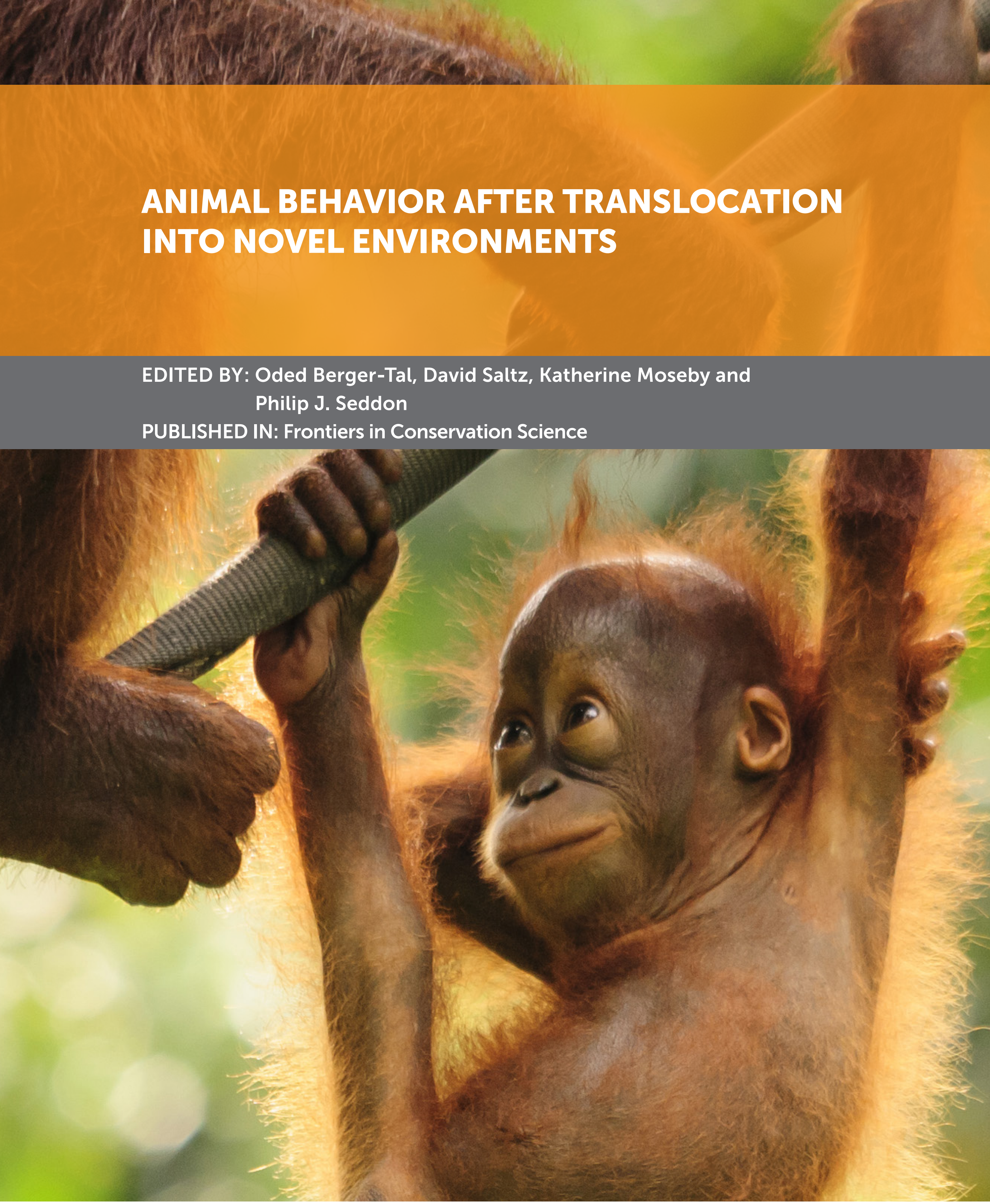

# ANIMAL BEHAVIOR AFTER TRANSLOCATION INTO NOVEL ENVIRONMENTS

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PUBLISHED IN: Frontiers in Conservation Science

frontiers Research Topics

ISSN 1664-8714
ISBN 978-2-88976-152-4
DOI 10.3389/978-2-88976-152-4

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# ANIMAL BEHAVIOR AFTER TRANSLOCATION INTO NOVEL ENVIRONMENTS

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**Citation:** Berger-Tal, O., Saltz, D., Moseby, K., Seddon, P. J., eds. (2022). Animal Behavior After Translocation Into Novel Environments.
Lausanne: Frontiers Media SA. doi: 10.3389/978-2-88976-152-4

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EDITORIAL
published: 25 April 2022
doi: 10.3389/fcosc.2022.888125

# Editorial: Animal Behavior After Translocation Into Novel Environments

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**Keywords: conservation behavior, exploration-exploitation, conservation translocations, HIREC, captive breeding**

**Editorial on the Research Topic**

**Animal Behavior After Translocation Into Novel Environments**

Imagine the following scenario: you have been invited to a conference in a foreign country, where you have never visited before and do not speak the language. A few hours after arriving at your hotel, you are abducted by a group of strangers. As you regain consciousness, you find yourself alone in a completely unfamiliar city. You realize that in order to survive, you urgently need to find a safe place and some food, and to evade the bands of marauding criminals that roam this part of the city.

While this scenario sounds like the plot of a typical scary movie or video game, it might also describe (albeit in an anthropomorphized fashion) the experience that translocated animals go through as they are released into a novel environment which might be vastly different to any environment they have ever known. Conservation translocation, the deliberate movement of organisms from one site with release into another (IUCN/SSC, 2013), is a commonly applied conservation tool aimed at recovering threatened populations, reducing extinction risk, or restoring ecosystem functions (Seddon et al., 2014; Hoffmann et al., 2015). Nevertheless, despite the popularity of this approach, translocating animals and releasing them into the wild is a challenging ordeal that often fails (Berger-Tal et al., 2020). Considering the disturbing scenario that we outlined above, the challenges of translocation projects might become clearer—the success of a translocation project depends on the ability of the released individuals to survive and later also to reproduce in an unfamiliar environment.

These challenges make the study of animal behavior in novel environments crucial to the success of most future conservation translocation projects (Berger-Tal and Saltz, 2016). By understanding how animals behaviorally respond to novel environments and whether these reactions are adaptive, researchers can design effective solutions that could increase translocation success. Such solutions are most crucial during the establishment phase of the translocation (Armstrong and Seddon, 2008), when survival, reproduction and dispersal of the released individuals closely depend on their responses their new environment. Knowledge on how animals behave in novel environments may help managers prior to the release, by helping them choose specific individuals for release, guiding them in the design of the captive environment, or directing them toward the appropriate pre-release behavioral training protocol that will increase the chances that the released animals will succeed in the new environment (Shier, 2016; Blumstein et al., 2019; Greggor et al., 2021). Alternatively, knowledge of animal behavior could help design effective solutions that could be implemented after the release, such as making modifications to the release site, release protocols, or

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**Specialty section:**
This article was submitted to Animal Conservation, a section of the journal Frontiers in Conservation Science

**Received:** 02 March 2022
**Accepted:** 05 April 2022
**Published:** 25 April 2022

**Citation:**
Berger-Tal O, Saltz D, Moseby KE and Seddon PJ (2022) Editorial: Animal Behavior After Translocation Into Novel Environments. Front. Conserv. Sci. 3:888125. doi: 10.3389/fcosc.2022.888125

the post-release conditions (Bell, 2016; Efrat et al., 2020; Resende et al., 2021). Detailed monitoring of released individuals might indicate the need for further adjustments to the release site or to the release protocol, since acclimatization to the new environment can take anywhere between several weeks to well over a year (Poirier and Festa-Bianchet, 2018; Bannister et al., 2020).

The articles in this Research Topic tackle different aspects of the behavioral responses of animals translocated to novel environments. They apply very different approaches and methodologies to better understand how animals cope (or fail to cope) with novel environments, and the ways in which we can harness this understanding to improve conservation translocation projects. Maor-Cohen et al. showed that reintroduced Persian fallow deer, *Dama mesopotamica*, change their habitat preferences over time as they become familiar with the novel landscape. They also found that individual variation in habitat selection can take a few years to be expressed because the initially perceived high risk in the months following the release overshadows any other individual preferences. Working on a completely different system, Picardi et al. had similar findings, showing that temporal dynamics of post-release habitat selection in translocated greater sage-grouse, *Centrocercus urophasianus*, can emerge in some individuals but not in others, highlighting the importance of accounting for both individual variation and the time since release in order to detect habitat selection patterns in translocated animals. The results of these two studies emphasize the central role that individual differences in behavior have in determining translocation success, which reflects a wider understanding within the field of conservation science, i.e., that measurements of inter- and intra-individual differences within populations should be incorporated into conservation and management programs in order to enhance their efficacy and increase their success rate (Merrick and Koprowski, 2017).

Goldenberg et al. studied the movement of African savannah elephants, *Loxodonta Africana*, calves following their release into a fenced wildlife sanctuary in northern Kenya, and found that the released calves tended to use fewer sites than their resident conspecifics, but that social context was an important driver of exploration in these individuals. Sociality was of key concern also in the study of Kaczensky et al. who investigated the movement patterns of kulan, *Equus hemionus kulan*, translocated to a vast novel habitat with no resident conspecifics, in the Torgai region of Kazakhstan. The authors found that the fission-fusion dynamics and low movement correlation within kulan groups increases the risk that the individuals will lose contact with each other and lead to translocation failure. Doden et al. studied the movement of translocated American beavers, *Castor canadensis*, and showed that day-to-day activities, such as foraging and resting, were largely unaltered by translocation, but translocated beavers exhibited coarse-scale movement behaviors most similar to dispersal by resident subadults.

Undin et al. studied the post-release mating behavior of North Island brown kiwi, *Apteryx mantelli*, on Ponui Island, New Zealand, and the implications for genomic admixture. Using genomic tools, the authors found that the kiwi did not mate randomly, but rather preferred individuals different than themselves, reducing inbreeding and increasing genetic variability in this translocated population. Lee et al. studied vigilance and foraging behavior in a cohort of captive-bred ʻAlalā, *Corvus hawaiiensis*, after their release to the Island of Hawaiʻi. They found that the vigilance of the birds overall increased over time since release, but that as group size increased, both vigilance and foraging decreased. They also found that the feeders used to provide supplementary food for the birds might have inadvertently increased the birds' susceptibility to predation. Dixon-MacCallum et al. presented taxidermic mounts of mammalian predators and non-predators to Vancouver Island marmots, *Marmota vancouverensis*, that were either wild-caught, or captive-born. They found that after only two generations in captivity, marmots begin losing their ability to discriminate predators from non-predators, suggesting that pre-release predator-recognition training might be needed to increase the survival of translocated individuals of this critically endangered species.

Finally, two studies in our Research Topic applied a theoretical or conceptual framework to the issue of animal behavior in novel environments. Saltz and Getz applied optimal stopping theory—a mathematical theory addressing the problem of when to stop a current activity and take a particular action so that expected net rewards are maximized—to the case of animals in a novel environment. Specifically, the authors asked "when should an animal stop exploring a novel habitat and "settle down" within a defined home range?". They provide a set of related predictions that are testable within the context of translocation projects. Hunter-Ayad et al. proposed two strategies for approaching and managing novelty in the context of conservation translocations. The conservative strategy, characterized by the avoidance and removal of novel conditions as much as possible, is best used for translocations of highly threatened species for which ensuring post-release survival is a priority. The extrapolative strategy deliberately allows exposure to novel conditions and monitoring outcomes to increase understanding of a species' ecology, which suits species that are in recovery and species facing novel and emerging threats that may require non-traditional translocations, such as assisted colonizations.

While our Research Topic focuses on conservation translocations, rapid anthropogenic changes to the environment makes the encountering of novel environments the rule rather than the exception for many species of animals, translocated or otherwise. Thus, the insights coming from this special topic go far beyond the practice of conservation translocations and might promote better conservation of wildlife in a rapidly changing world.

## AUTHOR CONTRIBUTIONS

The editorial was drafted by OB-T. All authors contributed to the editorial and approved the submitted version.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Conservation Science

HYPOTHESIS AND THEORY
published: 08 July 2021
doi: 10.3389/fcosc.2021.691714

# Novel Conditions in Conservation Translocations: A Conservative-Extrapolative Strategic Framework

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**Specialty section:**
This article was submitted to Animal Conservation, a section of the journal Frontiers in Conservation Science

**Received:** 06 April 2021
**Accepted:** 09 June 2021
**Published:** 08 July 2021

**Citation:**
Hunter-Ayad J, Jarvie S, Greaves G, Digby A, Ohlemüller R, Recio MR and Seddon PJ (2021) Novel Conditions in Conservation Translocations: A Conservative-Extrapolative Strategic Framework.
Front. Conserv. Sci. 2:691714.
doi: 10.3389/fcosc.2021.691714

In response to anthropogenic threats, conservation translocations are increasingly used to combat species' population and range declines. However, moving animals outside of their current distribution can mean introducing them to novel conditions, even in the case of reintroductions to formerly inhabited areas due to ecosystem changes following extirpation. This exposure to novel conditions introduces uncertainty that can undermine decision making for species conservation. Here we propose two strategies, which we define as conservative and extrapolative, for approaching and managing novelty and the resulting uncertainty in conservation translocations. Conservative strategies are characterised by the avoidance and removal of novel conditions as much as possible, whereas extrapolative strategies are more experimental, allowing exposure to novel conditions and monitoring outcomes to increase understanding of a species' ecology. As each strategy carries specific risks and opportunities, they will be applicable in different scenarios. Extrapolative strategies suit species in recovery which can afford some experimental management, or species facing novel and emerging threats which require less traditional translocations, such as assisted colonisations. We provide examples, applying our framework to two endemic New Zealand species with long histories of translocation management: tuatara (*Sphenodon punctatus*), a reptile and takahē (*Porphyrio hochstetteri*), a flightless bird.

**Keywords: translocation, restoration, novelty, ecological conservation, strategy, wildlife management, evidence-based conservation, adaptive management**

## INTRODUCTION

Anthropogenic ecosystem degradation has occurred throughout human history (Waters et al., 2016), resulting in species declines and extinctions. There has been an estimated 68% decrease in population sizes of mammals, birds, amphibians, reptiles, and fish between 1970 and 2016 alone (WWF, 2020). These population declines often go hand in hand with dramatic range contractions for many species (Faurby and Araújo, 2018). Conceptually this can be viewed as shrinkage of a species' realised niche as human activity reduces the portion of their fundamental niche space that is accessible (Scheele et al., 2017). Species are often excluded from core niche spaces and restricted to a peripheral realised niche representing marginally tolerable conditions for the species (Crooks et al., 2017). Such species typically persist in a relict distribution, representing areas of low habitat quality, but often with little human activity (Kerley et al., 2012, 2020).

Species that occupy only a fraction of their former geographical distribution are often conservation priorities, as without the factors driving their range contractions being halted and/or reversed, they remain at high risk of extinction (White et al., 2014; Hunter et al., 2016). The restoration of such range-reduced species increasingly includes conservation translocations, or the human-mediated movement of living organisms from one area, with release in another where the primary objective is conservation benefit. Reintroductions, to re-establish populations in areas of the species' indigenous range from which they had previously been extirpated, and reinforcements, the release of individuals into an existing population of conspecifics to increase population viability, are important forms of conservation translocations (IUCN/SSC, 2013; Seddon et al., 2014). There is inherent uncertainty in translocating range-reduced species, as most direct information of species' behaviour and environmental preferences will come from observations in their relict distribution (Mihoub et al., 2014). While reintroductions will typically aim to release animals into areas of their indigenous range, such areas will rarely be directly analogous to the relict distribution (Osborne and Seddon, 2012; White et al., 2014; Taylor et al., 2017). As such, there will always be a degree of novelty inherent in conservation translocations.

We suggest that strategies for dealing with novelty, and resulting uncertainty, can be conceptually classified into "conservative" and "extrapolative" at the two ends of a continuous spectrum of approaches. For translocations following a conservative strategy, novel conditions would be avoided as much as possible, with release sites selected to be as similar as possible to areas within the current (relict) distribution of the translocated species. In contrast, under an extrapolative strategy, more exploratory or experimental translocations would be considered, allowing species to encounter novel conditions. Here choices would be based on predicting species' behaviour through extrapolation from observed patterns. While we primarily propose these strategies for species restricted to a relict distribution, we note that they might also have relevance for other species and translocation objectives. For example, in translocations where individuals are relocated due to displacement by infrastructure, animal welfare concerns could promote a conservative strategy, as this could minimise stress for relocated animals (Teixeira et al., 2007). Alternatively extrapolative strategies in such translocations could be used as an opportunity to pursue more active ecosytem engineering objectives (Perring et al., 2015).

Multiple options for species conservation management could also be compared using a similar classification system. For example, threat management within a species relict distribution could be considered a conservative option compared with the alternatives of either translocating individuals or taking them into captivity (Snyder et al., 1996). However, here we are specifically referring to management following the decision to translocate animals, rather than considering translocations relative to alternative actions.

We identify the challenges posed by the novelty inherent in conservation translocations in relation to release-site selection and post-release habitat use, and provide a conceptual framework to explore how this novelty can be approached following either a conservative or an extrapolative strategy. We illustrate this framework using case studies of the translocation management of two endemic New Zealand species that have suffered dramatic anthropogenic range contractions; a reptile, the tuatara (*Sphenodon punctatus*), and a flightless bird, the South Island takahē (*Porphyrio hochstetteri*).

## NOVELTY

We define novelty at two levels: the individual level due to a founder animal's initial unfamiliarity with the specific features of the release area, and the species level when a release area differs considerably from the extant range of a species (Thatcher et al., 2006; Yott et al., 2011; Attum and Cutshall, 2015). These sources of novelty create uncertainty that can undermine the decision-making process for conservation translocations (Seddon et al., 2007). This uncertainty is manifest in two key areas:

- Reintroduction site selection, where choices based on relict distributions should identify areas where a translocated cohort is able to persist, but might potentially miss sites with conditions best able to support population growth and persistence (Kerley et al., 2012; Osborne and Seddon, 2012).
- Post-release resource use, where expectations based only on relict populations are unlikely to anticipate the full range of potential responses of the reintroduced population under novel conditions (Mihoub et al., 2014; Massaro et al., 2018).

These sources of novelty and consequent uncertainty are represented in two of the consequences for reintroductions listed in Osborne and Seddon (2012): "*present day locations might not indicate currently suitable habitat,*" and "*present day locations where a species is absent might not indicate unsuitable habitat*." Here we provide a framework for how each of these uncertainties can be approached, through making either relatively conservative or extrapolative inferences.

## CONSERVATIVE STRATEGY

Adopting a conservative strategy, candidate release sites are given priority based on their similarity to conditions within the current distribution of the species, regardless of past population declines and range contractions. As such, selected translocation sites will have conditions similar to those in which the species is known to survive, which should reduce the number of novel or unknown factors. Reinforcements may be considered a conservative translocation strategy, as the presence or proximity of conspecifics provides clear evidence that the species can survive in a release area. A conservative approach can increase confidence that the reintroduced population will be able to survive in selected release areas. However, this conservatism will inevitably reduce the number of potential release sites to be considered, and is likely to miss suitable, or even preferred, release sites that are not represented within a species relict distribution (Kerley et al., 2012, 2020).

Similarly, following a conservative strategy, predictions of resource selection and population growth for conservation translocations would be made and evaluated based on patterns observed within the focal species' current range. This would have the advantage of limiting novelty, and thus uncertainty, as the founding cohort would be expected to require the same resources as are available in their relict range. Where not all resources are available, management could focus on providing these. This could be through the provision of supplementary feed and/or breeding shelter, such as nest boxes (Panfylova et al., 2016), removal of pests and predators (Hegg et al., 2012; Taylor et al., 2018), vegetation management (Lloyd and Powlesland, 1994) and/or controlling human activity to reduce harvest or persecution (Chapron et al., 2014). This has the advantage of reducing uncertainty in post-release outcomes as the environment is managed to provide conditions known to be at least minimally adequate for species persistence (Seddon et al., 2014). Similarly, and particularly in the case of reinforcements, decisions relating to population carrying capacities and appropriate social and demographic structures would be based on and evaluated with reference to observed patterns in relict populations.

In addition to potential additional management costs associated with release site modifications, there are potential missed opportunities associated with a conservative post-release strategy. Reducing novel conditions in a reintroduction area will remove opportunities for adaptation, whether through behavioural plasticity or genetic mechanisms, which could benefit the survival and management of the species in the long term (Zeisset and Beebee, 2013). There will likely be cases where removing or reducing resource provision such as feeding or nest sites, while reducing population growth in the immediate term, could provide the impetus for animals to explore previously unexploited resources and might eventually lead to greater population growth and stability over subsequent generations (Mertes et al., 2019). Furthermore, conditions in a species' relict range might lie on the fringes of a species' niche if the relict range represents refugia from anthropogenic threats (Kerley et al., 2012). If these are used as a benchmark for identifying population growth and persistence potential, then it will be difficult to identify sub-optimal performance in reintroduced populations (Beauchamp and Worthy, 1988). Management practises could also inadvertently reinforce or perpetuate these sub-optimal conditions, thus limiting population growth. For example, a population growth rate at least as strong as that observed within the relict range might be considered satisfactory by managers, despite this potentially being well below the maximum biological rate for the species (Morris and Doak, 2002; Kerley et al., 2012, 2020).

## EXTRAPOLATIVE STRATEGY

In order to make predictions beyond currently observable conditions, extrapolative translocation management could consider additional data sources from outside the relict population. This could include indigenous distributions prior to range contractions (Lentini et al., 2017) or biophysical and behavioural information from captive animals (Mitchell et al., 2012). Alternatively, evidence could be sought from other species, e.g., from sister-species (Hunter-Ayad and Hassall, 2020), or trophically analogous species (Andelman and Fagan, 2000). However, while additional data sources can inform extrapolative translocations, they are not always available, or might not be considered reliable due to temporal, spatial, environmental, ecological, and/or taxonomic distance from the relevant management conditions (Osborne and Seddon, 2012; Svenning et al., 2016). Additional data are not always necessary to enable extrapolation, as trends within a species' relict distribution can be extended beyond observed conditions by expert inference (Beauchamp and Worthy, 1988; Kerley et al., 2012, 2020) or through statistical or biophysical models (Elith et al., 2010; Gallien et al., 2012). Regardless of the methods of extrapolation, confidence in predictions regarding translocation outcomes will be proportional to the differences between conditions at release sites relative to those in the input data, as more separation will necessitate a higher degree of extrapolation to generate predictions. As such, post-release establishment and persistence will tend to be less assured than under more conservative strategies.

Tolerating a higher degree of novelty when selecting release sites would mean that candidate sites would not be rejected simply because conditions differ from those in a species' relict distribution. This has the advantage of expanding the number and type of release sites that can be considered by conservation managers (Kerley et al., 2020). For reinforcements, while site selection is clearly based on the presence of conspecifics, extrapolative choices could be those that are considered more experimental with regards to the populations chosen for reinforcement. For example, rather than reinforcements being used as a tool to "save" struggling or declining populations, a common use (Hegg et al., 2012), they could be used to promote rapid growth in stable or increasing populations under extrapolative strategies. However, a key challenge under extrapolative strategies is determining *what* novelty is acceptable. Many novel conditions will render a release site clearly unsuitable, whereas other types of novelty could be suitable for a species. Ecological habitat models (e.g., correlative and mechanistic niche models) are a valuable tool in addressing this challenge as they can be used to estimate potential release site suitability even under novel conditions (Mitchell et al., 2012; Chauvenet et al., 2013; Lentini et al., 2017; Hunter-Ayad et al., 2020).

When predicting and evaluating post-release resource selection, extrapolative management would consider a broad array of resources as potentially usable in a release area. However, there might be considerable uncertainty in the degree to which any or all novel resources will be exploited, and when this might be. There might be temporal latency arising from the necessity for animals to explore novel resources and to adapt their behaviour appropriately (Osborne and Seddon, 2012). For example ʻAlalā, or Hawaiian crow (*Corvus hawaiiensis*) reintroduced to the island of Hawai'i steadily transitioned from reliance on familiar areas and supplementary feed, towards exploring novel areas and natural food sources over a 200 day post-release tracking period (Smetzer et al., 2021). Such adaptions to make use of novel resources could be useful in distinguishing whether certain resource uses observed in refugee populations are facultative or obligate in nature. For instance, apparent dietary specialisation in giant pandas (*Ailuropoda melanoleuca*) is potentially a consequence of a restricted breadth of suitable food in their relict distribution and, speculatively, they could adapt to make use of novel food sources were they translocated outside of this distribution (Kerley et al., 2020).

However, the risk with such conservation translocations is that the species is unable to adapt and exploit novel resources, and consequent high post-release mortality might increase the likelihood of the extinction of the founder cohort (White et al., 2014). Additionally, population, social, and demographic structures are likely to vary upon exposure to novel environments, or be altered via reinforcements, and should not be judged directly against patterns in extant populations. As such, reintroductions conducted following an extrapolative strategy will tend to have more open-ended predictions of post-release performance. This will also change the nature of any evaluation of the translocation; as expected goals and outcomes are less certain, post-release monitoring could be an opportunity to reveal new data regarding the species and to inform their conservation into the future, rather than checking whether focused goals are being met *per se*. The greater underlying uncertainty arising from the translocated species reaction to novel conditions will mean that such reintroductions carry a higher risk of failure and unintended or unforeseen outcomes.

## APPLYING THE STRATEGIES

Both conservative and extrapolative strategies have specific strengths and limitations, and thus will be suitable in different contexts (**Table 1**). For instance, the inflexibility of conservative strategies, basing management on observations only from a relict population, can hamper adaptive management and reduce the ability for species management to respond to emerging threats (Corlett, 2016). However, this is a long-term concern and there are many instances where maximising confidence in rapid actions is required to save a species from immediate extinction (Lloyd and Powlesland, 1994; Massaro et al., 2018; Mukhlisi et al., 2020). In contrast, extrapolative strategies can often fail to provide certainty or concrete recommendations, making them a less palatable option to inform high stakes conservation decisions. It would be more appropriate to consider extrapolative predictions of release site suitability as hypotheses which can be tested via a translocation and subsequent monitoring (Armstrong and Seddon, 2008). As such, extrapolative translocations can be useful in an adaptive management setting as effective monitoring of post-release performance can provide evidence and information for the long-term conservation management of the reintroduced species (Seddon et al., 2014). However, the scope to experiment with extrapolative translocations is often not a luxury afforded in conservation plans for many threatened species.

In addition to the conservation context of a species' being translocated, consideration should be given to the life-history traits of that species, as some species will be inherently more suited to conservative or extrapolative translocations, respectively. For instance, species with generally low adaptive potential (i.e., behavioural rigidity and/or genetic restriction) are likely to have little tolerance for novel stresses (Gillies and St. Clair, 2008; Heikkinen et al., 2015). Therefore, more adaptive species are inherently suited to more conservative translocation strategies. Whereas, species with high adaptive potential (i.e., behavioural plasticity and/or genetic diversity) are much more likely to be able to adapt to novel stresses encountered following a translocation (Gillies and St. Clair, 2010), so are inherently better candidates for extrapolative translocations. We note, however, that the inherent suitability of a translocated species must still be balanced with other factors that influence the suitability of a given strategy for each specific setting. The strategic challenge for conservation managers then becomes determining how to balance several conditions, which might produce conflicting views over which strategy should be pursued.

Our framework can also be considered at multiple levels (i.e., community, clade, genus, species, population, individual, and life-stage), as strategies are relevant both to developing both broad strategies (ecosystem management) and detailed decision making (make-up of release cohorts). In this way, these rules-of-thumb can guide practitioners in considering from the widest scope, ecosystem function and services (Hale and Koprowski, 2018), to the finest detail, individual personality and traits (Koolhaas et al., 2007; Boyer et al., 2010).

For species facing a high risk of extinction in the short-term due to a combination of species' traits and sustained or increasing threats within their relict range, a conservative approach is likely to be the most suitable. This would focus on securing stable populations to save the species in the short-term, which must be a management priority, albeit while perhaps limiting long-term population growth potential. However, species not under immediate risk of extinction, with stable or growing populations might be better served by an extrapolative strategy where novelty need not be avoided. Although this might seem counter intuitive, this situation does occur. For instance, species might maintain stable or growing populations over a large, but still reduced, range. An example are Eurasian cranes (*Grus grus*), which were reintroduced to South-West England in 2010 in order to restore and enhance ecosystems in this region. Cranes were extirpated from the British Isles in the sixteenth century, though large populations have persisted on the Eurasian mainland. As such, the species has never been threatened

**TABLE 1 |** Summary of conditions lending themselves to conservative and extrapolative translocation management.

| Features | More suitable for conservative translocation approaches | More suitable for extrapolative translocation approaches |
|---|---|---|
| Traits | • Ecological specialist<br>• Obligate rigid behaviour<br>• Poor genetic diversity<br>• Low fecundity<br>• Long generation times | • Ecological generalist<br>• Behaviourally plasticity<br>• High genetic diversity<br>• High fecundity<br>• Short generations |
| History | • Recent range contraction<br>• Causes known and remedied | • Extirpation in the distant past<br>• Uncertain drivers<br>• Ecosystem change since contraction |
| Population size/trend | • Small population<br>• Declining population<br>• High extinction risk | • Multiple protected populations<br>• Positive population growth<br>• Supported by captive breeding programmes |
| Current threats | • Direct anthropogenic actions (e.g., harvest, persecution or land-use change)<br>• Predation (e.g., introduced mammalian predators on offshore islands)<br>• Available release sites where threats are controlled, e.g., national parks or protected areas | • Novel/emerging threats<br>• Climate change<br>• Threats cannot be controlled in release areas |
| Timeframe | • One-off action<br>• No chance of "second try"<br>• No adaptive management for species<br>• Required as a proof-of-concept for further funding and support | • Long-term management prioritisation and funding<br>• Plans entailing several translocations with successive monitoring<br>• Can feed into adaptive management |

*Choices should be considered across features (i.e., most features make a species suitable for one translocation strategy), as different features will likely be split between conservative and extrapolative suitability for most species.*

and is listed as least-concern on the International Union for Conservation of Nature (IUCN) Red List for threatened species (Birdlife International., 2016; Soriano-Redondo et al., 2019). Alternatively, species could have stable or growing populations due to active management in captivity and/or in the wild (such as the tuatara and takahē case studies given below). In this case, growing populations provide opportunities for extrapolative translocations to be considered, even though species survival remains dependent on ongoing conservation efforts.

In cases where extinction is not an imminent concern there is scope to view conservation translocations as ecological experiments, enabling researchers and conservationists to learn more about the niche-breadth of the species, as well as aspects of species ecology such as dietary and behavioural plasticity (Sarrazin and Barbault, 1996). In such cases even a failed translocation attempt can provide valuable information for the conservation of the species (Taylor et al., 2017). For example, a "failed" translocation could perhaps confirm that at least one condition in the release area was outside of the species niche, or that the release procedure was unsuitable, without jeopardising species' survival. We expect the conservative and extrapolative strategies laid out above to be useful in clarifying decision-making processes for conservation managers and scientists. For instance, the choice of a conservative vs. extrapolative strategy can inform several key decisions in the building of ecological models (i.e., how models are set up, including what data used as model input and the kinds of relationships fitted to those data), a key tool in supporting conservation management (Hunter-Ayad et al., 2020).

To examine our conservative-extrapolative translocation framework, we use two case studies for species where conservation translocations have formed an integral part of their rehabilitation: the tuatara and the takahē. Both of these species are endemic to New Zealand (also known as Aotearoa New Zealand, hereafter NZ), which was discovered by humans only in ∼AD 1280 (Wilmshurst et al., 2008). Tuatara and takahē were extirpated from the majority of their indigenous range following the arrival of humans to NZ (**Figures 1**, **3**), with this largely attributed to predation by introduced mammals and habitat loss (Beauchamp and Worthy, 1988; Cree, 2014). Both species are of cultural significance in NZ to the indigenous Māori people as *taonga* (treasures), as well as to European communities (Lee and Jamieson, 2001; Cree, 2014). For several decades, conservation management of tuatara and takahē has included conservation translocations, making them suitable candidate species to examine our conservative-extrapolative framework. Tuatara management has been extensively documented in the published literature. Whereas, for takahē recent developments are largely unpublished outside of the grey literature. Ongoing takahē research will draw from and emulate the work to date with tuatara, developing quantitative models to identify potential impacts of climate change.

## TUATARA CASE STUDY

Tuatara (*Sphenodon punctatus*) are a lizard-like reptile endemic to NZ and of evolutionary significance as the sole living representative of Rhynchocephalia, the sister group to Squamata (Cree, 2014). Tuatara are diurno-nocturnal and adapted to cooler climates, being active at body temperatures from ∼5 to 30°C (Barwick, 1982; Thompson and Daugherty, 1998). Compared to most other reptiles tuatara have a long maturation time (∼13–20 years), lengthy inter-clutch intervals (∼2–9 years), a small clutch size (∼8 eggs; range 1–17), and a long life span of at least 100 years (Cree, 2014).

Once widespread across NZ's North and South Islands, as well as many offshore islands (**Figure 1**), tuatara became restricted to a relict distribution, being only found naturally on 32 offshore islands. Although taxonomy remained uncertain for living tuatara until recently (Hay et al., 2010), all living populations of tuatara are currently considered to be *S. punctatus* (Hay et al., 2010; Gemmell et al., 2020).

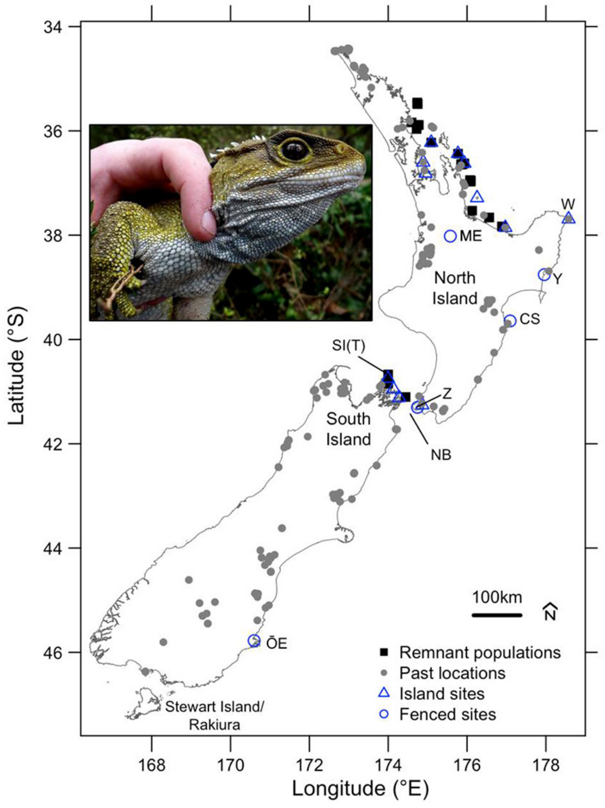

**FIGURE 1 |** Map: Tuatara remnant and past locations as well as translocation release sites. Past locations (grey circles) from Holocene-aged fossil deposits (last 11,650 cal years BP, as determined by biochronological reasoning, namely the dominance of the moa Anomalopteryx didiformis; Worthy and Holdaway, 2002) and other known or probable extinctions from offshore islands (Cree, 2014). The remnant populations (black squares) and translocation sites (blue outlines) are split into groups of island and fenced sites, as these entail more conservative and extrapolative translocations, respectively. Locations of key places mentioned in the text are listed from north to south: W, East Island/Whangaokeno; ME, Maungatautiri Ecological Island; Y, Young Nick's Head; CS, Te Matau a Maui—Cape Sanctuary; SI(T), Stephen Island (Takapourewa); Z, ZEALANDIA; NB, North Brother Island; OE, Orokonui Ecosanctuary; Inset, An adult male tuatara about to be reintroduced to OE; photo by SJ. Adapted from Cree (2014) and Jarvie et al. (2021).

Conservation translocations to islands from which introduced mammals have been eradicated (Gaze, 2001), and to mainland predator-fenced sanctuaries have been used to create insurance populations and to restore ecosystem function (Miller et al., 2012; Jarvie et al., 2021). Beginning in 1995, tuatara have now been translocated to 14 islands and 5 mainland fenced sanctuaries, increasing the number of populations to 47 (**Figure 1**; see Jarvie et al., 2021). Most conservation translocations of tuatara arose out of well-documented recovery planning during the 1990s and early 2000s (Cree and Butler, 1993, Gaze, 2001), although these recovery plans are now out of date. The long-term goal for tuatara from the most recent Recovery Plan is to preserve genetic diversity of all existing populations and to restore new populations throughout their pre-human range, including locations with increased accessibility to the general public (Gaze, 2001).

Following a conservative strategy, earlier conservation translocations of tuatara focused mainly on restoring populations within the same ecological region as the source population (Cree, 2014; Jarvie et al., 2014). These population restorations included both reintroductions and reinforcements. Initial reintroductions included establishing new populations with at-risk genetic stocks (Cree and Butler, 1993), such as the release of tuatara previously identified as a separate species (*S. guntheri* from North Brothers Island, which is now considered to also be *S. punctatus*; Hay et al., 2010).

With encouraging provisional results, a more extrapolative strategy was adopted for the reintroduction of tuatara to the predator-fenced mainland sanctuary of ZEALANDIA (formerly known as Karori Wildlife Sanctuary) in 2005 (**Figure 1**; McKenzie, 2007). The tuatara were released in the sanctuary, which was mostly free of introduced mammals, except for the house mouse (*Mus musculus*). Because of the possible impacts of mice, most of the translocated tuatara (60 of the 70) were released within a small (1 ha) mouse-proof enclosure within the larger sanctuary. The remaining 10 tuatara were released into the outer sanctuary (225 ha) and were monitored using radio-transmitters to assess the possible impacts of mice before further releases (McKenzie, 2007). Following high rates of survival of the released tuatara in both the mouse-proof enclosure and outer sanctuary, the population was reinforced in 2007 (Cree, 2014; Jarvie et al., 2021). In 2012, tuatara were translocated following an extrapolative strategy to considerably outside of the ecological region of the source population, to four predator-fenced mainland sanctuaries and an island (**Figure 1**; Cree, 2014; Jarvie et al., 2021). While mice are periodically detected at some mainland sites, their effects on tuatara remain uncertain. Several mainland locations have also had occasional incursions of larger introduced mammals such as Norway rats (*Rattus norvegicus*), ship rats (*R. rattus*), and stoats (*Mustela erminea*), but control of these predators has been needed to minimise the threat to tuatara. Preliminary survivorship of tuatara at monitored mainland locations is encouraging (McKenzie, 2007; Cree, 2014; Jarvie et al., 2015, 2016, 2021; Price et al., 2020), although continued vigilance and monitoring for introduced mammals remains necessary.

Prior to previous conservation translocations for tuatara, climatic suitability of release sites was considered on the basis of laboratory studies, field studies, and expert inference, and have been informed by knowledge of the Holocene fossil record (Cree, 2014; Jarvie et al., 2014, 2021). A recent study built correlative species distribution models (SDMs) using occurrence records from remnant populations and past locations from the Holocene (**Figure 1**) as well as paleoclimates, to estimate climatically suitable areas (**Figure 2**; Jarvie et al., 2021). By incorporating locations of Holocene deposits and/or knowledge of past locations in SDMs, larger areas of suitable climate were identified compared to SDMs derived from remnant populations only. These results highlight the need to consider data from outside relict distributions when assessing climate suitability for future conservation translocations for tuatara, and other relict species.

To support future conservation management of tuatara, research should be undertaken to inform translocations. Comparisons of remnant populations with translocated populations are useful to understand changes in demography (e.g., sex ratios, mating systems, and populations trends), phenotypic plasticity and phenology (e.g., Mitchell et al., 2008; Miller et al., 2012; Rout et al., 2013). Further development of mechanistic models for tuatara should be undertaken to explore responses of populations to climate change in existing and novel environments (e.g., Carter et al., 2018). The resulting mechanistic models could also be compared to results from correlative SDMs, potentially providing key insights into processes shaping the species' range limits (Tingley et al., 2014; Briscoe et al., 2016). Because the evolutionary consequences of translocations in long-lived species might not be apparent for centuries, confirming the accuracy of predictions based on correlative SDMs and mechanistic models could take decades. The continued measurement of responses of extant populations to climate change will be key for model validation.

Population viability analyses and gene retention modelling could be used to inform management of source and translocated populations, including investigating demographic responses to ambient temperature and population density. In some instances, the choice of founders from more than one source population might also be considered to maximise genetic diversity (Weeks et al., 2011; Miller et al., 2012). For example, where release sites are between remnant populations, founder populations could comprise individuals from adjacent genetic groups (Hay et al., 2010) to increase the adaptive population of any new population.

However, more extrapolative translocations might have benefits and unintended drawbacks (Miller et al., 2012). On one hand, there might be an increase in fitness due to greater genetic variation and hybrid vigour, and there could be microevolutionary responses because of adaptation to new local conditions (Jamieson et al., 2006). On the other, the resulting hybridisation could cause outbreeding depression or maladapted phenotypes, and expose founders from different populations to novel diseases (Miller et al., 2012). A mixed-stock approach to future translocations of tuatara would require careful monitoring, for example, of short-term survival and growth of founders, recruitment, and performance of hybrids relative to founder stock (Weeks et al., 2011). Intensive consultation with stakeholders and iwi (Māori tribes) partners prior to translocations would also be necessary (Miller et al., 2012).

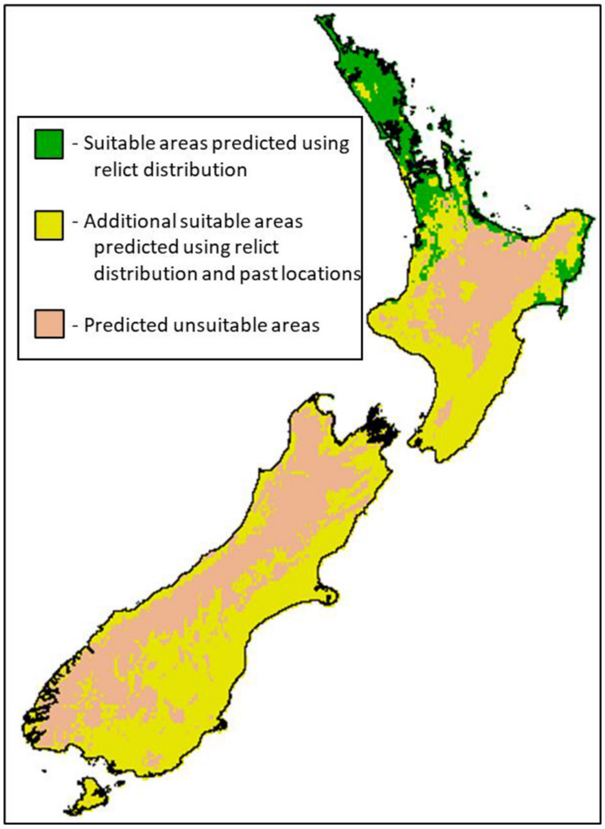

**FIGURE 2 |** Map of current climatic suitability from a maximum entropy model (Phillips et al., 2006) trained with remnant populations and past locations for tuatara (*Sphenodon punctatus*) across New Zealand. Green areas were identified as suitable by models using only data from remnant populations of tuatara **(Figure 1)**, whereas the yellow areas show the additional space predicted to be suitable when remnant populations and past locations (**Figure 1**; radio-carbon dated deposits, Holocene-age deposits, and known or probable extinctions) were also used as model inputs. For full methodological details see Jarvie et al. (2021), including with figures showing projections under climate change and with model uncertainty.

For selection of future release sites, an increasingly extrapolative approach could be considered if remnant populations remain secure and translocated populations become established within the indigenous range. While reintroductions and reinforcements should still be used for future translocations to establish populations within the indigenous range, consideration could also be given to introductions of tuatara to islands or mainland sites where habitat is predicted to be suitable under climate change. The combined use of correlative SDMs and mechanistic models could inform such translocations. Proposed release sites could include assisted colonisation (Brodie et al., 2021) of tuatara to locations such as Stewart Island/Rakiura, which is outside the indigenous range of the species.

## SOUTH ISLAND TAKAHĒ CASE STUDY

The South Island takahē (*Pophyrio hochstetteri)* is the world's largest extant rail species, characterised by their size and flightlessness. Takahē, along with the kākāpo (*Strigops habroptila*), represent the last vestige of NZ's unique pre-human guild of flightless herbivorous birds. They were presumed extinct in the early twentieth century and a high-profile rediscovery in 1948 instigated over half a century of conservation effort to preserve and restore the species (Lee and Jamieson, 2001).

Prior to the arrival of humans, the takahē's indigenous range was widespread across the South Island, with a distinct species, the North Island takahē (*Porphyrio mantelli*), on the North Island. However, following the arrival of humans NZ and the associated introduction of mammalian predators the North Island species was driven to extinction, while the South Island takahē was largely restricted to a single mountain range (the Murchison Mountains, Fiordland) by the early 1940s (Hegg et al., 2012, 2013; **Figure 3**).

The location of the relict population of takahē has been designated a special protected area since the 1950s. Despite this, the species remained vulnerable to extinction as it persisted only as a single population (Hegg et al., 2012). Consequently, conservation translocations began in the 1970s to create secondary, secure populations in predator-free reserves and small islands (hereafter "secure sites") in case of extirpation of the single relict population (Hegg et al., 2013). The primary recovery goal for the takahē is to establish sustainable wild populations of takahē within their natural range. The secure site populations play a critical role for genetic insurance and population growth purposes, and the use and extent of secures sites continues to be reviewed as wild population security grows (DOC Unpublished Strategies).

Between 1987 and 1992 a reintroduction of takahē was attempted to an open mainland site (hereafter "wild site"). This was to establish a population in the Stuart Mountains, neighbouring the relict population in the Murchison Mountains (Hegg et al., 2013). However, this reintroduction was ultimately unsuccessful, despite conservative site selection, as high mortality and dispersal prevented establishment of a population. This failure was attributed to the small size of annual release cohorts, unusually harsh winters in the early 1990s and high densities of mammalian predators (Lee and Jamieson, 2001; DOC Unpublished Records).

Following the failure of the Stuart Mountains reintroduction, focus shifted to conservation efforts within the Murchison Mountains relict population, as well as a continued establishment and management of small populations at secure sites. The most important criteria for selecting a secure site were the absence of introduced mammalian predators and operational access (as the remoteness of the Stuart Mountains hampered monitoring and management actions there). All secure sites represent novel conditions outside of the relict distribution in the Murchison Mountains, as they are different in terms of climate, ecological community and human activity. As a result, this site selection can be viewed as extrapolative. However, rather than being a preference of management this was due to the necessary focus on the major threat to takahē persistence, invasive predators, and the lack of conservative sites in which these predators could be effectively controlled. Takahē have now been established in 18 secure sites, removing immediate risks of extinction and beginning to reverse the decline of the species, such that today there are ∼500 living takahē, up from a low of 124 birds in 1981 (Hegg et al., 2012; DOC Unpublished Data). This resulted in a downgrading of the NZ species threat level, Nationally Critical to Nationally Vulnerable in 2016 (Robertson et al., 2016).

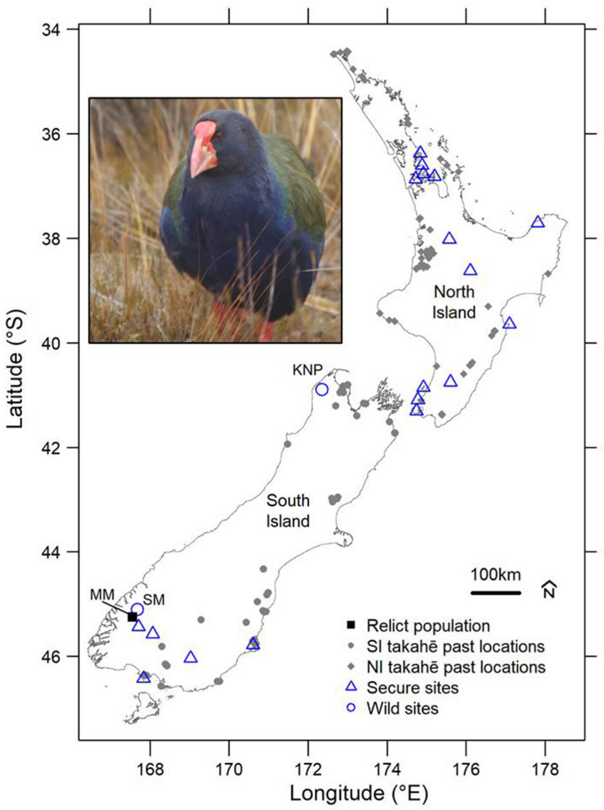

**FIGURE 3 |** Map: Takahē remnant and past locations as well as translocation release sites. Past locations (grey circles) from Holocene-aged fossil deposits (last 11,650 cal years BP, as determined by biochronological reasoning, namely the dominance of the moa Anomalopteryx didiformis; Worthy and Holdaway, 2002) are used to indicate of the pre/early human distribution of both North Island (NI) takahē (*Porphyrio mantelli*) and South Island (SI) takahē (*Porphyrio hochstetteri*). The relict population (Murchison Mountains, MM), wild sites (blue-outlined circles, SM, Stuart Mountains; KNP, Kahurangi National Park), and secure sites (blue-outlined triangles) are also shown. Inset: A South Island takahē following reintroduction to KNP; photo by JH-A.

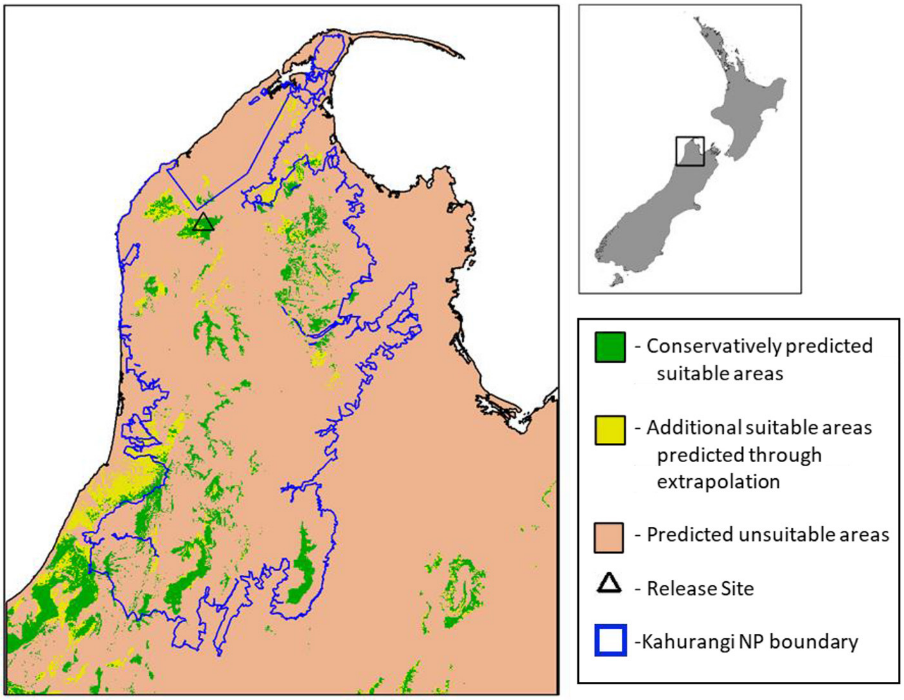

**FIGURE 4 |** Map of current environmental suitability from a maximum entropy model (Phillips et al., 2006) trained with records from South Island takahē (*Porphyrio hochstetteri)* relict population **(Figure 3)**. Green areas were identified as suitable by a conservatively fitted model, whereas the yellow areas show the additional space predicted to be suitable when the model fitting was relaxed to allow a greater degree of extrapolation. The conservative model only identifies habitat in environments analogous to those occupied in the models' input data, whereas the extrapolative model focuses on excluding areas only because they are analogous to unused areas in the species training data. For full details of the methods used to generate these predictions see **Supplementary Data Sheet 1**.

While selection of secure sites has been necessarily extrapolative, management of post-release resource selection has followed a more conservative approach. Habitat management for takahē has been employed when necessary at secure sites, particularly to prevent vegetation succession. Prior eradication and on-going exclusion of invasive mammalian predators has been essential, while supplementary food is also provided at some sites. Genetic resources and population densities are also strictly managed, with breeding pairs established to maintain current levels and patterns of genetic diversity (Greaves et al., 2020). This population admixture serves the purpose of avoiding inbreeding and genetic bottlenecks, but might also limit the ability of takahē to adapt to conditions in any one secure site as continual translocations between secure, relict and wild sites are used to maintain genetic diversity across the global takahē population (Lees et al., 2014; Zavodna et al., 2015; Greaves et al., 2020). However, despite this control, some local behavioural adaptations have been observed as takahē at secure sites expand their use of resources that have limited availability in the Murchison Mountains such as fallen fruits, exotic grasses, small reptiles, and the chicks of other bird species (particularly ducks). This has demonstrated that takahē are a more adaptable and generalist species than is evident from their behaviour and ecology within the relict population (Beauchamp and Worthy, 1988; Mills et al., 1991).

From the mid-late 2010s mainland reintroductions of takahē were again planned to establish new wild sites supporting larger populations and with less intensive management than at secure sites. This followed population growth across multiple secure sites and increased ecological understanding and refinement of management methods, enabling policy to become more ambitious in scope. The first reintroduction has been to Kahurangi National Park in 2018, in the north-west of the South Island. This site was chosen relatively conservatively as it bears similarities to takahē-inhabited areas in the Murchison Mountains. However, post-release management (particularly a lack of fencing/containment) allowed takahē to establish and roam as they pleased (except into farmland), making this aspect of the reintroduction more extrapolative than at secure sites. Ongoing research is building SDMs using occurrence records from the Murchison Mountain takahē population (**Figure 4**), to estimate environmentally suitable areas in Kahurangi for the species (**Figure 4**; **Supplementary Data Sheets**).

Although mammalian predators are controlled to low densities within Kahurangi, eradication was not considered essential for the release of birds. Thus far, no supplementary feed has been provided as the extensive tussock grasslands at the release site are intended to provide sufficient food for released takahē, though post-release monitoring will be crucial to confirming if this is the case. Additionally, having a relatively large release cohort of 30 individuals allowed for greater complexity in social structures and interactions to arise post-release than in previous translocations.

Early post-release monitoring of this population seems to indicate similar patterns of resource-use, population growth, and social structure to that of the relict population (DOC Unpublished Data). However, this was initially disrupted, possibly in part due to a female gender bias in the release cohort. Single females were observed to disturb established breeding groups, causing them to disband prior to and during the first post-release breeding season, potentially contributing to low population growth. Dispersal away from the release site was also observed predominantly in unpaired birds, rather than in stable pairs (DOC Unpublished Data). Further investigation of post-release resource use in Kahurangi is planned, using methods such as faecal analyses, stable isotope analysis, and eDNA to provide more information on dietary composition and changes over time (DOC Unpublished Proposals).

The conservation management plan for takahē considers that future reintroductions will be essential to maintain and restore the species, with an increasingly extrapolative attitude being considered as the species becomes more secure from historic threats while encountering new threats from climate change. The Takahē Recovery Programme is continuing to use existing sites to improve *in-situ* population performance and to predict likelihood of success at new sites. These new locations will be more extrapolative as takahē appear to prefer low-mid elevation and benign topography and climate. The primary focus is on likely predation pressure from introduced mammals and the feasibility of mitigation, ease of access and minimising excess dispersal through natural barriers.

## DISCUSSION

In this paper we have sought to develop a strategic framework to inform translocation strategies in terms of environmental novelty, highlighting the risks and rewards of opposing attitudes. We separate strategies into two broad categories based on defining novel conditions as those not represented within a species relict distribution. We define these as conservative (novelty avoidance) and extrapolative (novelty exposure) strategies, suggesting that each strategy has specific advantages and drawbacks, so will be suited to different species and conservation contexts. Our case studies demonstrate how previous translocation decisions can be viewed through the lens of our conservative-extrapolative framework. Management of both tuatara and takahē has shown a general trend of moving from initial conservative, cautious translocations, and towards generally more extrapolative, experimental manipulations. For tuatara this progress has followed this trend relatively clearly, with more recent translocations establishing populations further outside of their relict distribution than ever before. Whereas, for takahē, specific setbacks and practical restrictions meant that earlier site-selection decisions were extrapolative by necessity while population management was conservative, and more recent translocations have become more conservative in terms of site-selection while post-release management has become more extrapolative. We hope that these case-studies will demonstrate how our proposed framework can provide a lens through which both historic and future translocations decisions can be viewed.

As each of our developed strategies create specific opportunities and risks, they are intrinsically better suited to certain species, situations, and management objectives. It will remain a challenge to assess and balance numerous factors that will suggest a more conservative or a more extrapolative approach is suitable (**Table 1**). These factors are likely to counteract one another in many instances. For example, a species that has been through a population bottleneck, such as the alpine ibex (*Capra ibex ibex*), might have low genetic diversity and adaptive potential, suggesting suitability for conservative translocations, despite having a large and growing population, suggesting they could be candidates for extrapolative reintroductions (Stüwe and Nievergelt, 1991). Balancing such conflicting conditions will remain a significant challenge for translocation management, and we emphasise two key aspects to bear in mind: firstly, these strategies can be considered as "rules-of-thumb" or guiding principles, and secondly that, although we have defined the strategies categorically for convenience, they in fact characterise the ends of a continuum of attitudes to novelty exposure. Based on these considerations we propose that our strategies are best applied at the discretion of management when opportunities and conditions allow. Furthermore application of the strategies in the face of conflicting factors can be flexible. Choices here would be based either on a judgement call from conservation practitioners based on their priorities or be a compromise where applied strategies are somewhat intermediate, conservative in some respects but more extrapolative in others. This ability to be flexibly applied should make our framework potentially useful in many settings and given many constraints.

Historically, reintroduction has mostly been the limit of ambition for ecosystem management and restoration by managers and scientists, although there have been key exceptions (Lloyd and Powlesland, 1994; Greuber et al., 2012; Carter et al., 2017). We expect that strategies for dealing with novelty in translocations will become much more extrapolative in the future, as the scope and ambition of emerging management goals will allow less room for the strict control of resources and conditions that conservative strategies require. Thus, our framework provides a structure for the development of adaptive management strategies for conservation translocations (Osborne and Seddon, 2012; Smith et al., 2012). We expect this to facilitate the development of strategies where the exposure to risk from novel conditions is explicitly considered in terms of species traits, and population conservation status (Kennedy et al., 2013). However, a cautious, conservative approach will likely be most appropriate for the early stages in the restoration of highly threatened species, as securing a stable population and removing the imminent threat of extinction must be a priority in such cases. Conservative translocations will also be viewed more favourably by the public, indigenous peoples, and other stakeholders, whereas extrapolative translocations are likely be more controversial (e.g., Ricciardi and Simberloff, 2009).

Extrapolative strategies have particular importance in the context of ongoing anthropogenic climate and land-use change. To combat emerging threats, increasingly more extensive ecosystem manipulations are suggested, including *assisted colonisation* (Brodie et al., 2021), the translocation of individuals outside of their established range as a response to threats such as climate change (IUCN/SSC, 2013). These sorts of translocations, moving organisms outside of both their current and indigenous ranges are inherently extrapolative, as managers are knowingly creating unprecedented conditions and ecological interactions (Rendall et al., 2018; Bouma et al., 2020).

We urge caution in the application of extrapolative translocation strategies, particularly with regard to assisted colonisation and rewilding projects that seek to create novel ecosystem conditions (Corlett, 2016). In these cases, where there is so much inherent uncertainty, we suggest that decisions should always be informed by what data are available, and that even the most experimental translocations should be based on evidence-based hypotheses regarding the potential success and risks of the translocation (Armstrong and Seddon, 2008; Bouma et al., 2020). This is due to the cautionary tales from the field of invasive species management, in which many species that have been introduced outside of their native range, whether accidentally or intentionally, are a major driver of ecosystem degradation and biodiversity decline, costing conservation management vast resources to reduce and reverse the resulting damage (Brook et al., 2008; O'Donnell et al., 2017). We strongly suggest that a minimum requirement for conservation introductions be that there is evidence that the focal species will not only survive, but will also have (at least) no negative impact on the overall biodiversity and ecosystem functioning of the release area.

We further suggest that the principles developed in our framework can be applied to other areas of conservation practise, beyond conservation translocations. For example, distinguishing a similar continuum of conservative to extrapolative measures could usefully refine and clarify decision making for predator/pest control (Recio et al., 2015; Roy et al., 2016; O'Donnell et al., 2017), resource extraction (Peres et al., 2016) and tourism volume (Daily et al., 2009). Relating these choices to specific ecological evidence and considerations. These strategies can be framed generally as an application of cost-benefit analysis to conservation management (Chee, 2004; Fletcher et al., 2011) and could usefully enhance the clarity and transparency of risk management in decision making processes (Sutherland et al., 2004).

Inherent risks and uncertainties emphasise the need for caution in planning conservation translocations. We add to previous calls to view translocations as ecological experiments, following a mindset whereby explicit *a priori* predictions are made and then tested, even in cases where scientific enquiry is not the primary objective of management (Seddon et al., 2007; Taylor et al., 2017). We believe the conservative-extrapolative framework presented here will help with the application of this concept. Following this framework can help to ensure that predictions are appropriately framed in terms of the confidence that can be placed on them and that "tests" from post-release monitoring are also viewed and incorporated into adaptive management plans in a suitable way. We expect a conservative-extrapolative framework will have increasing relevance as conservation practise is developing away from traditional, preservationist approaches, so called "fortress" conservation, towards goals with increasing ambition and scope to include ecosystem services, ecological restoration, and rewilding as key objectives (Seddon et al., 2014; Corlett, 2016).

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

## AUTHOR CONTRIBUTIONS

JH-A, PS, MR, and RO conceived the idea and scope of the work. JH-A reviewed the literature and led the writing of the manuscript. SJ led the writing of the tuatara case-study, while AD and GG provided crucial comments towards the takahē case study, as well as the manuscript as a whole. All authors contributed critically to the draughts and gave final approval for publication.

## FUNDING

Funding support was provided to JH-A by a University of Otago Doctoral Scholarship. Monitoring of takahē in the Murchison Mountains provided species data for corelative models presented in the takahē case study. This population monitoring was supported by Fulton Hogan, commercial partner of the Takahē Recovery Programme, who provided funding for operational costs.

## ACKNOWLEDGMENTS

For prior consultation that helped to clarify our ideas, we thank New Zealand's Department of Conservation Te Papa Atawhai, Ngāti Koata [kaitiaki or guardians of tuatara from Stephens Island (Takapourewa)] and Kāti Huirapa Runaka ki Puketeraki (mana whenua or indigenous people of Orokonui Ecosanctuary). We would also like to thank Alison Cree and Lynn Adams for discussions on conservation translocations of tuatara, and Trevor Worthy and Paul Scofield for providing Holocene occurrence records for tuatara and takahē. Finally we would like to thank our reviewers, CC and TW for their help in improving a previous draft of the paper.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2021.691714/full#supplementary-material

**Supplementary Data Sheet 1 |** Takahe models.

**Supplementary Data Sheet 2 |** Takahe environmental data.

**Supplementary Data Sheets 3–10 |** ENMeval replicate data.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Conservation Science

ORIGINAL RESEARCH
published: 05 August 2021
doi: 10.3389/fcosc.2021.701490

# Anti-Predator Vigilance as an Indicator of the Costs and Benefits of Supplemental Feeding in Newly Released ‘Alalā (*Corvus hawaiiensis*)

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**Specialty section:**
This article was submitted to
Animal Conservation,
a section of the journal
Frontiers in Conservation Science

**Received:** 28 April 2021
**Accepted:** 06 July 2021
**Published:** 05 August 2021

**Citation:**
Lee HN, Greggor AL, Masuda B and
Swaisgood RR (2021) Anti-Predator
Vigilance as an Indicator of the Costs
and Benefits of Supplemental Feeding
in Newly Released ‘Alalā (Corvus
hawaiiensis).
Front. Conserv. Sci. 2:701490.
doi: 10.3389/fcosc.2021.701490

Although supplemental feeding is commonly used as a conservation strategy during animal translocations, it comes with a number of pros and cons which can be hard to quantify. Providing additional food resources may lead to improved physical health, survivorship, and reproduction. However, offering predictable food sources could make individuals more conspicuous to predators and less aware of their surroundings, disrupting their natural predator-prey dynamic. Decisions such as release cohort size and supplemental feeder design could influence the balance of these costs and benefits, depending on how animals behave in the face of predation risk and static food sources. Additionally, animals released to the wild from long term human care must balance foraging and predation risk while adjusting to a novel environment. To help conservation managers make informed decisions in light of these potential costs, we studied the behavior of a cohort of 11 conservation-bred ‘alalā (*Corvus hawaiiensis*) at supplemental feeding stations after release into the wild. Vigilance, foraging behavior and social group size was quantified *via* 1,320 trail camera videos of ‘alalā over the span of 12 months. We found that vigilance increased over time since release, suggesting that ‘alalā learn and adjust to their novel surroundings. Both vigilance and eating decreased with group size, indicating that although conspecifics may share the burden of scanning for threats, they also increase competition for food. We also found that the design of the feeder may have limited birds’ abilities to express anti-predator behavior since less vigilance was observed in individuals that manipulated the feeder. Yet, birds may have been able to offset these costs since they increasingly scrounged for food scraps next to the feeder as time progressed. We discuss how changes to behavior over time, social interactions, and feeder design should all be considered when planning supplemental feeding as part of wildlife translocations.

**Keywords: corvid, conservation behavior, group size effect, post-release monitoring, translocation**

## INTRODUCTION

Humans often disrupt the natural balance between predators and their prey (Carthey and Blumstein, 2018). By inadvertently introducing non-native predators into delicate ecosystems, or subsidizing natural predators by introducing abundant non-native prey, we increase the vulnerability of native prey to predation. Furthermore, bringing animals into human care as part of conservation efforts can disrupt and erode natural anti-predator responses (McPhee and Carlstead, 2010; Crane et al., 2015; Shier, 2016). Accordingly, an unstable predator-prey relationship can be a major factor leading to species decline or can impede recovery efforts. In the case of conservation translocations, animals are released into novel environments and are highly vulnerable to predation due to a lack of specific knowledge about predators, and the locations of cover, refuge and other habitat features that help prey avoid detection or evade threats. Predation can have direct negative effects on translocation outcomes since naïve animals easily succumb to predation (Berger-Tal et al., 2020) or indirect effects, since time spent engaged in anti-predator behavior, such as vigilance, may prevent animals from gaining fitness benefits from foraging or breeding (Lima and Dill, 1990; Brown et al., 1999). These costs of translocation are likely to be more severe in the initial period following release, before animals have fully adjusted to the novel environment and become familiar with predators, varying predation risks on the landscape, and effective anti-predator behaviors.

One translocation tool that has the potential to influence predator/prey dynamics is supplemental feeding. Supplemental feeding is commonly used at release sites as a strategy to increase food resource availability for species that are resource-limited due to anthropogenic habitat change or for naïve reintroduced animals that have not yet learned to exploit wild food (Boutin, 1990; Ruiz-Miranda and Swaisgood, 2019). Thus, supplemental feeding is often prioritized in the initial period following release to counter the challenges of learning to forage in a novel environment. If done well, supplemental feeding can also help anchor animals to the release site, which can increase survival (Lockwood et al., 2005; Liu et al., 2016) and reproduction (Rodriguez-Hidalgo et al., 2010), facilitate monitoring and help animals take advantage of other management actions that may occur there, such as invasive predator control, or habitat restoration. However, provisioning food to animals also comes at a cost. Supplemental feeding can influence space use (Mertes et al., 2019), spread disease (Sorensen et al., 2014), and potentially increase predation risk if predators learn prey are concentrated at a resource (although evidence for the latter is slim; see Robb et al., 2008). These costs are not always straightforward to predict, however, because supplemental feeding could also decrease predation if food resources decrease time spent in dangerous foraging activities or good nutritional condition renders evasive actions more effective. As a consequence, supplemental feeding should be discontinued once animals have learned to forage and exploit the release environment for food resources sufficiently for survival and reproduction.

Prey species can also adopt behavioral strategies for avoiding predation. Vigilance is a behavioral adaptation in which animals monitor their surroundings for potential threats (Quenette, 1990; Treves, 2000; Beauchamp, 2015). While engaging in vigilance may reduce vulnerability to predators and competitors, excessive vigilance takes time away from foraging, social behavior, and other survival-relevant activities (Lima, 1987; Lima and Dill, 1990). Documenting how animals balance vigilance and eating at supplemental feeders can offer a window into the risk assessment of released animals, whereby an increased level of vigilance behavior through time may indicate learning about predation. Therefore, assessing vigilance at feeders can help evaluate the behavioral competency of reintroduced animals and how elements of the release strategy may interact with a species' basic behavioral biology. For instance, decisions made about release cohort size may influence the likelihood of animals exhibiting a beneficial balance of vigilance and feeding, since having larger groups of animals influences vigilance levels in many species (Colagross and Cockburn, 1993; Roberts, 1996). This group size effect predicts that individuals in larger groups have less need for vigilance since larger groups have more eyes to look out for threats and offer a reduced individual likelihood of predation (Saino, 1994; Ward and Low, 1997). However, larger groups also deplete resources more quickly, can be more conspicuous, and have other associated costs, such as conspecific aggression (Robinette and Ha, 2001).

Additionally, animals' anti-predator responses are often not static. Many species respond flexibly to changes in predation risk, therefore the perceived costs of foraging in translocation contexts may change over time as animals gain more information about their novel environment. During initial release periods, animals may have to take riskier strategies, if they are unable to locate alternative food sources. Yet, as animals become more aware of the activity of predators, presence of conspecifics or foraging options, they may be able to more safely exploit resources (Berger-Tal and Saltz, 2014). Being able to learn post-release has been shown to help boost survival (Krochmal et al., 2018), but animals commonly fail to learn the behaviors they need (Berger-Tal et al., 2020). Therefore, identifying changes in how animals interact with or use supplemental feeders over time may serve as one marker of their adjustment to the novel dangers of the wild, and a sign of learning. Specifically, the temporal pattern of post-release changes in reliance on supplemental food and vigilance behavior provide insights into patterns of learning how to forage on natural foods and accumulation of knowledge about predation risk.

We illustrate the utility of investigating the complex interactions between social and antipredator behavior at supplemental feeders, with newly released 'alalā (*Corvus hawaiiensis*). 'Alalā, i.e., the Hawaiian crow, are the only extant endemic corvid species in the Hawaiian Islands. They are the sole seed disperser for many native plants (Culliney et al., 2012), and they have a complex social system, which varies with age. Younger birds are gregarious with a hierarchy of dominant and submissive birds. As they mature, they form pair bonds and establish territories which they defend from conspecifics (Banko et al., 2002). Their only native predator is the 'io, the

Hawaiian hawk (*Buteo solitarius*). ʻAlalā declined severely in the late twentieth century due to threats of predation by non-native mammals such as mongooses, rats, and feral cats, habitat degradation, disease and human conflict (U. S. Fish Wildlife Service, 2009). Despite conservation breeding and releases for the ʻalalā in the 1990s (Keuhler et al., 1995), ʻalalā were declared extinct in the wild in 2002 (U. S. Fish Wildlife Service, 2009). A new wave of reintroductions began in 2016 once the conservation breeding population had stabilized. Release strategies have thus far explicitly targeted the gregarious juvenile stage for release, in the hope that larger groups of birds would help each other in anti-predator defense, as has been documented in some, but not all corvid species (Dlaz and Asensio, 1991; Henderson and Hart, 1991; Ward and Low, 1997; Rolando et al., 2001). However, the extent to which corvid comparisons on the group size effect translate to ʻalalā may depend on the social system being compared, which varies greatly between corvid species. Also, it was anticipated that release birds' conservation breeding background might impact their anti-predator behavior since they did not develop with the same predation threats as their ancestors (McPhee and Carlstead, 2010; Crane et al., 2015; Shier, 2016). In attempts to combat their potential predator naivety, all birds were exposed to anti-predator training prior to release (Greggor et al., 2021).

As part of post-release monitoring efforts for ʻalalā, and to better assess the anti-predator costs of providing supplemental food, we measured the prevalence of vigilance and eating behavior within naturally forming social groups at feeding stations. We used camera trap videos taken during the 1st year post-release of the 11 birds released in 2017. By doing so, we hoped to determine whether the birds' vigilance for aerial threats changed over time and was influenced by the size of foraging groups. We hypothesized that the ʻalalā would either exhibit lower vigilance over time as they overcame any initial post-release stress in response to novelty, or would increase vigilance over time if the birds discovered elevated predation risk. Additionally, should the custom plastic food feeder impose costs in terms of anti-predator behavior, we would expect to see decreased vigilance when birds interact with it. However, having multiple group mates around could offset this cost, if ʻalalā are able to be less vigilant and eat more food when conspecifics are present. Such a group effect would support the management strategy of releasing larger, socialized, juvenile cohorts as a way of combatting predation risk.

## MATERIALS AND METHODS

### Study Area

This study examines trends in vigilance in ʻalalā at supplemental feeding stations from October 2017 to September 2018 in the Pu'u Maka'ala Natural Area Reserve. The study covered 11 newly released ʻalalā: seven males and four females. They were hatched in 2016 from the Keauhou Bird Conservation Center on Hawaiʻi island, and were reared either by hand with ʻalalā puppets or by adult ʻalalā in large outdoor aviaries. Each bird was identified with a unique combination of a metal and three colored plastic leg bands. The 11 birds were released in two separate groups, one late September 2017, the other in early October 2017. The habitat surrounding the release site is primarily mesic and wet forest. ʻOhiʻa trees (*Meterosideros polymorpha)* dominate the forest canopy, with a variety of native fruiting trees and ferns composing the lower tiers. Historically, cattle grazed portions of the reserve, resulting in patches of grassland and shrubland. The reserve is also home to ʻio, and other potential predators include introduced mammals such as small Indian mongooses (*Herpestes javanicus*), feral cats (*Felis catus),* and rats (*Rattus* sp.).

Daily supplemental food was provided in the forest near the release site at three to four stations. The stations consisted of an elevated platform upon which sat a feeder (made by Tuft Plastic Molders) which birds were trained to open prior to release (see video in **Supplementary Material**). Due to the size, weight, and design of the hopper, ʻalalā were the only species in the area capable of manipulating the lid. Other species were only recorded at the station in rare instances, but their data was not used as part of this study. Throughout the day as ʻalalā foraged from the feeder, food scraps would accumulate on the feeding platform. The platforms were cleaned daily when the feeder was removed at dusk or in the late afternoon, leaving no food available until the following morning. Each station was periodically moved around the site as needed for management reasons.

### Data Collection

On any given day, up to three of the supplemental feeding stations were equipped with a Bushnell Trophy Trail Camera. The cameras collected 10 s of video footage when they detected motion at stations, with 2 s gaps between consecutive videos. Collecting data *via* non-obtrusive trail cameras increased the likelihood that we would obtain a representative sample of feeding events, and that vigilance behaviors would not be biased by human observers. Each day field monitoring staff reviewed the footage, saved clips with identifiable ʻalalā and named the videos with the date and birds' band combinations. This study focuses on a subset of the tens of thousands of videos collected during the first full year post-release. Ten videos per bird per month were randomly selected in R (R Core Team, 2019), for a total of 120 videos per bird. In videos with multiple ʻalalā present, the focal bird was labeled as the first in view of that video sequence or the closest to the camera. Videos in which the focal bird's behaviors were obscured were replaced with a new video chosen at random for the same bird within the same month.

A group of three researchers coded the behaviors in each video according to an ethogram (**Table 1**), noting the total number of ʻalalā present, and behaviors such as: aerial vigilance level (**Figure 1**), and whether the focal bird ate, opened the feeder, scrounged food removed from the feeder by others, flew away, or engaged in social behaviors. Vigilance was coded as an ordinal variable, to help capture an increasing expression of wariness, based on head angle, and with or without the presence of head movements (scanning), which would afford a wider field of view. We did not record duration or frequency for any of the behavioral variables because although the trail camera videos were a standard duration (10 s), the random subset we selected varied in whether they caught birds at the beginning, middle or end of a given behavior, which would mean that duration

**TABLE 1 |** ʻAlalā vigilance ethogram with information and definitions used for video coding.

| | |
|---|---|
| Bird ID | Individual identified based on color band combination. |
| Total birds | Total number of ʻalalā at the feeder station. |
| Vigilance for aerial threats | 0—None: Bird does not raise beak at a 90-degree angle or higher for the entire duration of the clip.<br>1—Low: Bird raises bottom edge of beak at a 90-degree angle or higher in a single direction, regardless of the length of time or number of glances.<br>2—High: Bird raises bottom edge of beak at a 90-degree angle or higher in more than one direction, regardless of the length of time or number of glances. |
| Eats | Yes: Bird interacts with food. Examples include: Food visible inside the beak. Visibly swallowing food. Leftover food on beak. Movement inside feeder after opening lid. Scrounging behind feeder out of view.<br>No: Bird does not meet criteria for interacting with food. |
| Opens feeder | N/A: feeder lid is not present or visible, or is already open at start of video clip.<br>No: Focus bird does not lift or prop up feeder lid during the video clip.<br>Beak: Bird opens feeder as trained, using only the beak to open feeder lid, and beak/head to prop open lid, regardless of whether food was obtained or not.<br>Foot: Foot comes in contact with feeder lid, and either opens or props lid.<br>Other: Another part of the bird's body comes in contact with feeder lid, and either opens or props lid. |
| Scrounges | Passive: Bird attempts or is successful at obtaining food without opening feeder lid and without direct interaction with another bird. Examples include: Eating food not directly from feeder, such as leftover food around feeder/or feeder lid. Eating from an already open feeder lid that stays ajar without bird's assistance. Pecking for food behind feeder out of view.<br>Active: Bird attempts or successfully obtains food by taking from another bird without begging. Examples include: Stealing from another bird. Begging and being fed from another bird. Taking food from feeder when another bird opens lid.<br>None: Bird does not attempt any of the above. Includes instances when bird is already eating, but the method of obtaining food is unknown. |
| Flight | Yes: Focus bird flies to the feeder station or away from the station during video clip.<br>No: Focus remains at the feeder station during the whole video clip.<br>Note: Instances such as small hops or travel from one part of station to the other do not count as flight. |
| Social behaviors | Flutters Wings: A bird flutters wings. Indicate if focus bird initiates or receives behavior.<br>Steals: A bird attempts to take food currently or previously held in another bird's beak or foot. Indicate if focus bird initiates or receives behavior.<br>Harm: A bird inflicts potentially harmful physical contact with another bird. Indicate if focus bird initiates or receives behavior. |

and frequency would often fail to accurately capture the full behavioral bout. When we recoded a subset of videos (16%), we found that the total number of birds and behaviors were consistently recorded (no. of birds, 97% concurrence between coders; vigilance, 89%; eats, 93%; opened feeder, 93%).

## Analysis

The behavioral data were used to determine if vigilance, eating, and the effect of conspecifics on behavior changed over time. Specifically, we aimed to answer three main questions: (1) what predicted the occurrence of vigilance for aerial threats at the feeding stations, (2) what conditions predicted birds eating at the feeding stations, and (3) did birds adopt different feeding strategies depending on the number of conspecifics present? A separate model was built for each question and all were investigated with regards to time since release. Social behaviors, such as aggression or submission, occurred too infrequently for robust statistical analysis (7.6% of videos).

Vigilance behavior was separated into three categories, with birds showing no (0), low (1), or high levels of vigilance (2), and was analyzed using a Cumulative Link Mixed Model (CLMM) with a logit link function, using the "ordinal" package (Christensen, 2019). The total number of birds in the video, sex of the focal bird, time in months since release, the type of contact with the feeder, whether or not the bird ate, and whether they took flight during the video were all included as fixed, explanatory variables. Bird identity was used as a random effect to account for repeated measures of individuals over time. Controlling for individual variation is necessary since vigilance levels can vary at the individual level, even when group size effects are present (Carter et al., 2009).

The factors that influenced whether or not a bird ate (Y/N) were analyzed with a Generalized Linear Mixed Model (GLMM) with a binomial error structure and a logit link function. The total number of birds present in the videos, sex of the focal bird, time in months since release, and whether or not the bird opened the feeder were all considered as explanatory variables. Similar to the vigilance model, individual ID was used as a random effect.

Finally, using just the observations where birds were observed eating at the feeding stations, we investigated whether ʻalalā were more likely to scrounge from the platform than eat from the plastic feeder (scrounge Y/N), based on the number of birds present. Scrounging behavior, i.e., taking advantage of a resource provided by a "producer" (Barnard and Sibly, 1981), could be advantageous for ʻalalā if birds are able to consume scraps left by others without having to interact with the feeder itself. Since active scrounging via social interaction with a conspecific occurred exceedingly rarely (2.8%), only passive scrounging was considered. We used a GLMM with a binomial error structure and a logic link function. We included the additional covariates of sex, and time in months since release. Individual ID was used as a random effect.

All models were simplified using backwards stepwise elimination, based on changes to AIC values (Burnham and

**FIGURE 1 |** Photo depictions of vigilance levels. Each pane shows a different level of vigilance. Birds either **(A)** spent the entire video with their head oriented downwards, **(B)** glanced upwards in one direction at some point during the video, or **(C)** oriented their head in multiple directions during the video.

Anderson, 2002). If dropping a given term did not increase the AIC by more than 2 points, then the term was excluded from the final model. Model selection was then confirmed by comparing Akaike weights between models with the MuMIn package (Barton, 2020).

# RESULTS

## What Predicts the Occurrence of Vigilance?

'Alalā displayed some level of vigilance toward aerial threats in 87.6% of observations, but were not equally likely to be vigilant in all situations. Individual 'alalā were less likely to be vigilant as group size increased at the food platforms (CLMM, $N = 1{,}320$, coef $= -0.32 \pm 0.1$, $z = -3.16$; **Figure 2**). Vigilance slowly and slightly increased the longer the birds spent in the wild (coef $= 0.06 \pm 0.02$, $z = 3.08$; **Figure 3**). Also, regardless of whether they used their beak or foot to open the feeder, 'alalā were less likely to be vigilant when interacting with the feeder (beak, coef $= -0.59 \pm 0.17$, $z = -3.42$; foot, coef $= -0.83 \pm 0.23$, $z = -3.64$), but there was no relationship between whether or not they were seen eating and their vigilance levels. Birds who took flight during videos were less likely to be vigilant (coef $= -0.60 \pm 0.23$, $z = -2.57$), meaning that birds were less likely to be vigilant immediately before leaving the feeder. Finally, sex had no effect on vigilance (**Table 2**).

## What Predicts Eating?

The more birds present on the food platforms, the less likely any individual ate (GLMM, $n = 1{,}320$, $B = -0.49 \pm 0.10$, $z = -4.73$). Also, focal individuals were less likely to be observed eating if they were seen taking flight during the video ($B = -1.09 \pm 0.22$, $z = -5.03$). 'Alalā were more likely to be seen eating if they were interacting with the feeder ($B = 0.37 \pm 0.18$, $z = 2.06$). Sex, and time since release had no effect on the likelihood that birds ate during the videos (**Table 3**).

## What Influences Scrounging?

The number of birds present on the food platform did not influence the likelihood that birds would scrounge from the platform rather than eat from the feeder (**Table 4**). However, birds became increasingly likely to scrounge as the months passed since release (GLMM, $n = 982$, $B = 0.15 \pm 0.02$, $z = 6.76$). Sex also had no effect on the likelihood that birds would scrounge.

# DISCUSSION

Supplemental feeding can provide translocated individuals with additional food resources in a novel environment, but it may come at the cost of an increased risk of predation. We studied 'alalā antipredator vigilance, eating behavior, and group size over time to assess the potential benefits and risks of supplemental feeding. Overall, the 'alalā were often vigilant at the feeding stations, with 87.6% of observations showing some form of scanning behavior. However, the birds' vigilance levels depended on a number of factors. Individual likelihood of vigilance decreased with group size, but increased over time since release. The supplemental feeding setup also added potential costs as birds showed decreased vigilance while using the feeder, but 'alalā appear to have several feeding strategies which can offset these costs, such as scrounging. We discuss the relative costs and benefits of supplemental feeding that we documented, in the context of potential release strategies, as well as changes through time that may inform when to adjust supplemental feeding.

Releasing larger groups of birds has the potential to offer anti-predator benefits if birds are more likely to share vigilance duties among a group and have greater opportunities to feed when together. In 'alalā we found that group size was linked to both vigilance and eating, but not in a fully advantageous way. Individual 'alalā were less vigilant as the group size increased, consistent with a large body of literature (Dlaz and Asensio, 1991; Henderson and Hart, 1991; Ward and Low, 1997; Rolando et al., 2001). However, 'alalā also showed a decrease in the likelihood of eating as the group size increased, suggesting that while there may have been anti-predator benefits, foraging together also posed energy intake costs. This is a departure from the general assumption that individuals will spend more time feeding if they are spending less time scanning for threats (Henderson and Hart, 1991; Saino, 1994), and may be due to other factors such as competition (Saino, 1994). However, perhaps feeding more efficiently, and safely, over shorter time periods, could negate any energy intake lost due to conspecific distraction.

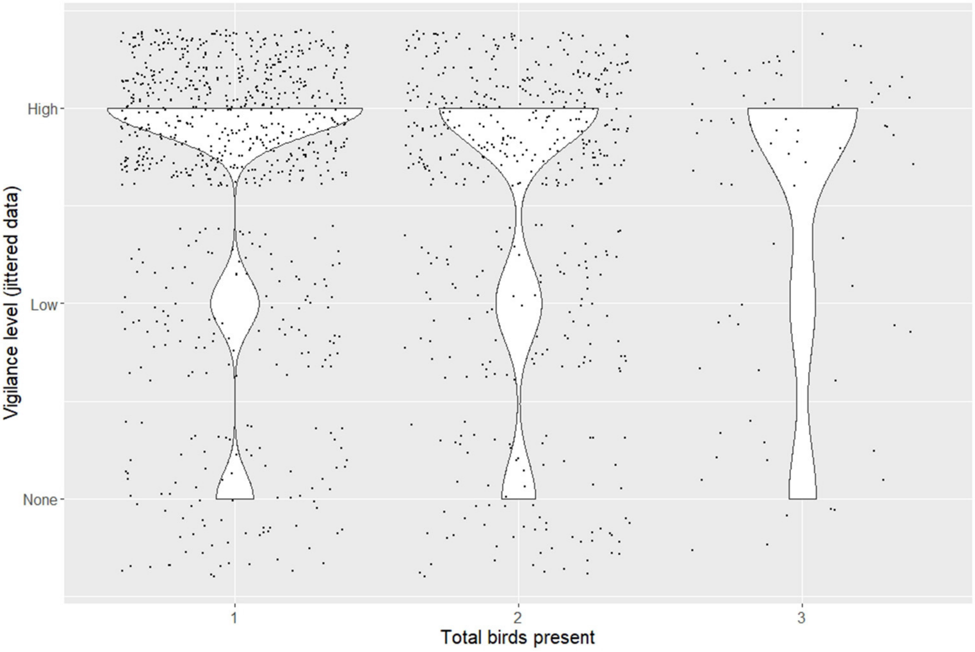

**FIGURE 2 |** Ordinal levels of vigilance depending upon the number of birds present. Violin plots and raw data, jittered around their category, using the geom_jitter function from the ggplot2 package, are included to illustrate the distribution of the data between vigilance categories. The total number of birds present represent 1, 2, and 3 or more individuals. In videos with more birds present, vigilance levels were less skewed toward the highest category of vigilance (2).

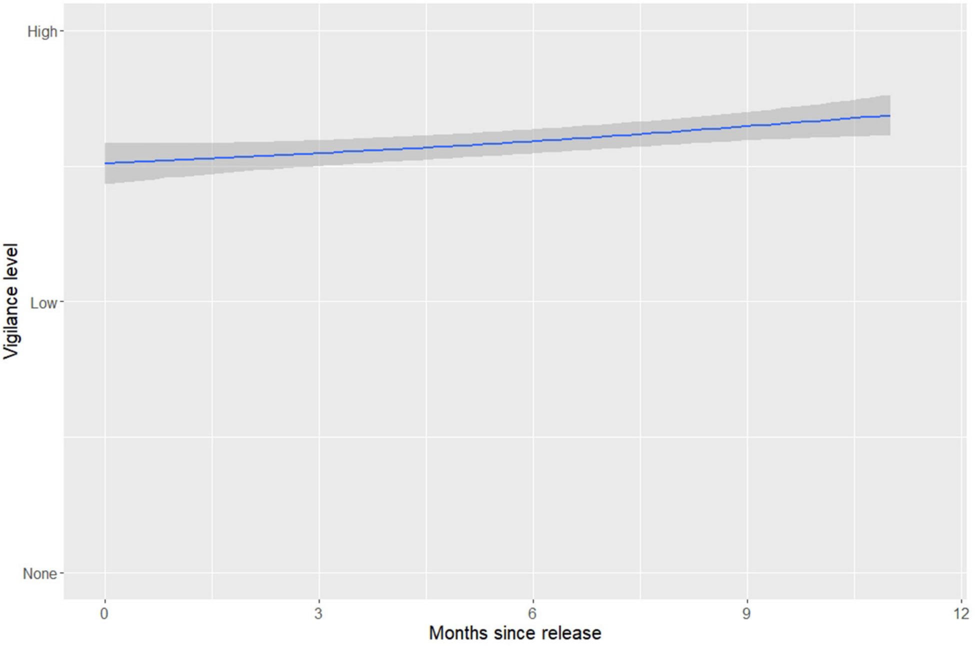

**FIGURE 3 |** Likelihood of vigilance based on months elapsed since release. Vigilance was a ordinal variable with a range of 0–2. The shaded region shows the standard error around the raw data mean for each month since release.

Alternatively, the feeder setup, not social distraction, limited birds' ability to eat in groups. Many factors must be considered when designing bird feeding stations, such as: limiting heterospecific foraging, making food accessible to the target species, and preventing food from spoiling. To reduce these potential side effects, ʻalalā were trained to open custom

**TABLE 2 |** Model selection process for analysis of vigilance.

| CLMM, $n = 1{,}320$ videos | ΔAIC | Akaike weight |
|---|---|---|
| Vigilance ∼ Sex + Flight + Opens_feeder + Total_birds + Time_since_release + Eat + (1\|Bird.ID) | 0.0 | 0.119 |
| Vigilance ∼ Sex + Flight + Opens_feeder + Total_birds + Time_since_release + Opens_feeder +(1\|Bird.ID) | −1.86 | 0.297 |
| **Vigilance ∼ Flight + Opens_feeder + Total_birds + Time_since_release + Opens_feeder + (1\|Bird.ID)** | **−2.86** | **0.502** |
| Vigilance ∼ Flight + Opens_feeder + Total_birds + Time_since_release + (1\|Bird.ID) | +1.34 | 0.060 |
| Vigilance ∼ Flight + Total_birds + Time_since_release + (1\|Bird.ID) | +13.74 | 0.00 |
| Vigilance ∼ Flight + Opens_feeder + Time_since_release + (1\|Bird.ID) | +5.00 | 0.010 |
| Vigilance ∼ Flight + Opens_feeder + Total_birds + (1\|Bird.ID) | +4.80 | 0.011 |

*The ΔAIC value represents the difference in AIC from the full model.*
*The final model, i.e., the one with the lowest AIC value and highest Akaike weight is represented in bold text.*

**TABLE 3 |** Model selection process for analysis of eating.

| GLMM, $n = 1{,}320$ videos | ΔAIC | Akaike weights |
|---|---|---|
| Eats ∼ Sex + Time_since_release + Interact.feeder + Flight + Total.Birds + (1\|Bird.ID) | 0.0 | 0.245 |
| Eats ∼ Time_since_release + Interact.feeder + Flight + Total.Birds + (1\|Bird.ID) | −0.60 | 0.317 |
| **Eats ∼ Interact.feeder + Flight + Total.Birds + (1\|Bird.ID)** | **−0.70** | **0.336** |
| Eats ∼ Flight + Total.Birds + (1\|Bird.ID) | +1.70 | 0.101 |
| Eats ∼ Interact.feeder + Total.Birds + (1\|Bird.ID) | +12.4 | 0.001 |
| Eats ∼ Flight + Interact.feeder + (1\|Bird.ID) | +22.1 | 0.000 |

*The ΔAIC value represents the difference in AIC from the full model.*
*The final model, i.e., the one with the lowest AIC value and highest Akaike weight, is represented in bold text.*

**TABLE 4 |** Model selection process for analysis of scrounging behavior.

| GLMM, $n = 982$ videos | ΔAIC | Akaike weights |
|---|---|---|
| Scrounges ∼ Time_since_release + Total.birds + Sex + (1\|Bird.ID) | 0.0 | 0.166 |
| Scrounges ∼ Time_since_release + Total.birds + (1\|Bird.ID) | −1.5 | 0.361 |
| **Scrounges ∼ Time_since_release + (1\|Bird.ID)** | **−0.6** | **0.472** |
| Scrounges ∼ 1 + (1\|Bird.ID) | +45.3 | 0.000 |

*The ΔAIC value represents the difference in AIC from the full model. The final model, i.e., the one with the lowest AIC value and highest Akaike weight is represented in bold text.*

plastic feeders at the feeding stations. While this prevented other bird species from foraging on the food, it limited the number of ʻalalā that could access the feeder at once. When more dominant birds feed from the feeder, others would have to wait for access. Thus, there was little competitive advantage to eating efficiently for dominant birds in this scenario. The design of the supplemental feeding stations also likely influenced the ability or motivation of birds to engage in anti-predator behavior. Birds that were seen interacting with the feeder displayed less vigilance. Manipulating the lid required diverting attention away from potential threats and the lid obscured the surrounding view (see video in **Supplementary Material**). There is the potential that the feeder could serve as an ecological trap, if it increases their susceptibility to predation (Robb et al., 2008; Robertson et al., 2013). However, all 11 birds survived the 12-month study period, despite the persistent presence of ʻio in the surrounding forest (Greggor et al., 2021). Therefore, while the feeder setup did not appear detrimental during the initial year of release, future designs may want to consider ways of allowing vigilance while accessing food, and facilitating safe scrounging, to reduce the potential costs of the feeder.

Despite the relatively stable costs and benefits of using the feeders during the study period, the vigilance behavior of ʻalalā increased slowly over the 1st year post-release. Since the released ʻalalā had been raised in human care, their greater vigilance over time may signify an adjustment to the wild and its predators. Such behavioral acclimatization periods are common in translocations (Shier, 2016), and in other species, being able to learn post-release has been shown to help boost survival (Krochmal et al., 2018). The increase in vigilance we documented does not mirror a classic learning curve, which suggests that ʻalalā were not entirely naïve or defenseless upon release and may only have needed to fine-tune their anti-predator behavior over time. In tandem to increases in vigilance, we also saw a greater reliance on scrounging behavior over time. By foraging on food scraps discarded from the feeder, birds may have learned to avoid the vigilance costs imposed by sticking their head into the feeder. These two behaviors together suggest that the management strategy of releasing juveniles ahead of sexual maturity and territorial conflict may have allowed for a period of relative safety in numbers while birds learned new strategies, which helped the cohort survive and adjust. However, the relative costs and benefits we documented of supplemental feeding likely change as birds mature and become territorial, around 3–4 years of age (Banko et al., 2002). As conspecific aggression becomes more prevalent, group feeding may require additional vigilance directed toward conspecifics rather than predators, or it may not be tolerated by dominant individuals. Older birds would be expected to favor solitary or pair feeding to offset these social costs, which could make supplemental feeders more dangerous. Therefore, the feeding strategies that work early in a release process may not always be ideal in later stages.

A common criterion employed for withdrawing supplemental food is evidence for reduced reliance on this food resource as the reintroduced animals learn to exploit natural food resources. While we could not quantify the volume of food consumed in each foraging bout, our findings indicate that there was no change over time in the likelihood ʻalalā would be seen eating at the feeding platforms when caught on camera. Despite their static foraging likelihood, spatial analyses suggest they spent increasing time away from the feeders (Smetzer et al., 2021) and unpublished data have documented ʻalalā foraging on a diversity of native fruits and "bark flaking" to obtain insect prey (Masuda et al.). Therefore, it is yet unclear whether ʻalalā had preferences for supplemental food, or simply continued to exploit its ready availability. While the 1 year period of this study exceeds the supplemental feeding duration of many translocation programs, in some programs long-term food supplementation for >1 year has been shown to be beneficial (Chauvenet et al., 2012; White et al., 2012). Future research is required to determine whether birds' wild foraging ability was compromised, wild foods were insufficient, or some other factor was involved in the continued reliance on provisioned food for reintroduced ʻalalā. Comparisons of vigilance levels during wild-type foraging to those seen at the supplemental feedings will also be useful for determining whether the relative perceived risks differed between food types.

Supplemental feeding is used in many translocation projects (Boutin, 1990; Ruiz-Miranda and Swaisgood, 2019), but the costs of offering supplemental food are less often considered than the potential benefits (Ferrer et al., 2018). Our results highlight how evaluating anti-predator vigilance, foraging, and social environment can illuminate translocation outcomes in the supplemental feeding context. While we cannot ascertain from our data how supplemental feeding affects predation and survival, we can learn how recently released birds use their behavior to adapt to the potential risks of feeding at supplemental food stations, and how their behavioral choices may offset costs and change through time as they gain knowledge of relative risks of feeding at concentrated food sources.

In applying these results to other species or systems, there are several factors that need to be considered which may influence responses to supplemental food. Specifically, social dynamics and conspecific tolerance will determine whether and when larger group size is a positive or negative influence. In the early stages of a translocation program before sufficient data on predation and mortality are available, animals' choice of when to remain vigilant vs. when to feed can be informative, and perhaps predictive. ʻAlalā can remain vigilant, interrupting feeding to scan for potential predators, and adjust their level of vigilance adaptively in a manner suggesting they rely on conspecifics to detect predators while feeding. These are promising signs indicative of threat-sensitive anti-predator behavior. If such vigilance and adjustments to situational changes in risk are not observed in translocated animals, this may be an early warning sign that their behavior is maladaptive. Further, animals' behavior should change over time following release as they learn and adapt to novel circumstances (Berger-Tal and Saltz, 2014); if these temporal changes in behavior patterns are not observed, this may indicate that the translocated animal's ability to learn is deficient. Because predation—and anti-predator behavior—varies as a function of habitat features that influence detection by predators or escape options (Lima and Bednekoff, 1999; Valeix et al., 2009; Cooper and Blumstein, 2015), microhabitat should be carefully considered when locating supplemental feeders. Nearby cover may make escape options available or provide hiding places for predators, depending on the nature of the predator-prey relationship. If feeders are placed in areas that are too risky, released animals may become prey or may become so vigilant that they are not able to effectively utilize the feeder. An animal's vigilance behavior may be a sensitive assay of the risk associated with varying habitat features, increasing in riskier environment. Thus, monitoring how anti-predator vigilance varies with habitat type could help inform site selection for supplemental feeders. Due to its sensitivity and close relationship with potential fitness impacts, anti-predator vigilance is a particularly promising behavior to use as an indicator for behavior-based management (Berger-Tal et al., 2011). This case study with ʻalalā underscores the value of measuring behavior as part of post-release monitoring to inform evidence-based conservation management and improve translocation outcomes.

## DATA AVAILABILITY STATEMENT

The data and R code used for the original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

## ETHICS STATEMENT

The animal study was reviewed and approved by San Diego Zoo Wildlife Alliance's IACUC (NIH A3675-01, USDA 93-R-0151, project 16-009). Permits for the release and subsequent monitoring of ʻalalā include a Threatened and Endangered Species Recovery permit (#TE060179-6) an MBTA permit (#MB09204C-1), State of Hawaii Natural Area Reserves Special Use Permit (#I1296), and a BBL permit (#24020) for capture, handling, holding, banding, and auxiliary marking of ʻalalā.

## AUTHOR CONTRIBUTIONS

AG, BM, and HL designed the study. HL collected video behavioral data. AG conducted the statistical analysis. HL and AG wrote the manuscript, with input from all authors. BM and RS secured funding. All authors contributed to the article and approved the submitted version.

## FUNDING

This research was supported by the Pacific Internship Programs for Exploring Science (PIPES) through funding from the National Science Foundation Research Experiences for Undergraduates (DEB 1757875). Funding for the ʻalalā release and monitoring during data collection for this study was provided by the National Fish and Wildlife Foundation, Moore Family Foundation, Max and Yetta Karasik Foundation, anonymous donors, and San Diego Zoo Wildlife Alliance. Funding for ʻalalā conservation breeding efforts was provided by the U.S. Fish and Wildlife Service, Hawaii Division of Forestry and Wildlife, anonymous donors, and San Diego Zoo Wildlife Alliance.

## ACKNOWLEDGMENTS

We would like to thank Amy Durham and Kawai Navares for help with video coding and discussing ethogram development. We also thank the dedicated ʻalalā field team for swapping, maintaining and archiving trail camera data, alongside general bird care. Finally, we thank the many members of the ʻalalā working group, without whom, the ʻalalā would not be alive today.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2021.701490/full#supplementary-material

**Table S1 |** All R code used for analysis and plot creation in Lee et al., 2021.

**Video S1 |** Video illustrating the field of view obstructed by feeder usage. Camera angles used for video analysis are reflected in **Figure 1**.

**Datasheet 1 |** All data used for analysis in Lee et al., 2021.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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in Conservation Science

ORIGINAL RESEARCH
published: 10 August 2021
doi: 10.3389/fcosc.2021.702128

# Mixed Mating in a Multi-Origin Population Suggests High Potential for Genetic Rescue in North Island Brown Kiwi, *Apteryx mantelli*

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**Specialty section:**
*This article was submitted to Animal Conservation,*
*a section of the journal Frontiers in Conservation Science*

***Received:*** *29 April 2021*
***Accepted:*** *15 July 2021*
***Published:*** *10 August 2021*

**Citation:**
*Undin M, Lockhart PJ, Hills SFK, Armstrong DP and Castro I (2021) Mixed Mating in a Multi-Origin Population Suggests High Potential for Genetic Rescue in North Island Brown Kiwi, Apteryx mantelli. Front. Conserv. Sci. 2:702128. doi: 10.3389/fcosc.2021.702128*

Reinforcement translocations are increasingly utilised in conservation with the goal of achieving genetic rescue. However, concerns regarding undesirable results, such as genetic homogenisation or replacement, are widespread. One factor influencing translocation outcomes is the rate at which the resident and the introduced individuals interbreed. Consequently, post-release mate choice is a key behaviour to consider in conservation planning. Here we studied mating, and its consequences for genomic admixture, in the North Island brown kiwi *Apteryx mantelli* population on Ponui Island which was founded by two translocation events over 50 years ago. The two source populations used are now recognised as belonging to two separate management units between which birds differ in size and are genetically differentiated. We examined the correlation between male and female morphometrics for 17 known pairs and quantified the relatedness of 20 pairs from this admixed population. In addition, we compared the genetic similarity and makeup of 106 Ponui Island birds, including 23 known pairs, to birds representing the source populations for the original translocations. We found no evidence for size-assortative mating. On the contrary, genomic SNP data suggested that kiwi of one feather did not flock together, meaning that mate choice resulted in pairing between individuals that were less related than expected by random chance. Furthermore, the birds in the current Ponui Island population were found to fall along a gradient of genomic composition consistent with non-clustered representation of the two parental genomes. These findings indicate potential for successful genetic rescue in future *Apteryx* reinforcement translocations, a potential that is currently under utilised due to restrictive translocation policies. In light of our findings, we suggest that reconsideration of these policies could render great benefits for the future diversity of this iconic genus in New Zealand.

**Keywords: aves, assortative mating, breeding behaviour, conservation management, hybridisation, mate choice, translocation**

# INTRODUCTION

Translocations are increasingly utilised in conservation management to reintroduce species within their former ranges, introduce them to new sites predicted to be suitable for them, or reinforce already existing populations (IUCN/SSC, 2013). Foreseeing the outcome of such interventions remains challenging, partly due to the complexity of the interface between genotype, phenotype, environment, and post translocation behaviour (Renan et al., 2018; Undin et al., 2021b). Post translocation breeding behaviour, such as mating system, and mate choice, warrant special attention, for instance, thanks to its direct link to the post translocation effective population size ($N_e$; Anthony and Blumstein, 2000).

Mate choice will directly impact reinforcement translocation outcomes. These translocations commonly involve the movement of individuals from a genetically distinct source into a target population. When such interventions result in a fitness increase and/or increased population growth rate, it is referred to as genetic rescue (Ingvarsson, 2001; Hedrick et al., 2011; Whiteley et al., 2015; Bell et al., 2019). Support is growing for genetic rescue being an effective conservation tool, especially for target populations showing symptoms of inbreeding depression (Weeks et al., 2011; Frankham, 2015; Whiteley et al., 2015; Bell et al., 2019; Ralls et al., 2020). Yet, several recent publications argue that genetic rescue has not been attempted as often as it should (Frankham, 2015; Ralls et al., 2018, 2020). One reason for hesitation toward this deliberate admixture of individuals, is the perceived high risk of causing outbreeding depression and loss of unique genetic diversity through homogenisation or genetic replacement (Love Stowell et al., 2017; vonHoldt et al., 2018; Ralls et al., 2020). A fundamental factor determining whether a translocation results in rescue, homogenisation, or replacement is whether, and at what rate, introduced, and original individuals interbreed (Vila et al., 2003; Hedrick and Fredrickson, 2010; Adams et al., 2011; Weiser et al., 2013; Bateson et al., 2014; Mussmann et al., 2017; Thavornkanlapachai et al., 2019). Consequently, post translocation mate choice, and, specifically, the presence of assortative mating, has the potential to greatly affect the outcome of this type of management (Bradley et al., 2014; Engler et al., 2019).

Assortative mating is defined as a positive or negative correlation between phenotypic or genetic traits of paired males and females (Jiang et al., 2013). Some level of positive assortative preference ("like mates alike") is fundamental in biology since this is a key mechanism for generating new as well as preserving existing species, subspecies, and ecotypes (Verzijden et al., 2005; Kopp et al., 2017; Schumer et al., 2017; Janicke et al., 2019). However, the results of positive assortative mating are context- and situation-dependent (Schumer et al., 2017). For instance, in birds as well as other groups, this behaviour has been shown to maintain sharp morphological separation in hybrid zones (Semenov et al., 2017) but has also been suggested to explain cases of instant speciation through hybridisation (Melo et al., 2009; Hermansen et al., 2011). This mating strategy has been linked to a preference for matching plumage colouration or pattern in several bird species (Andersson et al., 1998; Masello and Quillfeldt, 2003; Semenov et al., 2017; Sun et al., 2019). Yet, the most discussed and studied type of positive assortative mating is size matching between males and females, generally resulting in big individuals mating with other big individuals and small with small (Delestrade, 2001; Helfenstein et al., 2004; Jiang et al., 2013; Ippi et al., 2018; Janicke et al., 2019).

The opposite of positive assortative mating is negative assortative mating, also known as disassortative mating. This mating behaviour results in pairing between individuals less genetically and/or phenotypically similar than expected by chance, and/or between individuals with dissimilar or "opposite" traits (Jiang et al., 2013). Several studies of birds have found strong evidence for disassortative mating being a key mechanism for ensuring high fitness of offspring, for instance, since it manifests as incest-avoidance, reduced risk of inbreeding, and/or as a way of matching beneficial genotypes (Walters et al., 1988; Nelson-Flower, 2009; Nelson-Flower et al., 2012; Riehl and Stern, 2015; Riehl, 2017). Most research on this topic has focused on the major histocompatibility complex (MHC; Brown, 1998; Bonneaud et al., 2006; Kamiya et al., 2014; Santos et al., 2016; O'Connor et al., 2019). Growing evidence suggests a strong heterozygotic advantage for these immune system genes, resulting in fitness benefits for pairs with differing or otherwise compatible MHC profiles (Strandh et al., 2012; Kamiya et al., 2014; Brambilla et al., 2018; Hoover et al., 2018). However, disassortative mating has also been linked to other traits. A famous example is the white-throated sparrow (*Zonotrichia albicollis*). Within this species, mating almost exclusively occurs between individuals of the opposite of the two prevalent colour morphs (Hedrick et al., 2018).

Whether positive or negative, assortative mating is by necessity linked to mechanisms for detecting compatibility, phenotypic similarity, and/or genetic kinship (Kopp et al., 2017). The mechanisms behind such kin-recognition vary greatly between species but can be based on visual (Walters and Garcia, 2016; Sun et al., 2019), audible (Humphries, 2013), and/or scent cues (Zelano and Edwards, 2002; Bonadonna and Sanz-Aguilar, 2012; Strandh et al., 2012; Hoover et al., 2018), and the ability to detect (dis)similarity can be learnt or innate (Riehl and Stern, 2015). For many species, the mechanism(s) for kin-recognition remain unknown but, there is, for instance, growing support for MHC linked mate choice being based on scent cues in birds as well as mammals (Zelano and Edwards, 2002; Bonadonna and Sanz-Aguilar, 2012; Strandh et al., 2012). More specifically, Zelano and Edwards (2002) speculated that the most likely birds to evolve the ability to make active mate choice based on MHC identity would (1) lack the opportunity for kin-recognition based on social recognition, for instance, due to having precocial young leaving the parents at an early stage, (2) have at least one parent whose only or main contribution to the offspring is genetic material, (3) be long-lived, (4) be monogamous, and (5) have the highly developed olfactory sense. Part of the reasoning behind this is that a long life-span and high partner fidelity generates selection for mechanisms for identifying optimal partners (Kvarnemo, 2018).

One group matching all five of these criteria is *Apteryx* or kiwi birds; in particular, the focus species of this paper North Island brown kiwi, *Apteryx mantelli* (1) has super-precocial chicks, allowing conservationists to collect eggs and hatch them in captivity without the presence of a parent (Colbourne et al., 2005), (2) has male-only incubation (Colbourne, 2002), (3) can live for at least 40 years (Barlow, 2011; Robertson and de Monchy, 2012), (4) shows high levels of pair fidelity and monogamy (Taborsky and Taborsky, 1999), and (5) uses scent as their primary sense (Cunningham et al., 2009; Castro et al., 2010).

Here we exploit research opportunities provided by the unique high-density *A. mantelli* population on Ponui Island that has been thoroughly researched for the last 17 years. This population is the result of two translocation events over 50 years ago. The origin of the translocated birds was Hauturu-o-Toi (also known as Little Barrier Island) and the Waipoua Forest (**Figure 1**). The birds at these sites now belong to two of the four management units recognised within *A. mantelli*, the Northland and Western management units, respectively (Craig et al., 2011; Scrimgeour and Pickett, 2011; Germano et al., 2018). This division into management units followed the identification of four genetically separate taxa (lineages) within *A. mantelli* (Northland, Western, Eastern, and Coromandel; Weir et al., 2016). The study by Weir et al. (2016) found a Pairwise Hudson's $F_{\mathrm{st}}$ of 0.139 (95% CI 0.120–0.158) between the Northland and Western taxa, and dated the split between these management units, and thus between the parental populations of Ponui Island, to between 100,000 and 220,000 years ago. Whilst local adaptations might have evolved over this period of temporal divergence, the extent and nature of any local adaptation remains unknown (Undin et al., 2021a).

The unique features of *A. mantelli*, the island's long history of continuous research, and the population's multi-origin background make the *A. mantelli* on Ponui Island ideal for research of behaviour after translocation into a novel environment and, in particular, of mate choice. We examine size matching and genetic (dis)similarity of 17 to 23 Ponui Island pairs by utilising morphometric data collected over 17 years combined with high-density SNP data obtained through genotype-by-sequencing (GBS; a method for reduced representation sequencing; Elshire et al., 2011). We then utilise the SNP data to infer breeding behaviour over time on a population level by investigating whether or not there is evidence for cryptic clusters within the population. Finally, we discuss what the results suggest about *A. mantelli* mate choice and the plausible implications of this behaviour for future conservation efforts. We focus on reinforcement translocations which are aimed at achieving genetic rescue in this species. However, discussion of our findings is applicable for all species in need of augmented gene flow.

## MATERIALS AND METHODS

### Study Sites, Blood Sampling, and Morphometric Measurements

Ponui Island is 1770 ha, and its kiwi density is estimated to one bird per ha. Over the last 17 years, at any given time between 30 and 50 adult *A. mantelli* on the island have been tagged with radio transmitters. Tracking these birds with transmitters, combined with detailed studies of their habitat use, foraging, and breeding (partly using camera traps) has provided extensive data on individual features as well as on mating and pair identities. The datasets utilised herein contained morphometric data from 53 birds from Ponui Island including 17 pairs, and blood samples from 117 birds including 23 pairs (see further below). Most of these birds—paired birds as well as reference birds—were first caught as adults (>4 years old) over 10 years ago (**Table 1**). However, the true age was only known for the 12 reference birds that were caught as juveniles between 2004 and 2011. Based on the population being founded in 1964, and an estimated generation time of 8–15 years, the analysed birds can be expected to belong to between the 4th and 6th generation born on the island. However, the oldest known *A. mantelli* individual was over 40 years old and with a maximum lifespan of 80 to 100 years suggested for *Apteryx*, it is possible that some of the originally released birds and/or their offspring may still be alive. Blood samples have been collected in four separate cohorts: in 2004, 2006–2008, 2010, and 2017–2019. When multiple samples were available from the same bird, the newest was used to increase the likelihood of high quality. While paired and reference birds had a similar age spread, newer blood samples tended to be more available for the paired birds (**Table 1**).

The Ponui Island population was founded through two translocations in 1964 of eight birds from the Waipoua Forest (now belonging to the *A. mantelli* Northland management unit) and six birds from Hauturu-o-Toi (Hauturu; Colbourne, 2005). The Hauturu birds are usually considered as belonging to the *A. mantelli* Western management unit, but some claim their origin is hybrid or unclear (Burbidge et al., 2003; Colbourne, 2005; Scrimgeour and Pickett, 2011; Germano et al., 2018).

Unfortunately, data could not be collected directly from the Waipoua Forest due to arduous terrain and a substantial reduction in population density since the early 1990s (Craig et al., 2011). Fortunately, we were able to source both blood samples ($n = 20$) and morphometric data ($n = 15$ adults) from the Trounson Kauri Park (hereafter Trounson). Trounson is about 10 km in a straight line, south of the Waipoua Forest, which is within the known dispersal distance of this species (Forbes, 2009). Banded birds have also been observed moving between the two areas on several occasions (Meduna and Donovan pers. comm. 2020) suggesting high potential for sufficient gene flow between the areas to consider them as representing one gene pool.

Morphometric measurements were also collected from 16 adult kiwi on Hauturu-o-Toi. Five additional Hauturu morphometric samples and 13 blood samples for genetic analyses were collected from the Remutaka Forest and the Pūkaha National Wildlife Centre (also known as Mt Bruce) from birds that were translocated to these sites from Hauturu in 2010 and 2008, respectively. Throughout this text, these birds will jointly be referred to as Hauturu birds to reduce confusion.

Blood sampling and morphometric measurements of the birds were conducted in accordance with the Kiwi Best Practise Manual (Robertson and Colbourne, 2017), the Massey University Animal Ethics Committee (MUAEC) permits 06/05, 07/144, 16/92, and 18/83, and the Department of Conservation Wildlife

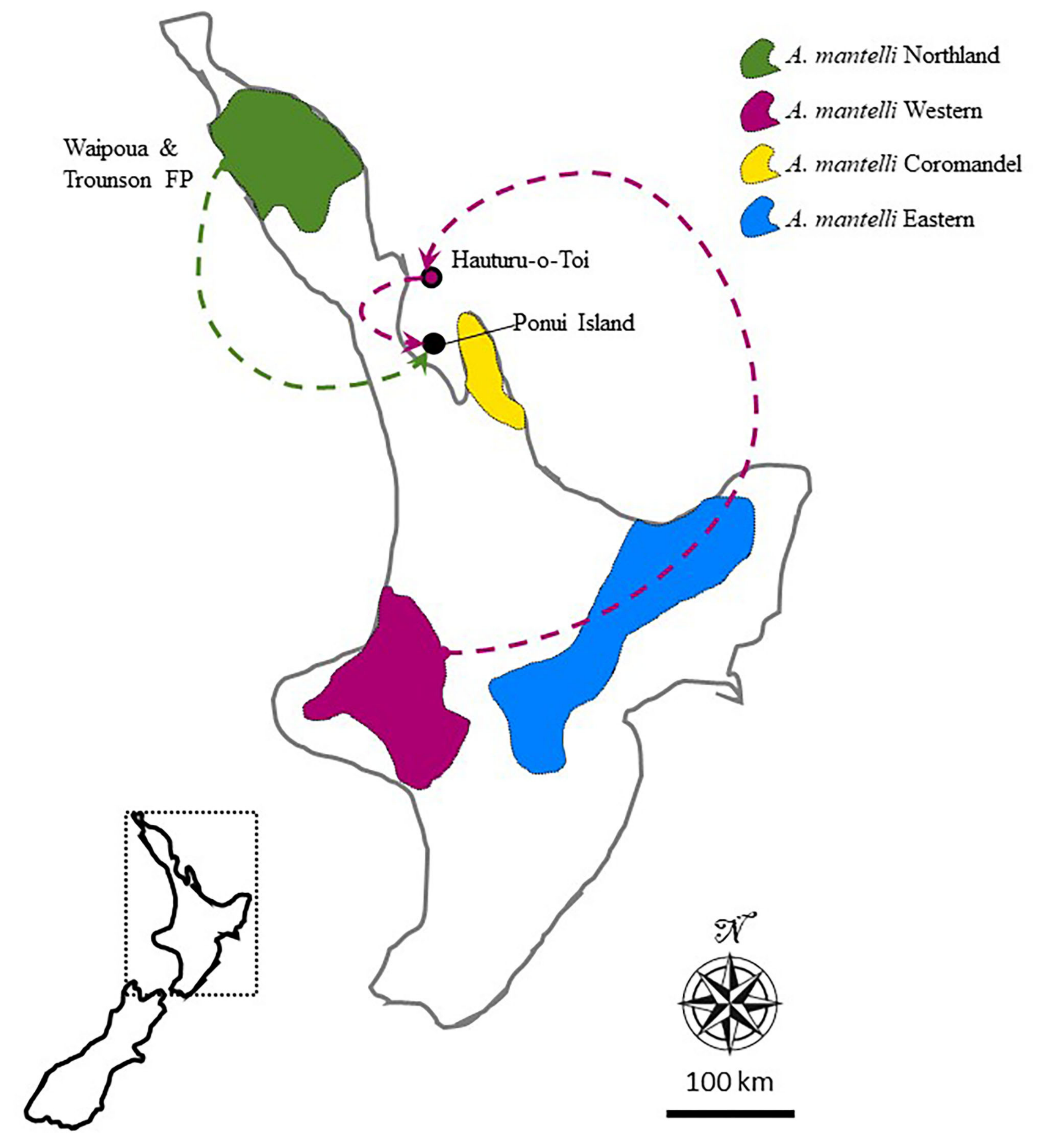

**FIGURE 1 |** Map of New Zealand's North Island illustrating the approximate distribution of the four management units (also referred to as taxa) recognised within this species. The location of Ponui Island, its parental populations, and the origin of the Hauturu birds are indicated. Modified from Undin et al. (2021b).

permits AK-14969-RES, AK-21519-FAU, 50249-FAU and 70875-RES. Samples from the parental populations were collected in 2020 and 2021. For birds fitted with transmitters (most of the Ponui Island birds analysed, all the studied pairs, and most of the Hauturu birds from the Remutaka Forest and the Pūkaha National Wildlife Centre), blood sampling, and measuring occurred together with the annual transmitter replacement. A licenced kiwi dog assisted with catching the remaining birds, which were caught specifically for this study. The density of kiwi has been estimated to be around one kiwi per three ha both

**TABLE 1 |** Number of birds and samples collected at three-time intervals for paired and reference Ponui Island birds in this study, illustrating that the majority of birds were initially caught at least 10 years ago.

| | Paired birds | | Reference birds | |
|---|---|---|---|---|
| **Years** | **Initial capture** | **Sample collected** | **Initial capture** | **Sample collected** |
| 2004–2009 | 56 | 3 | 78 | 17 |
| 2010–2014 | 36 | 17 | 17 | 63 |
| 2015–2019 | 8 | 81 | 5 | 20 |

*Kiwi reach adulthood at about 4 years old and can live for over 40 years.*

in Trounson and on Hauturu (in 2007 and 2008, respectively; Holzapfel et al., 2008). Age of the birds was mostly unknown, hence individuals were considered adults if they were known to have bred or, when the breeding status was unknown, based on their sex, size, and weight combined; females were considered adult if weighing >2000 g, or >1700 g if having a tarsus width (TW) >11 mm or a bill >113 mm; males were considered adults if weighting >1700 g, or >1400 g if having a tarsus length (TL) >90 mm or a bill >90 mm.

## Size Assortative Mating

Bill length, tarsus length, and the ratio between these measurements were used to explore differences in size distribution among adult birds from Hauturu, Trounson, and Ponui Island. Linear modelling (lm) in R (R core team version 3.6.2) was used for this analysis. To analyse size assortative mating, Pearson correlations between female and male morphometric values were investigated. The measurements analysed were TL, TW, bill length, weight to TL ratio, bill length to TL ratio, and body condition was used for 17 Ponui Island pairs. Body condition was calculated based on weight and TW following Taborsky and Taborsky (1999).

## DNA Purification, Sequencing, and SNP Calling

DNA was extracted from 10 to 50 µl thawed *A. mantelli* blood using a High Pure PCR Template Preparation Kit (Roche, Basel, Switzerland). The manufacturer's instructions were followed with the exception that the DNA was eluted twice using 50 µl of elution buffer for each centrifugation round. The DNA extraction success and quality were validated using agarose gel electrophoresis (1% (w/v) agarose in 1x TAE buffer) and the concentration of DNA was measured with a Qubit 2.0 fluorometer using the dsDNA High Sensitivity assay (Life Technologies, CA, USA).

Pair-ended Genotype-by-sequencing (GBS) library, sequencing preparation, and associated quality cheques were done by The Elshire Group Limited. GBS libraries were constructed using 100 ng of genomic DNA, 1.44 ng of adapters, the restriction enzyme EcoT22i, and 18 PCR cycles, and otherwise following the protocol presented in Elshire et al. (2011). For this study, sequencing of 150 unique birds across three 96-well plates were analysed. Sample location within plates was randomised and each plate contained one positive and one negative control. Sequencing was performed on an Illumina HiSeq XTen with 2 × 150bp paired-end reads.

The previously published *A. mantelli* genome (Le Duc et al., 2015) was deemed suboptimal as a reference genome for our study based on being (1) highly fragmented and (2) a composite genome of multiple individuals representing two separate management units within the species. Raw short-read data generated by Le Duc et al. (2015) was accessed from the European Nucleotide Archive (Study Assession RJEB6383) and the ERR519283_1.fastq.gz date file was used to re-assemble a reference genome based on a single individual. Raw reads were aggressively trimmed using trim_galore (https://github.com/FelixKrueger/TrimGalore) before assembly with Meraculous 2.2.5.1 (Chapman et al., 2011) using a kmer size of 35 and heterozygous mode 1. The resulting reference genome utilised for our analyses was haploid, with heterozygous regions collapsed into a single haplotype chosen at random between the two possible sequences.

Processing of raw read data, including filtering, trimming, alignment, and SNP calling was conducted by Tea Break Bioinformatics. The 1,538,639,658 raw sequencing reads were de-multiplexed using Axe (axe-demux; Murray and Borevitz, 2018), adapters and barcodes were trimmed using the batch_trim.pl script (https://github.com/Lanilen/GBS-PreProcess) using default parameters. Forward and reverse reads were pair-matched and aligned to the reference genome using Bowtie 2 (Langmead and Salzberg, 2012) using default parameters.

SNP-calling was conducted in STACKS 2.5 (Catchen et al., 2013) using the populations program set for the EcoT22i enzyme, bootstrapping, and site merging. Initially, this was done for each plate separately. The graphical output from Kinship-using-GBS-with-Depth-adjustment program (KGD; Dodds et al., 2015) and Tensorflow Projector (https://projector.tensorflow.org/) were then used to verify the absence of bias or batch effects after which Stacks 2.5 was rerun for the combined dataset of all three plates using the following command line: –vcf -r 0.1 –min-maf 0.1 -e ecoT22I –ordered-export –bootstrap –merge-sites –genepop –structure –fasta-loci –fasta-samples –fasta-samples-raw –write-single-snp. These settings allowed for up to 90% missing data per locus (-r 0.1) to maximise the number of individuals included in the resulting dataset. SNPs derived from different cut sites that had overlapping read coverage were combined into single loci (–merge-sites). To ensure robust SNP identification and to restrict noise, the minimum minor allele frequency was set to 10% (min-maf 0.1). The output was filtered to only include the first variable site per locus (–write-single-snp) resulting in 51691 SNPs that were utilised for analyses with an average depth of 24 reads (with a standard deviation of 12), and an average call rate of 0.6 (with a standard deviation of 0.07). The generated output provided as text files formatted for genepop (see below), and fasta files for loci and samples (–genepop –fasta-loci –fasta-samples).

## Relatedness of Paired Birds

For relatedness analyses, known first-degree relatives (known offspring and siblings) were excluded and these analyses contained 20 known pairs and a total of 74 Ponui Island individuals. Unscaled pairwise relatedness values were derived using KGD (Dodds et al., 2015). This matrix of relatedness values is based on pairwise proportional allelic similarity but accounts for read depth (including missing data) which can lead to values $>1$ and below zero. These values were used to evaluate whether paired individuals were more or less related than expected under a scenario of random mating in two ways. Test one explored whether the relatedness of paired individuals to their partner was higher or lower than the average relatedness of the paired individuals to all other Ponui Island birds in the data set. This approach provided an indication of whether paired individuals were more closely related than expected by chance (a prediction of assortative mating) or more distantly related than expected by chance (a prediction of disassortative mating). To account for possible bias caused by cryptic clusters (in particular if a few paired individuals belonged to a cluster very distantly related to the rest), test one was complemented with test two. Test two involved ranking the relatedness of the female to the male and *vice versa* for each pair and then comparing these results to expectations based on a computer simulation of ranked relatedness under a scenario of random mating. A ranking of 1 suggested that the partner of a paired bird was the least related individual within the dataset to that paired bird and a ranking of 73 that the partner was the most related in the dataset Random mating was simulated using 10*40 randomly drawn ranks between 1 and 73. $T$-tests were used for both these tests.

In addition, the average relatedness of the male and female in each pair on Ponui Island ($n = 23$ Ponui Island pairs) to the birds from Hauturu, was used to categorise pairs as being "similar" or "different" in their genetic makeup). Based on the average relatedness to the Hauturu birds for 106 Ponui Island, the relatedness space was split into four quadrants to categorise pairs. Birds were classified as "similar" when both male and female were found to be less related or both more related to Hauturu than the average value. Birds were classified as "different" when the male was more and the female less related than the average or *vice versa*.

## Genetic Differentiation

Lastly, we examined genetic differentiation of the Hauturu, Trounson, and Ponui Island populations. Using the R package genepop (Rousset, 2008) we calculated pairwise $F_{st}$ values between the parental populations and between each parental population and the population on Ponui Island. Low $F_{st}$ values between the parental populations and the current population on Ponui Island would be expected if allelic variation from both parental genomes remains present on the island. Since presence of admixture on Ponui Island would be a crucial step in achieving genetic rescue (Weiser et al., 2013), the relatedness values derived from KGD were then used to calculate the average relatedness to the Hauturu and the Trounson birds for each of the Ponui Island birds in the sample ($n = 106$ Ponui Island birds). These two factors of relatedness were then linearly normalised to span from 1 to 0; i.e., the Ponui Island birds most related to Trounson had a value of 1 and the bird least related a value of 0, and the same was done for the relatedness of Ponui Island birds to Hauturu birds. The relatedness of each Ponui Island bird to Hauturu was then plotted against the same bird's relatedness to Trounson to explore potential skews toward either parental population and/or patterns of discontinuous spread (or clustering) along the relatedness gradient suggestive of positive assortative mating over time having generated cryptic subpopulations on the island.

# RESULTS

## Morphology

For bill length and bill to tarsus ratio, the birds from Hauturu were found to be significantly smaller compared to birds from Trounson, while the distribution of individual morphometric values of the Ponui Island birds spanned the range of both parental populations (**Figures 2A,C**; Bill: $F = 8.00$, df $= 2$, $p = 0.001$; Bill/TL: $F = 11.10$, df $= 2$, $p < 0.001$). A bimodal distribution for both these characteristics was due to the size difference between the sexes (**Figures 2A,B**; Robertson and Colbourne, 2017); accounting for this difference, the trait distributions within the Ponui Island population was continuous. The difference in tarsus length was not found to be statistically significant (TL: $F = 2.60$, df $= 2$, $p = 0.08$).

None of the analysed morphometric characteristics (bill length, weight, tarsus length, tarsus width, bill to tarsus and weight to tarsus ratio, or body condition) showed any support for size assortative mating among the Ponui Island pairs ($n = 17$ pairs; **Figure 3**).

## Relatedness of Partners

Overall, the allelic similarity within pairs was found to be significantly lower compared to the paired individuals' average relatedness to all other Ponui Island birds in the dataset (0.057 vs 0.011, respectively; t $= -4.06$, df $= 39$, $p$-value $< 0.001$; $n = 20$ pairs and 74 birds overall; **Figure 4A**). Looking at individuals, 75% of the paired birds had a lower value of allelic similarity to their partner compared to their average similarity to the full dataset. The results based on ranked relatedness further supported that pairs were less related than expected under random mating ($t = 2.43$, df $= 73.25$, $p$-value $= 0.018$; **Figure 4B**). On average across paired birds, 69% of the birds in the full data set had a higher ranked relatedness than the partner of that individual. In five cases, the partner was in fact one of the top three least related individuals in the data set. However,

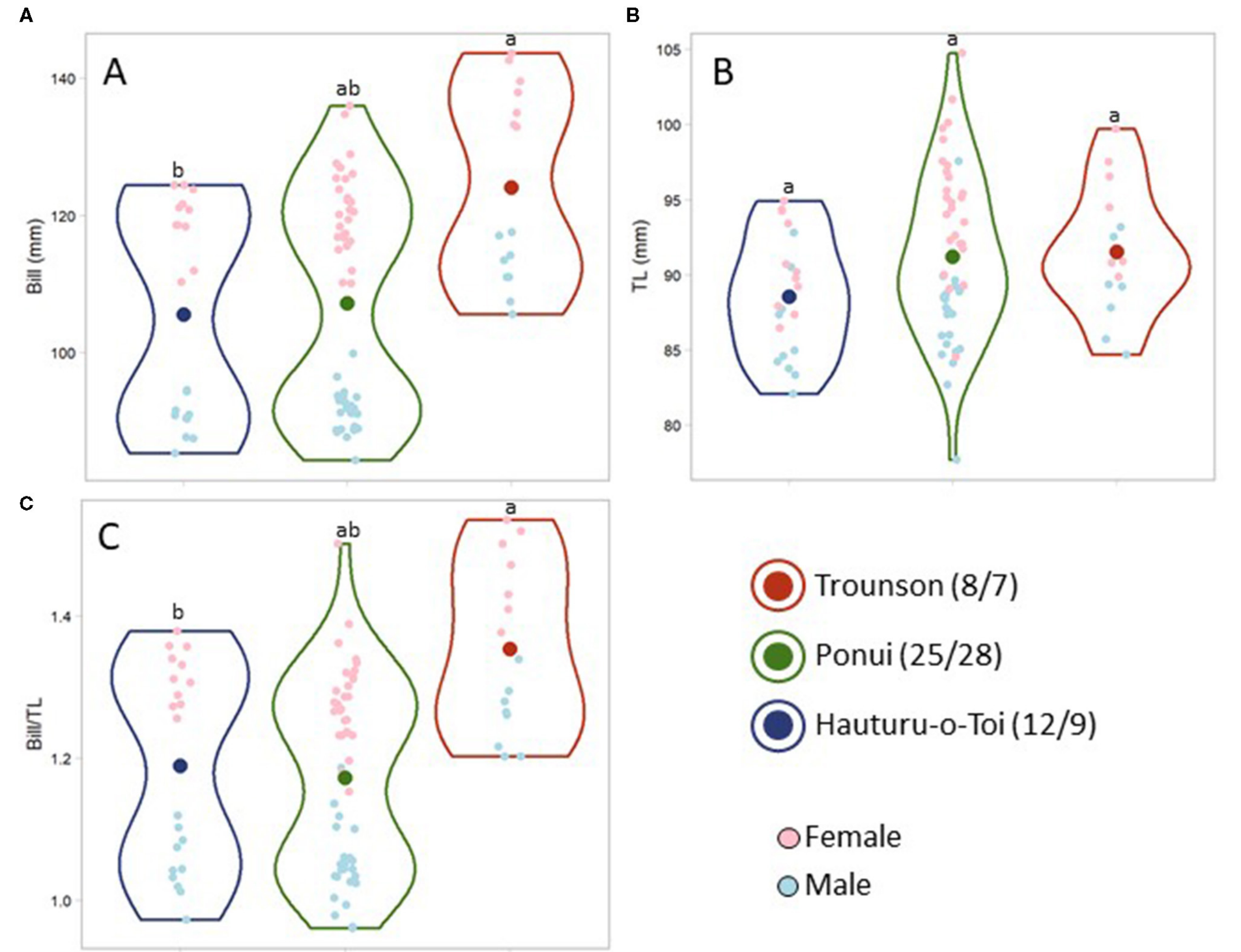

**FIGURE 2 |** Violin plots comparing morphometrics of adult *A. mantelli* from Hauturu-o-Toi, Ponui Island, and Trounson Kauri Park, specifically bill length **(A)**, tarsus length **(B)**, and the ratio between the two **(C)**. Different lowercase letters indicate significant difference. Small dots represent each data point and dot colour indicates the sex. Large dots represent the average size or ratio estimated for each population. The shape of the violin outline indicates the distribution of the data points. Sample size for males/females is indicated in the legend for each population.

there was large variation, and one pair was found to have an allelic similarity close to that of first-degree relatives.

Based on the paired individuals' average relatedness to Hauturu birds, an equal number of pairs could be classified as similar (both male and female over or under the average relatedness to Hauturu) and different (one bird less and one more related to Hauturu than average; 10 pairs vs. 10 pairs; **Figure 5A**). The remaining three pairs were placed in neither category due to either or both partners falling on the threshold value (0.07; **Figure 5A**).

## Genetic Differentiation and Evidence for Admixture

The pairwise $F_{st}$ value between Trounson and Hauturu was found to be 0.159 while that between Ponui Island and Trounson was 0.101 and between Ponui Island and Hauturu was 0.092. These values indicate less genetic differentiation between both source populations and the Ponui Island population compared to between the two source populations. A strong negative correlation in relatedness for Ponui Island birds to Hauturu and Trounson was observed. The relatedness values formed a continuous gradient of allelic similarity. Thus, there was no indication of the Ponui Island birds clustering into cryptic subpopulations with individuals either mostly related to Hauturu or to Trounson birds (**Figure 5B**). These results are consistent with a lack of assortative mate choice over time, generating repeated mixing and backcrossing and resulting in a genetic structure on Ponui Island expected in a hybrid swarm (Hwang et al., 2011).

# DISCUSSION

Taken together we found no evidence for positive assortative mating in *A. mantelli*. This finding was supported both by

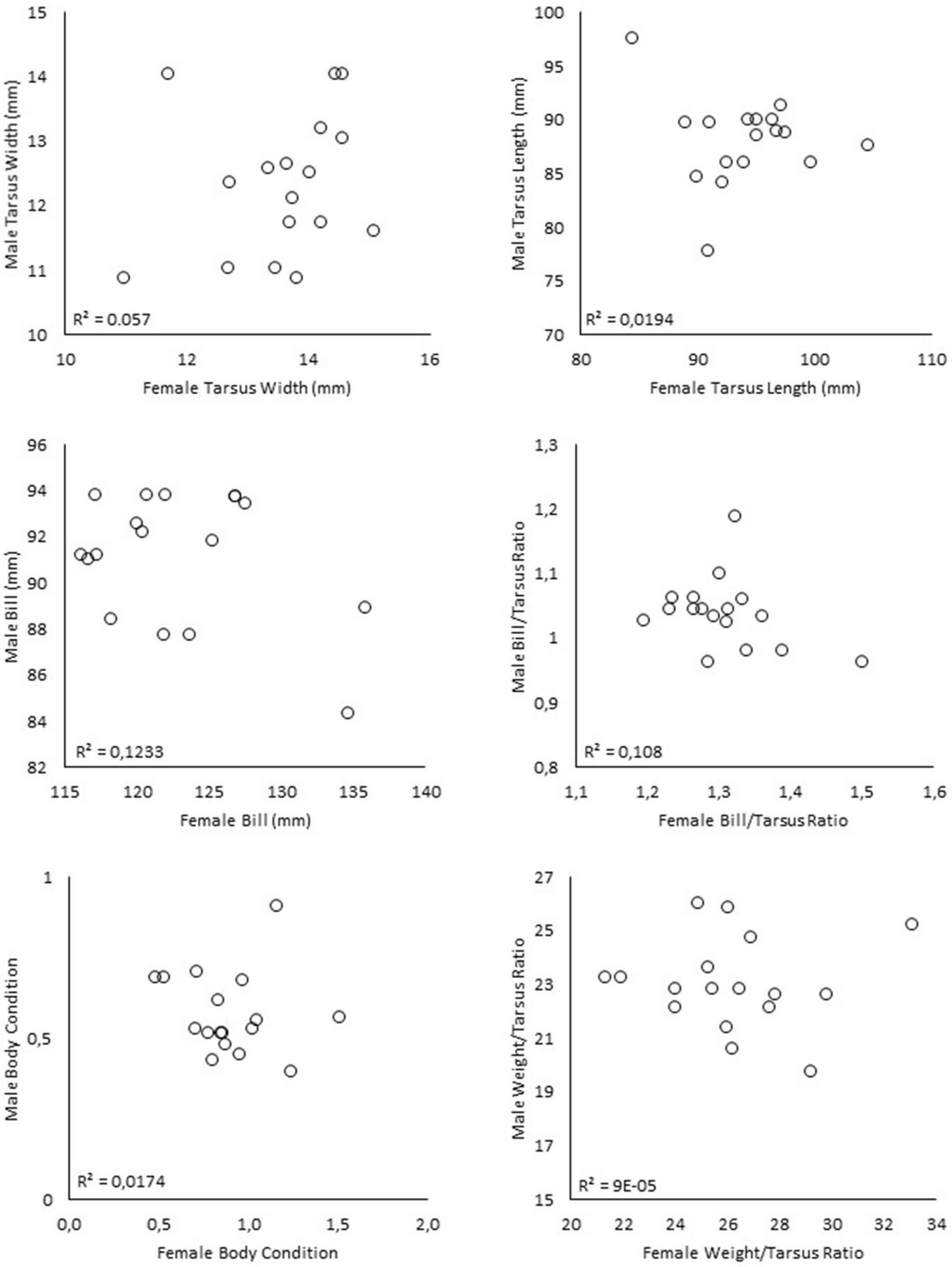

**FIGURE 3 |** Correlations between morphometric measurements of paired male and female *A. mantelli* from Ponui Island. The unit of weight is grams. Bill, tarsus length, and tarsus width are given in millimetres. Body condition is based on a combination of weight and tarsus width (Taborsky and Taborsky, 1999). None of the correlations were found to be significant. $R^2$ values refer to linear regression.

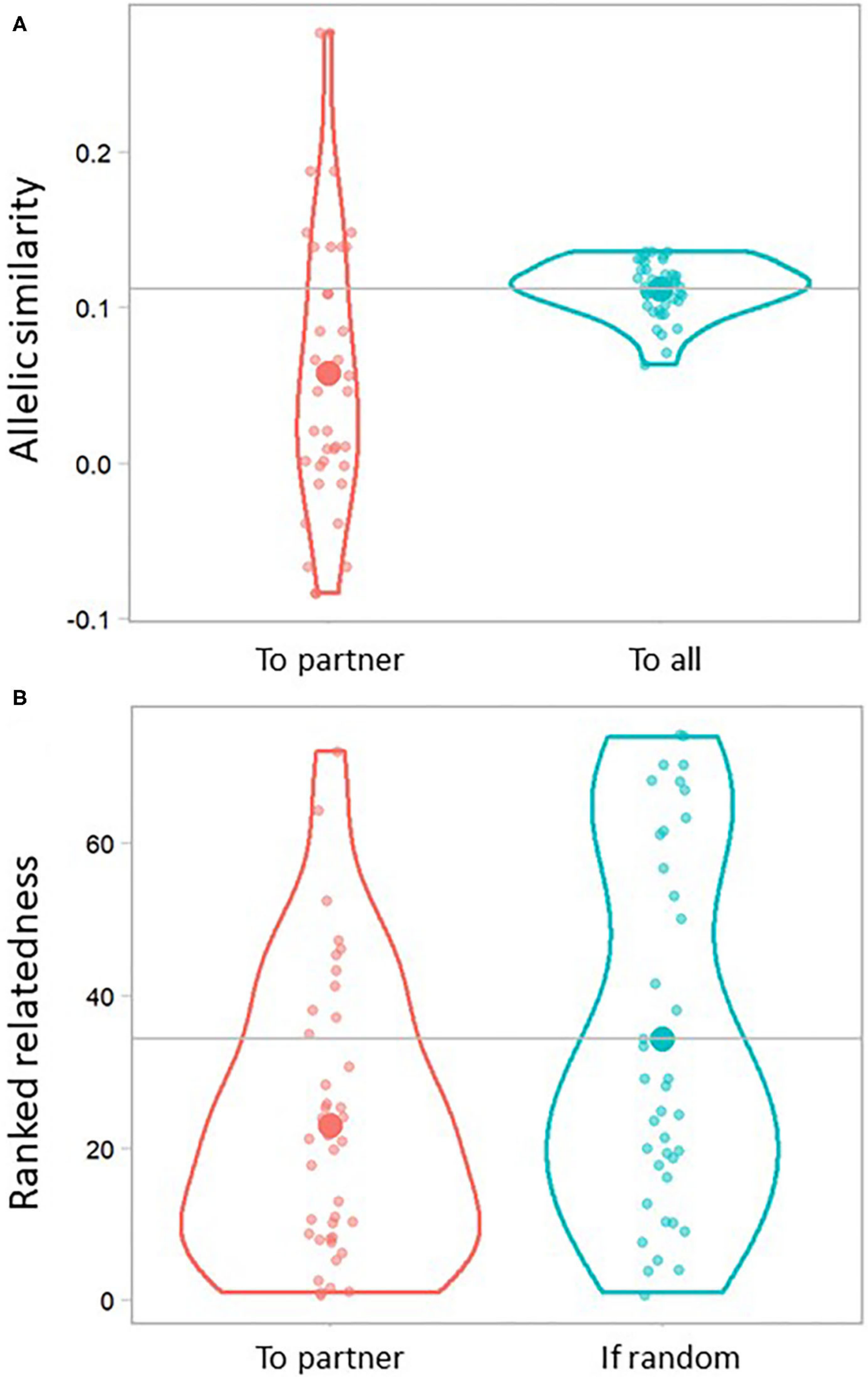

**FIGURE 4 |** Violin plots illustrating relatedness of paired individuals to their partner (*n* = 40 datapoints representing 20 pairs). **(A)** Pairwise relatedness based on allelic similarity between each paired bird and its partner (left) and the average pairwise relatedness based on allelic similarity of each paired bird to all other birds in the entire sample set (right; *n* = 74). **(B)** Ranked (or relative) relatedness of each paired bird to its partner (left) compared to one example iteration of 40 randomly generated rank values. A ranking of 1 indicates that the partner of a paired bird was the least related individual in the sample set, while a ranking of 73 indicates that the partner was the most related bird in the data set. Small dots represent each data point, and the shape of the violin outline represents their distribution. Large dots represent the average. Horizontal grey lines indicate average allelic similarity and ranked relatedness, respectively, expected under the null hypothesis of random mating.

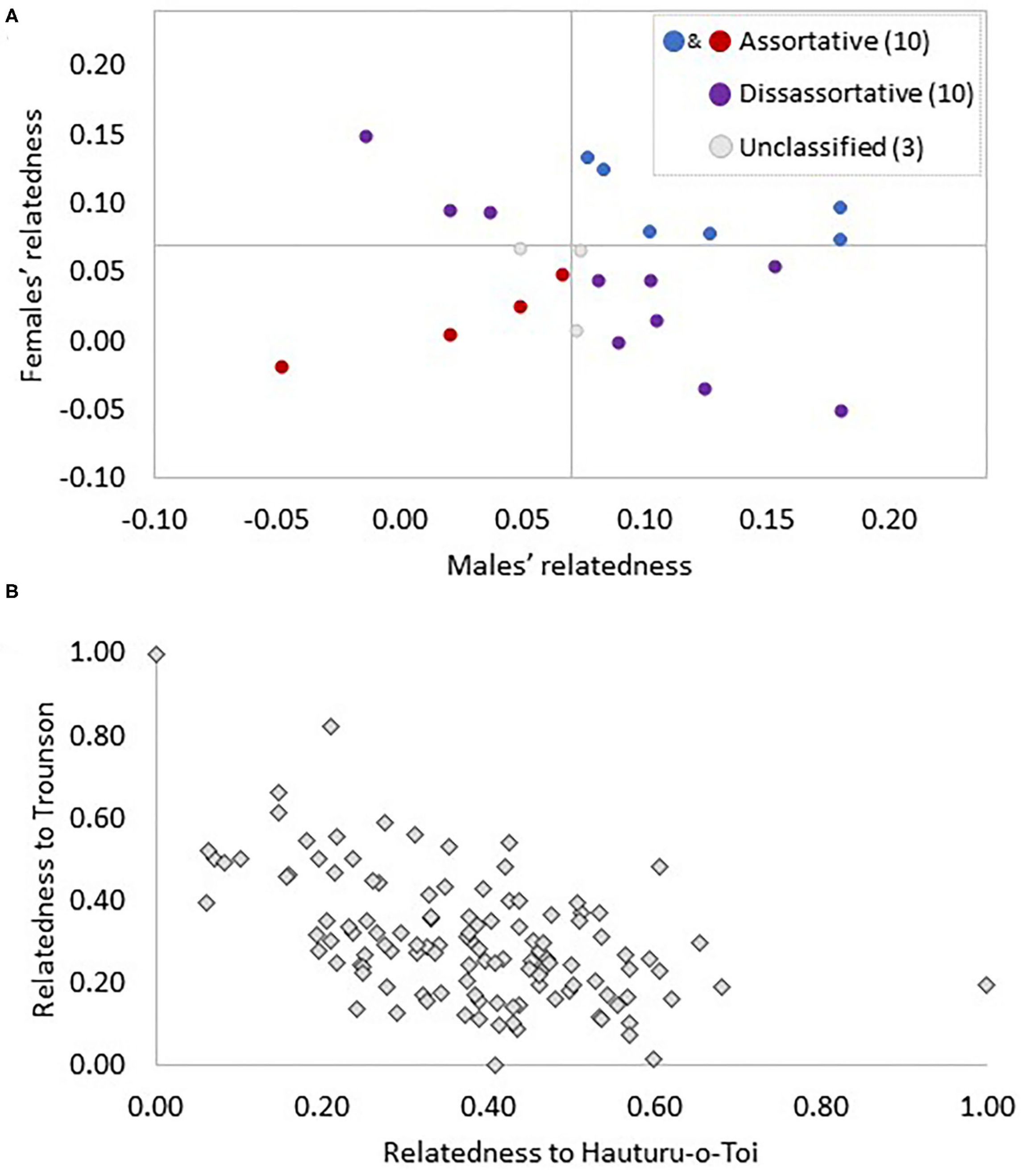

**FIGURE 5 |** Illustration of the genetic makeup of Ponui Island pairs **(A)** and the Ponui Island population overall **(B)**. In panel **(A)** 23 Ponui Island pairs are represented by one dot each and grey lines divide the graph into quadrants using the average relatedness of 106 Ponui Island birds to the Hauturu birds as a threshold value. In pairs falling in the lower left quadrant (red dots), both the male and female are less related to Hauturu than the average Ponui Island bird and, thus, are classified as "assortative" or "similar". Pairs in the upper right quadrant (blue) are also "assortative" or "similar" (both less related to Hauturu than the average Ponui Island bird), while the top left and bottom right quadrant contains pairs where the male and the female fall on opposite sides of the threshold and are, hence, referred to as "disassortative" or "different" pairs (purple). Three pairs fall on the threshold value and remain unclassified (grey). In panel **(B)** each of the 106 Ponui Island birds is represented by a diamond indicating their normalised relatedness to Hauturu and Trounson birds. Relatedness values were spread uniformly across the gradient, i.e., the scatter plot indicates no genetic clustering suggestive of positive assortative mating.

morphometric data, which indicated no size assortative mating, and genetic data, which suggested an equal likelihood of pairing with an individual of similar or dissimilar overall genetic makeup. The Ponui Island population originated from two genetically distinct taxa (Colbourne, 2005; Weir et al., 2016; Germano et al., 2018). Our morphometric sample set from Hauturu and Trounson suggested that these populations differ morphologically with Hauturu individuals being smaller. If size assortative mating occurred with limited admixture after the translocations to Ponui Island, we would thus expect to observe (cryptic) sub-populations on the island. However, we found no evidence for this. Morphological variation of individual Ponui Island birds spanned that of both parental populations. Furthermore, our genetic analyses indicated high level of shared diversity between both Ponui Island and both two founder genomes (based on $F_{\mathrm{st}}$ values) and a continuum of relatedness without clustering between the Ponui Island birds and the parental populations (based on allelic similarity). These results are expected if there is little genetic, preferential, or behavioural barriers to admixture following multi-origin translocations. Based on this, we suggest that the extant population in 2019—close to six decades after the translocation—has retained allelic variants from both parental populations, and that the population today constitutes a successful hybrid swarm in which there is large individual variation in genomic makeup and no evidence for lingering cryptic separation into a Hauturu and a Waipoua cluster.

In fact, pairwise allelic similarity and ranked relatedness suggested that paired individuals on Ponui were, on average, less related to each other than expected by chance. This disassortative mating is interesting for two reasons. Firstly, it is indicative of a post translocation behaviour that has the potential to increase the speed of admixture between genetically distinct groups, and this rate of admixture is directly linked to the potential for genetic rescue. Mate choice and mating system will drastically impact translocation outcomes (Anthony and Blumstein, 2000; Renan et al., 2018; Zecherle et al., 2021). Promiscuity, polygamy, and/or consecutive alteration of breeding units will all potentially increase the speed of admixture and reduce the long-term impact of initial mating after translocation events (Sander et al., 1997). However, *A. mantelli* has been described as monogamous with relatively high pair fidelity, thus, initial pairing post translocation will have comparatively larger impact on admixture and thus on the chances of achieving genetic rescue (Taborsky and Taborsky, 1999; Colbourne, 2002). It is possible that the initial scenario on Ponui Island following the translocations in 1964 was artificially bimodal with birds from the two source locations representing two strict groups. Unfortunately, important information of sex distribution and post translocation survival in the two cohorts is missing. However, the lack of genetic clustering on Ponui today indicates that paring between individuals with different degrees of mixed ancestry has happened over time. Thus, the lower-than-expected relatedness between birds in current pairs, cannot be explained by random chance impacting a small initial population. Furthermore, the population of *Apteryx* on Ponui Island today represents one of very few *Apteryx* populations that exhibit what is thought to resemble kiwi densities found before the introduction of exotic predators (Potter, 1990; McLennan and Potter, 1992; Miles et al., 1997; Craig et al., 2011; Germano et al., 2018) and, consequently, a comparatively "natural" frequency of mate choice opportunity suggesting that disassortative mate choice might have been more pronounced in the past.

The second reason the lower-than-expected relatedness between paired individuals is interesting is that it is suggestive of kin-recognition in *A. mantelli*, and that this mechanism is being utilised to reduce inbreeding and increase diversity. Such disassortative mating based on phenotype has been found to be rare (Jiang et al., 2013), and *A. mantelli* fit the profile of a bird expected to exhibit mate choice linked to MHC compatibility exceptionally well, not the least thanks to its well-developed sense of smell (Zelano and Edwards, 2002; Cunningham et al., 2009; Castro et al., 2010; Corfield et al., 2014; Le Duc et al., 2015). In fact, when comparing across Aves, Zelenitsky et al. (2011) noted that two extant groups stand out due to the large size of their olfaction bulb and inferred positive selection for this part of the brain compared to their sister clades: *Apteryx* and the order Procellariiformes (the petrels and allies, including albatrosses and shearwaters). Furthermore, Zelano and Edwards (2002), in studies of Procellariiformes have, indeed, found olfaction-based kin-recognition in European storm petrels, *Hydrobates pelagicus*, and blue petrels, *Halobaena caerulea* (Bonadonna et al., 2004; Bonadonna and Sanz-Aguilar, 2012) as well as MCH-based disassortative mating in Leach's storm-petrel (*Oceanodroma leucorhoa*) and *H. caerulea* (Strandh et al., 2012; Hoover et al., 2018). Studies of MHC diversity and structure in *Apteryx* have so far focused on the two species with the most drastic bottleneck history: *A. rowi* and *A. owenii* (Binney, 2007; Miller et al., 2011). The MHC diversity in *A. owenii* was found to be extremely low (Binney, 2007; Miller et al., 2011). If MHC profiles are important for *Apteryx* mate choice as well as fitness, this low diversity could provide an additional hurdle to *A. owenii* recovery. On the contrary, MHC diversity in *A. rowi* was found to be higher than expected based on their small current population size and recent tight bottleneck (Binney, 2007). This finding could suggest that a population reduction to about 150 birds (as in *A. rowi*) was still sufficient for mate choice to keep MHC diversity high, while a population minimum as low as five breeding birds (as in *A. owenii*) left little or no variation for mate choice to act upon. In view of these findings, we suggest that further studies into MHC diversity, compatibility, detectability, and preference in *Apteryx* should receive high priority. A first step would be to further examine the genetic dissimilarity between partners and investigate if it is predominantly linked to and/or exaggerated in certain regions of the genome (Beaumont and Balding, 2004; Fitzpatrick et al., 2010; Keller et al., 2013). Such studies would not only increase our understanding of *Apteryx* breeding but also take us closer to understanding the significance and nature of the genetic differences observed between *Apteryx* taxa today (see Undin et al., 2021a).

Hesitation toward translocations between genetically distinct lineages (populations, subspecies, or species) remains widespread. This is despite the fact that an increasing number of empirical studies, theoretical studies, and meta-studies suggests that admixture reduces genetic load and symptoms of inbreeding depression, increases heterozygosity and genetic diversity, boosts resilience and recovery rates, and can introduce favourable genetic variation that can increase the ability to cope with change especially in a situation of environmental change (Frankham et al., 2011; Weeks et al., 2011; Frankham, 2015; Jamieson, 2015; Whiteley et al., 2015; Ralls et al., 2018; Zecherle et al., 2021). An interesting parallel to the *A. mantelli* population on Ponui Island is the population of burrowing bettongs (or boodie, *Bettongia lesuer*) in Matuwa (Western Australia). This population was established in 2010 through the translocations of individuals from Barrow Island and Dryandra (Thavornkanlapachai et al., 2019). Similar to the case of Ponui Island, the Barrow Island and Dryandra populations represent two distinct taxa within *B. lesuer* (sometimes referred to as different subspecies; Thavornkanlapachai et al., 2019). A second similarity is that the Dryandra population, like Hauturu, was the result of a previous translocation, in this case from Dorre Island. Thirdly, these taxa show marked differences in phenotype, with the Barrow Island bettongs being substantially smaller (Short and Turner, 1999; Donaldson et al., 2017). When exploring the results of this multi-origin introduction, Thavornkanlapachai et al. (2019) and Rick et al. (2019) discovered that the first breeding at Matuwa happened almost exclusively within the two taxa. However, thanks to their low-fidelity breeding system, over half of the offspring in the Matuwa population were found to be of mixed origin after three years (Thavornkanlapachai et al., 2019). Despite their differences, the *A. mantelli* on Ponui Island and the *B. lesuer* in Matuwa can both be seen as examples of (1) that neither genetic nor phenotypic differences need to be hurdles for generating successful and genetically diverse populations through active augmented geneflow, translocations, and admixture, and (2) that breeding behaviour post translocations is directly influencing outcomes (Frankham, 2015; Frankham et al., 2017; vonHoldt et al., 2018; Rick et al., 2019; Hoffmann et al., 2020). Further studies are needed into the mechanisms of genetic rescue and outbreeding depression to increase the predictability of translocation outcomes (Undin et al., 2021b). In relation to behaviour, particular focus is needed to elucidate the effects of source site identity, translocation timing, number of individuals released, as well as population density for post translocation on mate choice and thus on the rate of admixture (see further Zecherle et al., 2021).

## CONCLUSION

Our results suggest that *A. mantelli* do not mate assortatively with genetically or morphologically similar mates. In fact, pairs were on average found to be less related than expected. This behaviour has the potential to work as a counterforce that reduces inbreeding in general (Walters et al., 1988; Nelson-Flower, 2009; Nelson-Flower et al., 2012; Riehl and Stern, 2015; Riehl, 2017), and, importantly, it suggests that interbreeding between resident and introduced kiwi after reinforcement translocations is likely. This creates potential for genetic rescue. Currently, a discussion is ongoing about the potential impact of inbreeding on *Apteryx* fitness and viability (Weiser et al., 2013; Innes et al., 2015, 2016; Germano et al., 2018). At the same time, policy around translocations is restrictive, strongly recommending minimisation of the geographic as well as the genetic distance between target and source populations (Craig et al., 2011; Scrimgeour and Pickett, 2011; Innes et al., 2016; Kiwis for Kiwi, 2016; Germano et al., 2018; Taylor et al., 2021). Arguments for this policy include that mixing populations that are too different risks resulting in outbreeding depression, loss of local adaptation, and overall loss of diversity. We recognise that mixing could result in undesirable outcomes and that this depends on the nature of the difference between source and target population (Undin et al., 2021a,b). However, our results presented herein indicate that genomic admixture can be a steady but slow process that retains diversity from both parental populations and that the Ponui Island population represents a successful balancing of the two key conservation goals of introducing genetic material without eradicating local diversity or homogenising population differences. Further support that there is currently underutilised potential for genetic rescue in *Apteryx* is the astonishing success of the Ponui Island population. This hybrid population has, on average, exhibited 9% annual population growth for over 50 years and is now one of the densest in the country despite the presence of some species of introduced predators and competitors (Cunningham and Castro, 2011; Strang, 2018). Additional study of this population should be prioritised to elucidate the particular factors that generated this success to enable practitioners to optimise strategy for future translocations.

We agree with other recent publications stressing that behaviour in the context of conservation needs more attention (Caro and Sherman, 2011; Renan et al., 2018; Zecherle et al., 2021). Consequently, we hope that this case study can contribute to the ongoing discussions concerning (1) attempting genetic rescue, (2) identifying suitable source populations for translocations, (3) the usefulness of genomics and epigenomics to take behavioural research to a population level and add a temporal scale, (4) how knowledge of social behaviour post translocations is important for appropriate conservation management design, and (5) how conservation management plans would benefit from incorporating the opportunity to express the full range of natural behaviours as an explicit goal and a part of how conservation success is defined. For instance, the presence of active mate choice in kiwi raises concern that, for the vast majority of *Apteryx*, the opportunity for mate choice today is substantially restricted either due to low population densities, small population sizes, reduced connectivity, and/or artificial settings such as so-called kohanga kiwi sites (sites where predators have been excluded, and the goal is to breed kiwi and harvest juveniles for introduction, reintroduction, and/or reinforcement translocations; Innes et al., 2016).

## DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: Dryad https://datadryad.org/stash/share/4VAEtkWXTdMm7vlU5jG5qDr_iBNyPZoT1l8C-xpRu-E. The following data files associated with this publication is available *via* Dryad. (1) Morphometric data compared between adults of three populations; (2) Morphometric data compared among 17 pairs of birds; (3) A relatedness matrix including all 150 individuals analysed; (4) Relatedness values and ranked relatedness values among 20 analysed pairs. Requests for raw reads from the underlying GBS sequence library should be made to Richard Witehira: richardwitehira@xtra.co.nz or Andre Witehira: andre.witehira@gmail.com. Permission would then be sought from the kaitiaki (guardians) representing hapu (sub-tribes) that affiliate with the areas of sample collection. Kiwi are taonga (treasures) to the indigenous Māori people of Aotearoa New Zealand. All individuals, samples, or genomic data obtained from taonga species have whakapapa (genealogy, connections, and belonging) and are considered taonga in their own right. Tikanga Māori (Māori customary practices) determines their use.

## ETHICS STATEMENT

The animal study was reviewed and approved by Massey University Animal Ethics Committee (MUAEC).

## AUTHOR CONTRIBUTIONS

MU performed the literature search, analysed the data, and wrote the first draft of the manuscript. IC is the leader of the long-term Ponui Island Kiwi Research and led the fieldwork and sample collection for this study. All authors jointly developed the concept for the article, contributed to the interpretation of the data, commented on previous versions of the manuscript, and approved the final manuscript.

## FUNDING

Funding for the many projects on Ponui Island over the years was provided by an anonymous donor, Kiwis for kiwi, Forest and Bird, and Massey University Research Fund. We are also very grateful to Bernard Sabrair and Elka Gouzer-Waechter who funded part of this research through the Massey Foundation. Kiwi Rescue's MBIE Program C09X1609, the New Zealand Marsden Fund MAU1707 and the Ngā Pae o te Māramatanga Kia Ārohi Kia Mārama grant id 18SCO17 provided specific funding for the last 4 years.

## ACKNOWLEDGEMENTS

First, we want to acknowledge the people of the land, in particular Te Patukeha, Ngati Kuta Hapū and Richard Witehira—without you, this project would never have started. We thank the Chamberlin family for allowing us to have a program of research to study the Ponui kiwi for the last 21 years.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Conservation Science

ORIGINAL RESEARCH
published: 19 August 2021
doi: 10.3389/fcosc.2021.703358

# Post-release Movement Behaviour and Survival of Kulan Reintroduced to the Steppes and Deserts of Central Kazakhstan

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OPEN ACCESS

**Edited by:**
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**Specialty section:**
This article was submitted to Animal Conservation, a section of the journal Frontiers in Conservation Science

**Received:** 30 April 2021
**Accepted:** 28 July 2021
**Published:** 19 August 2021

**Citation:**
Kaczensky P, Salemgareyev A, Linnell JDC, Zuther S, Walzer C, Huber N and Petit T (2021) Post-release Movement Behaviour and Survival of Kulan Reintroduced to the Steppes and Deserts of Central Kazakhstan. Front. Conserv. Sci. 2:703358. doi: 10.3389/fcosc.2021.703358

Asiatic wild ass, or kulan (*Equus hemionus kulan*) were once a key species of the Eurasian steppes and deserts. In Kazakhstan they went extinct by the 1930s. Early reintroductions have reestablished the species in two protected areas, but the species has reclaimed <1% of their former range and remained absent from central Kazakhstan. To initiate restoration in this vast region, we captured and transported a first group of nine wild kulan to a large pre-release enclosure in the Torgai region in 2017, and two more in 2019. We used direct observations and post-release movement data of four kulan equipped with GPS-Iridium collars to document their adaptation process in a vast novel habitat without conspecifics. For comparison with movements in the source populations, we additionally equipped two kulan in Altyn Emel National Park and six in Barsa Kelmes State Nature Reserve. The nine transported kulan formed a cohesive group with very high movement correlation in the enclosure. After release, the group initially stayed tightly together but started to break up by mid-May and all kulan travelled independently by mid-August. With 48,680–136,953 km$^2$, the 95% Autocorrelated Kernel Density Estimation ranges of the reintroduced kulan were huge and about 10–100 times larger than those in the source populations. The reintroduced mares never reconnected, there was no evidence of successful reproduction, and two of the four collared mares were killed by poachers and one died of natural causes. At least one stallion survived in the wild, but the fate of the other uncollared animals remains unclear. We speculate that the fission-fusion dynamics and low movement correlation of kulan societies and the need for migratory movements harbours the risk that animals released into a novel environment loose contact with each other. This risk is likely enhanced in steppe habitats where movement constraining factors are absent. Further kulan reintroductions to the steppes and deserts of central Kazakhstan should aim to release larger groups and build up the free-ranging population quickly to reach a critical mass, increasing the chance of kulan encountering conspecifics to successfully breed and increase their chances of survival.

**Keywords:** ***Equus hemionus kulan***, **kulan, Kazakhstan, reintroduction, social cohesion, soft release, post-release movement**

## INTRODUCTION

Old-growth steppe ecosystems store large amounts of carbon and support a great diversity of plant and animal taxa (Török et al., 2016; Wesche et al., 2016; Nerlekar and Veldman, 2020), including a diversity of charismatic ungulates, many of which are migratory (Kauffman et al., 2021). However, land conversion, degradation, and fragmentation has made temperate grasslands one of the most endangered terrestrial biomes. Most of the remaining near-natural grasslands are found in Central Asia, especially in Kazakhstan (Kamp et al., 2016). With the dissolution of the Soviet Union, Kazakhstan experienced dramatic socio-economic changes. While some of these changes have been negative for species conservation (e.g., through the breakdown of management structures that prevented overhunting or controlled poaching; (Milner-Gulland et al., 2003), others, such as large scale rural-urban migration of the human population, have created new opportunities for landscape-level biodiversity conservation and species recovery (Baumann et al., 2020; Freitag et al., 2021).

Large herbivores are important species for the functioning of steppe ecosystems but require large areas to accommodate their seasonal movements (Kauffman et al., 2021). Asiatic wild ass, or kulan (*Equus hemionous*), were once a key species in the assemblage of large herbivores [along with saiga antelope (*Saiga tatarica*), several gazelle species and Przewalski's horses (*Equus ferus przewaskii*)] that ranged the Eurasian steppes and deserts, stretching from the eastern shores of the Mediterranean to China (Bennett et al., 2017). Overhunting and habitat conversion decimated their populations and today they are only found on less than 3% of their historic global distribution range. While it is still possible to see large herds of kulan (*E. h. hemionus*) in the Gobi Desert of Mongolia (Buuveibaatar et al., 2017), the species only persists in small, isolated fragments in the rest of Central Asia. Consequently, the Central Asian subspecies or ecotypes (*E. h. kulan* and *E. h. onager*) are listed as Endangered on the IUCN Red List (Kaczensky et al., 2015).

In Kazakhstan, kulan became extinct in the 1930s, but reintroduction initiatives already started in the early 1950s. Today, kulan are again found in two separate locations, in Barsa Kelmes State Nature Reserve (SNR) in south-western Kazakhstan and in Altyn Emel National Park (NP) in south-eastern Kazakhstan. Two additional reintroduction attempts at different localities (Akatau-Buzachy and Andassay Sanctuary) were not successful (Kaczensky et al., 2016). With an estimated 500 and 3,000 kulan in Barsa Kelmes SNR and Altyn Emel NP respectively, Kazakhstan has become the most important stronghold for this endangered subspecies/ecotype of the Asiatic wild ass (Kaczensky et al., 2018a). Nevertheless, kulan have only reclaimed a tiny fraction of their former range in Kazakhstan and remain absent from the vast steppe and desert regions of central Kazakhstan, so that plans for further kulan reintroductions have been ongoing for decades.

The early reintroduction of kulan to Barsa Kelmes island was well documented (Rashek, 1966; Bannikov, 1981). Subsequent reintroductions, which lacked the confining borders of an island, were less well documented and radio collars were not used on kulan in Kazakhstan. Hence, there is very limited understanding of the factors which lead to the success of a kulan reintroduction (Kaczensky et al., 2016). There is also a total lack of baseline data on kulan movements and range sizes from Kazakhstan against which to evaluate the movements of translocated kulan. Historic observations from central Kazakhstan suggest that kulan migrated between the steppe regions in the north in spring and the desert-steppe regions in the south in fall (Bannikov, 1981, Bekenov and Fadeev, 1984). The same movement strategy is still employed by the Betpak-Dala saiga population to track greenery in summer and avoiding deep snow in winter (Bekenov et al., 1998; CMS, 2019).

In Mongolia range sizes of kulan are huge, and animals move in a nomadic fashion, travelling cumulative annual distances of 6,000–7,000 km and roaming over areas of 7,000–70,000 km$^2$, which makes them one of the most mobile terrestrial mammal species (Kaczensky et al., 2011a; Tucker et al., 2018; Joly et al., 2019; Nandintsetseg et al., 2019). The large scale-movements of kulan make them particularly vulnerable to habitat fragmentation and linear infrastructure with high traffic volume or fences constitute serious barriers to their movements (Linnell et al., 2016; CMS, 2020). Other factors known to negatively influence kulan range use are human activities (Buuveibaatar et al., 2016), and steep terrain (Kaczensky et al., 2011a). Kulan live in fission-fusion groups of frequently changing membership (Rubenstein et al., 2015; Renan et al., 2018) and individual kulan seem to show little overall movement coordination (Calabrese et al., 2018). However, kulan movements are strongly influenced by their need to access water, restricting pasture use to within commuting distances of waterpoints, but also resulting in kulan converging at these localities (Nandintsetseg et al., 2016; Payne et al., 2020) facilitating fission-fusion group dynamics and potentially allowing for social learning, including movement strategies (Brakes et al., 2021).

Little data is available on individual post-release movements of reintroduced kulan, but experiences with other large mammals suggest that "soft release" helps create social bonds and reduces the likelihood of homing and large-scale exploratory movements (Mertes et al., 2019; Resende et al., 2021) in line with natal habitat preference induction (NHPI, Stamps and Swaisgood, 2007). Captive-bred kulan reintroduced in Israel following a soft release approach, initially settled in a ca. 200 km$^2$ area close to the release site where water and good food were available, although bachelor males were observed as far as 70 km away (Saltz et al., 2000). However, reintroduced kulan in Israel seem to generally have small home ranges closely associated with artificial water points (Giotto et al., 2015) and more cohesive societies due to the scarcity of resources (Rubenstein et al., 2007).

Reintroducing ungulates into habitats where they showed migratory movement in the past - as kulan did along the steppe to desert gradient in central Kazakhstan - is even more challenging as there is a lack of understanding if, under what circumstances, and how quickly migratory or far-ranging behaviour can be restored with naïve animals (Kauffman et al., 2021, in press). Evidence from bighorn sheep reintroductions in North America suggest that learning and cultural transmission are the key mechanisms behind their migratory behaviour and it took generations for reintroduced populations to resume this behaviour (Jesmer et al., 2018). Hence, movement behaviour in the early stage of a reintroduction may not yet reflect the original and most adaptive movement behaviour, potentially also because reintroduced animals may initially key in on cues from their natal range rather than track seasonal food availability (Stamps and Swaisgood, 2007).

The Altyn Dala Conservation Initiative aims to conserve and recover nationally and internationally important flagship species and their habitats in the steppe and semi desert zones of Kazakhstan (Zuther et al., 2018). Although the main focus has been on the conservation of the autochthonous saiga populations, the initiative also aims to reintroduce kulan and Przewalski's horse to re-establish the original large ungulate assemblage along the steppe, desert steppe, and desert habitats of Kazakhstan, particularly along the steppe to desert gradient south of Torgai (subsequently referred to "Torgai region") (Kaczensky, 2011).

The three-year pilot phase of the kulan reintroduction anticipated the transport of 16-18 kulan per year in 2017, 2018, and 2019 using a large transport helicopter to quickly build up a breeding population (Kaczensky et al., 2017). However, we were met by a series of logistical problems which in the end only allowed us to airlift nine wild captured kulan from Altyn Emel NP in October 2017 and transport two additional wild captured kulan by truck from Barsa Kelmes in October 2019 (Kaczensky et al., 2018b, 2020). The first group of kulan transported in 2017, was kept in a large pre-release enclosure in the Torgai region over the winter and was released in April 2018, while the two kulan from Barsa Kelmes have remained in the enclosure since arrival in 2019.

To document the fate of the first group of reintroduced kulan and inform future translocations to the Torgai region, we analysed the movement data of reintroduced kulan and compared it with those of kulan in the two source populations. We expected reintroduced kulan to:

(1) Show a fission-fusion group dynamics and low movement coordination, but re-connection of animals in places they had previously explored together or in the vicinity of the pre-release area.
(2) Show exploratory movements followed by establishing a movement routine and decreasing proportions of new areas visited.
(3) Show the following movement characteristics:

- Initially, show movements similar to those in the source populations, especially given the abundance of pasture and water at the release site.
- Over time, re-establish migratory behaviour as described for historic kulan or seen in the Betpak-Dala saiga population.
- Be constrained in their movements by topography, rivers, linear infrastructure and human presence.

# MATERIALS AND METHODS

## Study Areas

### Torgai Region

The Torgai region is located in central Kazakhstan in the south part of the Kostanay province. The release site with the 55-ha pre-release enclosure is located at the abandoned village of Alibi on the Uly-Zhylanshyk river about 80 km southeast of the town of Torgai. Alibi is strategically located in the Torgai region within a ca. 40,000 km$^2$ network of protected areas (Altyn Dala and Irgiz-Torgai SNR), ecological corridors, and two hunting areas managed for conservation (**Figure 1**).

The climate is strongly continental with hot summers and cold winters, the average annual temperature is 7°C, annual precipitation averages 200 mm and is relatively evenly distributed throughout the year, with slight peaks in spring and fall/winter. About 25% of the precipitation falls as snow, with snow cover lasting on average from December through March and reaching up to 20 cm but varying considerably among years (from 7 to 30 cm; all climate data from the meteorological station in Torgai).

The Torgai region is located at the transition zone between the steppe and the semi-desert zone. Geologically it is part of the Torgai basin, which stretches towards the Aral Sea basin in the south. The terrain is flat, and elevations rarely exceed 200 m. Two larger perennial rivers flow through the area; the Torgai river in the north and the Uly-Zhylanshyk river in the centre. There are also several permanent large lakes, a multitude of small ones, and many artificial ponds which were created as livestock watering places during the Soviet era (and most of which retain water year-round).

There is a clear north-south gradient in precipitation and pasture productivity. While in the north steppe plant communities dominate, there is a gradual shift towards desert communities, typical for semi-desert and desert vegetation, towards the south. The vegetation cover in the area is not homogeneous, and in many places sharp boundaries between vegetation communities can be found, caused by the meso- and microrelief in combination with varying soil conditions and the influence of wildfires. The richest vegetation communities are along the Uly-Zhylanshyk river valley.

Human population density in the region is extremely low, ranging from 0.05 to 0.32 inhabitants/km$^2$, and is declining. Many settlements have become abandoned (Lenk, 2008). No major roads cross the Torgai region, but a new, unfenced, single-track railway (Zhezkazgan-Saksaulskiy corridor) was built in 2013–2014 near the southern edge and has been operational since 2015 (Olson, 2014).

The Torgai region is an important core habitat for the Betpak Dala saiga apopulation, which is currently recovering after a *Pasteurella multocida* induced mass-die off in 2015 (Kock et al., 2018). Other large mammals found in the Torgai region include Siberian roe deer (*Capreolus pygargus*), wild boar (*Sus scrofa*), and grey wolf (*Canis lupus*).

### Altyn Emel

Altyn Emel NP is located in south-eastern Kazakhstan in Almaty province. The NP was established in 1996 and covers 5,700 km$^2$. Its southern boundary is the Illy river and the Kapchagai reservoir and its northern boundary is made up of the Sholak mountains, a spur of the Dzungarian Alatau mountain range. Elevations range from 470 to 2,900 m, the average annual temperature on the plains is 8°C and average annual precipitation is 370 mm with peaks in May and October. The habitat in the plains is characterised by semi-desert and desert vegetation dominated by

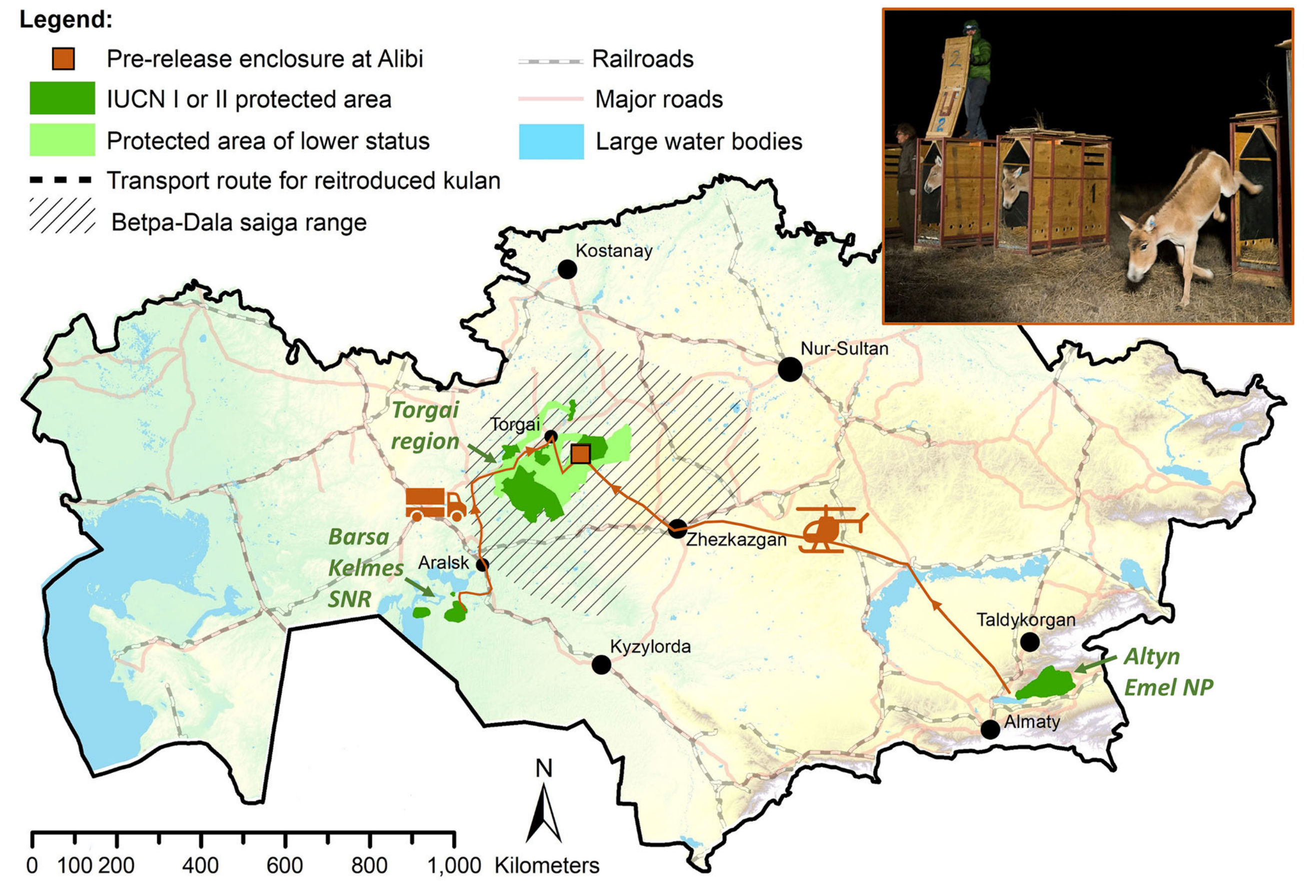

**FIGURE 1 |** Study areas of kulan in Kazakhstan. Nine kulan were reintroduced to the Torgai region in central Kazakhstan from Altyn Emel National Park (NP) in 2017 and two kulan from Barsa Kelmes State Nature Reserve (SNR) in 2019. Photo: Daniel Rosengren, Frankfurt Zoological Society.

shrubs and semi-shrubs. The NP is subdivided by a central valley with irrigation agriculture and a string of small villages. The eastern part is extremely dry with only minimal water sources. The western part has several oases on the plains and springs in the foothills of the Sholak mountains. The Ily river is flanked by large reed beds, but the shore of the Kapchagai reservoir allows relatively easy and open access to the water for plains ungulates (**Figure 1**; **Supplementary Figure 5**).

Kulan were reintroduced to Altyn Emel NP from 1982–1994 with 32 founders coming from the reintroduced population on Barsa Kelmes island in the Aral Sea (Kaczensky et al., 2018a). Besides kulan, the large ungulate community consists of goitered gazelle (*Gazella subgutturosa*), wild boar, a few Przewalski's horse (from a failed reintroduction) and grey wolf on the plains, and Siberian ibex (*Capra sibirica*), argali (*Ovis ammon*), and snow leopard (*Panthera uncia*) in the mountains. The kulan population is estimated to number ca. 3,000 animals (Kaczensky et al., 2018a).

## Barsa Kelmes

Barsa Kelmes SNR is located in Kyzylorda province in south-western Kazakhstan. It used to be a 133 km$^2$ island in the Aral Sea, established as a wildlife refuge in 1939. In the early 1950s, wild kulan from Badhyz, in south-eastern Turkmenistan, saiga antelopes and goitered gazelles were released on the island. In the 1980s, the water level of the Aral Sea started to drop rapidly, and salinity increased dramatically (Edelstein et al., 2012). Without access to suitable drinking water, kulan started to leave the island and found a new home in and around Kaskakulan, another former island with three man-made artesian springs. In 2006, the SNR was expanded to its current size of 1,601 km$^2$ which includes Kaskakulan and the surrounding area. The SNR includes no human inhabitation and is only accessible via unmaintained dirt roads.

Elevations range from 35 to 108 m, average annual temperature is 9°C and average annual precipitation is 132 mm with peaks in April and October–December. Vegetation is dominated by desert shrub vegetation, but also includes parts of the former seabed largely devoid of vegetation or covered by sand (Dimeyeva et al., 2012). Water is extremely scarce and largely limited to the artesian springs on Kaskakulan. Towards the west and north, outside the SNR, there are several lakes and irrigation channels, but these areas are also used by livestock herders, primarily for free-ranging domestic horses and cattle

(**Figure 1**; **Supplementary Figure 6**). Besides kulan, the large mammal community consists of small populations of goitered gazelle, wild boar, saiga antelope, and grey wolf. The kulan population was estimated at ca. 500 animals (Kaczensky et al., 2018a).

## Capture, Collaring, and Transport of Kulan

Kulan were captured by chasing them into large capture corrals at night using several jeeps and strong hand-held lights to guide their movements following methods described in Levanov et al. (2013) or by darting them with a $CO_2$-powered rifle from a pursuing jeep as described by Walzer et al. (2007); for further capture details see Kaczensky et al. (2018b, 2020). Kulan were anaesthetised for collaring and loading into the transport boxes with Etorphine in combination with Butorphanol and Detomidine as described in Walzer (2014).

The overall health status and condition of the animals were assessed visually and based on blood chemistry values (Gerritsmann et al., 2016) and leucocyte coping capacity [LCC; a proxy for stress (Huber et al., 2019)] obtained on-site with a portable VetScan® (VS2, Abaxis) on equine settings (Equine Profile Plus) and a high sensitivity chemiluminometer (Junior LB 9509, Berthold Technologies, Germany) respectively. During anaesthesia, all kulan were marked with coloured ear tags and fully grown adult kulan were equipped with GPS satellite collars (Vertex Lite or Vertex Plus, Vectronics Aerospace, Berlin, Germany; **Supplementary Table 1**). Kulan selected for transport also received long-acting neuroleptics (LANs; a mixture of Haloperidol and Perphenazine-decanoate) to keep them calm and stable during transport and in the initial release phase into the pre-release enclosure (Walzer, 2014).

In October 2017, the first group of nine wild kulan (four adult mares, four foals, one subadult stallion) were captured and airlifted by helicopter over 1300 km from Altyn Emel NP to a 55-ha pre-release enclosure at Alibi in the Torgai region (**Figure 1**), where they were held for 5 months over the winter until release in early April 2018 (Kaczensky et al., 2018b; Gliga et al., 2020). In 2019, two additional wild kulan (one adult mare, one subadult stallion) were successfully transported via truck over 850 km from Barsa Kelmes SNR to the pre-release enclosure (**Figure 1**; **Supplementary Table 1**; Kaczensky et al., 2020). In the pre-release enclosure, body condition and behaviour were observed twice a day. From late fall to early spring, kulan were provided with hay, and water in troughs during periods when the oxbow lake in the enclosure was frozen and there was no snow on the ground (Gliga et al., 2020).

With only 11 kulan transported 2017–2019, we fell short of the original plan to transport 16-18 kulan per year. Logistical problems during capture in 2017 resulted in the transport of only a small number of the kulan captured (Kaczensky et al., 2018a). A five-fold increase of the price for the transport helicopter in 2018 forced us to aim for a mixed truck–aeroplane–truck transport the following year, which only allowed for a narrow transport window, which we failed to meet because drought conditions made kulan capture in Altyn Emel NP very challenging. In 2019, we aimed for a truck transport from Barsa Kelmes SNR, which is much closer than Altyn Emel NP, but capture was hindered by issues with the capture corral and the treacherous terrain on the former Aral Sea seabed. Furthermore, with a transport time of 23 h non-stop driving under ideal conditions, the animals and crew were clearly coming to the limits of their endurance, with little safety margin left in case of problems with the transport vehicle or road conditions (Kaczensky et al., 2020).

## GPS Monitoring of Kulan

In the Torgai region we monitored the movement of four adult mares reintroduced from Altyn Emel NP in October 2017 and released from the pre-release enclosure in April 2018. We additionally monitored the movements of one adult mare reintroduced from Barsa Kelmes in 2019 in the pre-release enclosure, where she still is today and gave birth to a foal on 2 June 2021. We also monitored the movements of kulan in the two source populations: two kulan in Altyn Emel NP collared in 2017 (they had to be released back into the wild due to their exited behaviour when loaded into transport boxes) and of six kulan in the source population in Barsa Kelmes SNR collared in 2019 (**Table 1**; **Supplementary Table 1**; for further details see Kaczensky et al., 2018b, 2020). All collars were programmed to take 1 GPS location per hour and were equipped with pre-programmed drop-offs (CR-2A, Telonics, Mesa, AZ, USA).

After release from the pre-release enclosure, rangers attempted to locate and observe the collared kulan every two months. However, long-flight distances only made it possible to see collars whereas ear tags were largely invisible and numbers impossible to read. Once a collar became stationary, ACBK rangers checked the location for a dropped collar or a deceased kulan (for details on ground monitoring see: Kaczensky et al., 2020).

## Data Analysis

To assess how synchronised kulan movements were pre- and post-release, we calculated movement correlation, deconstructed into a drift (directional), a diffusive (social), and a summarised overall component with R package *corrMove* as described in Calabrese et al. (2018). The different models tested for were: (1) uncorrelated drift and uncorrelated diffusion (UU), (2) correlated drift and uncorrelated diffusion (CU), (3) uncorrelated drift and correlated diffusion (UC), and (4) correlated drift and correlated diffusion (CC). The algorithm further calculates the change date where movement correlation changes from one type to another.

To identify when kulan separated and whether they re-connected again, we calculated the pair-wise daily distances between all kulan pairs. To check for kulan association with the release site, we calculated the straight-line distance (net displacement—NSD) of locations to the pre-release enclosure.

To calculate range sizes, average distances travelled per day, and average range overlap among kulan, we used variograms and continuous-time movement models (ctmms) in the ctmmweb interface (Calabrese et al., 2021) of the R package *ctmm* (Calabrese et al., 2016). The ctmmweb interface allows for automated model fitting after visual inspection and calculates autocorrelated lifetime kernel density estimation (AKDE) home-range estimators and associated movement parameters with

**TABLE 1 |** Movement characteristics of kulan reintroduced to the Torgai region as compared to those in the source populations in Altyn Emel NP and Barsa Kelmes SNR (for full model results and CI see **Supplementary Table 2**).

| Kulan ID | Monitoring period | | N GPS locations | Range estimate (km$^2$) | | Mean % overlap of 95% AKDEs | Daily travel distance (km/day) | |
|---|---|---|---|---|---|---|---|---|
| | Start | End | | 100% MCP | 95% AKDE | | Cumulative | Modelled |
| **Reintroduced—Torgai region** | | | | | | | | |
| 26176 | 03.04.2018 | 20.10.2018 | 4,798 | 37,631 | 68,456 | 97 | 13.4 | 51.1 |
| 26855 | 03.04.2018 | 27.12.2018 | 6,430 | 34,551 | 48,680 | | 12.7 | 50.6 |
| 26859 | 03.04.2018 | 08.07.2020 | 19,843 | 43,507 | 112,808 | | 9.2 | 36.6 |
| 26860 | 03.04.2018 | 20.12.2019 | 14,940 | 64,350 | 136,953 | | 8.8 | 35.5 |
| **Reintroduced—enclosure** | | | | | | | | |
| 26176 | 25.10.2017 | 02.04.2018 | 3,820 | 0.54 | 0.63 | 100 | 1.2 | 7.7 |
| 26855 | 25.10.2017 | 02.04.2018 | 3,791 | 0.67 | 0.65 | | 1.3 | 8.4 |
| 26859 | 25.10.2017 | 02.04.2018 | 3,759 | 0.65 | 0.64 | | 1.2 | 8.1 |
| 26860 | 25.10.2017 | 02.04.2018 | 3,805 | 0.66 | 0.65 | | 1.3 | 8.5 |
| 32671 | 11.10.2019 | 01.12.2020 | 9,799 | 0.52 | 0.56 | | 1.5 | 18.3 |
| **Source population—Altyn Emel NP** | | | | | | | | |
| 26850 | 24.10.2017 | 30.11.2020 | 27,153 | 1,477 | 1,816 | 100 | 4.2 | 19.5 |
| 26852 | 24.10.2017 | 01.12.2020 | 27,203 | 1,562 | 2,061 | | 4.5 | 20.4 |
| **Source population—Barsa Kelmes SNR** | | | | | | | | |
| 26177 | 26.04.2019 | 25.09.2020 | 12,340 | 3,796 | 2,132 | 69 | 6.2 | 25.4 |
| 26851 | 03.10.2019 | 01.12.2020 | 10,193 | 3,061 | 2,218 | | 6.3 | 26.3 |
| 26854 | 28.09.2019 | 01.12.2020 | 10,292 | 4,902 | 4,881 | | 6.9 | 26.9 |
| 26857 | 03.10.2019 | 01.12.2020 | 10,196 | 1,525 | 1,462 | | 7.3 | 31.1 |
| 26861 | 25.04.2019 | 01.12.2020 | 14,044 | 5,574 | 4,122 | | 6.5 | 25.3 |
| 26863 | 25.04.2019 | 01.12.2020 | 14,046 | 4,092 | 5,543 | | 5.9 | 27.0 |

confidence intervals. For visualisation of movements, we used the R package *MoveVis* (Schwalb-Willmann et al., 2020).

To allow for comparison with conventional home-range estimates, we also calculated the minimum convex polygon around all GPS locations (100% MCPs) and also used this approach to visualise how much new area was incorporated into each kulan's range as consecutive weeks of GPS locations were included in the calculation.

# RESULTS

## Group Cohesion, Movement Coordination, and Fate of Kulan

Behavioural observations over the winter 2017/18 documented that the nine kulan in the pre-release enclosure formed a cohesive group (**Figure 2**; Gliga et al., 2020) which resulted in a very high level of movement correlation [97% correlated diffusion (UC) indicative of social correlation]. After release in early April, the group initially stayed tightly together (100% correlated diffusion UC) but started to split up in mid-May (mare 26860 on 21.05.2018, mare 26859 on 02.06.2018, and mare 26855 on 19.08.2018), which resulted in a drop of the UC to only 15%; the drift correlation remained 0% suggesting that there was no tendency for the kulan to move in the same direction. After the spilt-up, kulan rarely came within ≤10 km of each other again (**Figure 3**). Movement coordination among kulan in the source populations was similar in Barsa Kelmes SNR (UC = 13% with a change point on 20.05.2020) but was constantly higher among the two kulan in Altyn Emel NP (UC = 31%; see **Supplementary Figure 1**).

Ground monitoring of reintroduced kulan showed that after the split-up, mare 26860 and 26855 were travelling alone, mare 26859 with the subadult stallion, and mare 26176 with two yearlings (**Figure 4**). We did not document the presence of a new foal for any of the reintroduced mares during the monitoring period. Monitoring of the four collared mares successively ended with the pre-programmed drop of the collar of mare 26176 on 20.10.2018, and the subsequent deaths of mare 26855 on 27.12.2018 (poached), mare 26860 on 20.12.2019 (poached), and mare 26859 on 08.07.2020 (natural mortality). On 27.05.2021, the (formally subadult) stallion with ear tag #12 who had been seen travelling with mare 26859 in 2020 appeared outside the pre-release enclosure.

## Movement Relative to the Pre-release Enclosure

The first 7 days after release in April 2018, the group stayed within 20 km of the pre-release area, but then went on two exploration trips (10 April—5 May 2018) towards the desert ca. 140 km to the south-east of the pre-release area, both times returning to the vicinity of the pre-release enclosure. After the return from the second trip, the group immediately went to the desert-steppe and steppe north and east where they stayed until mare 26859 split off. After splitting up, kulan continued to

**FIGURE 2 |** Strong group cohesion and high movement correlation characterised the movement of kulan in the adaptation enclosure. Image taken by mare 26176's camera collar.

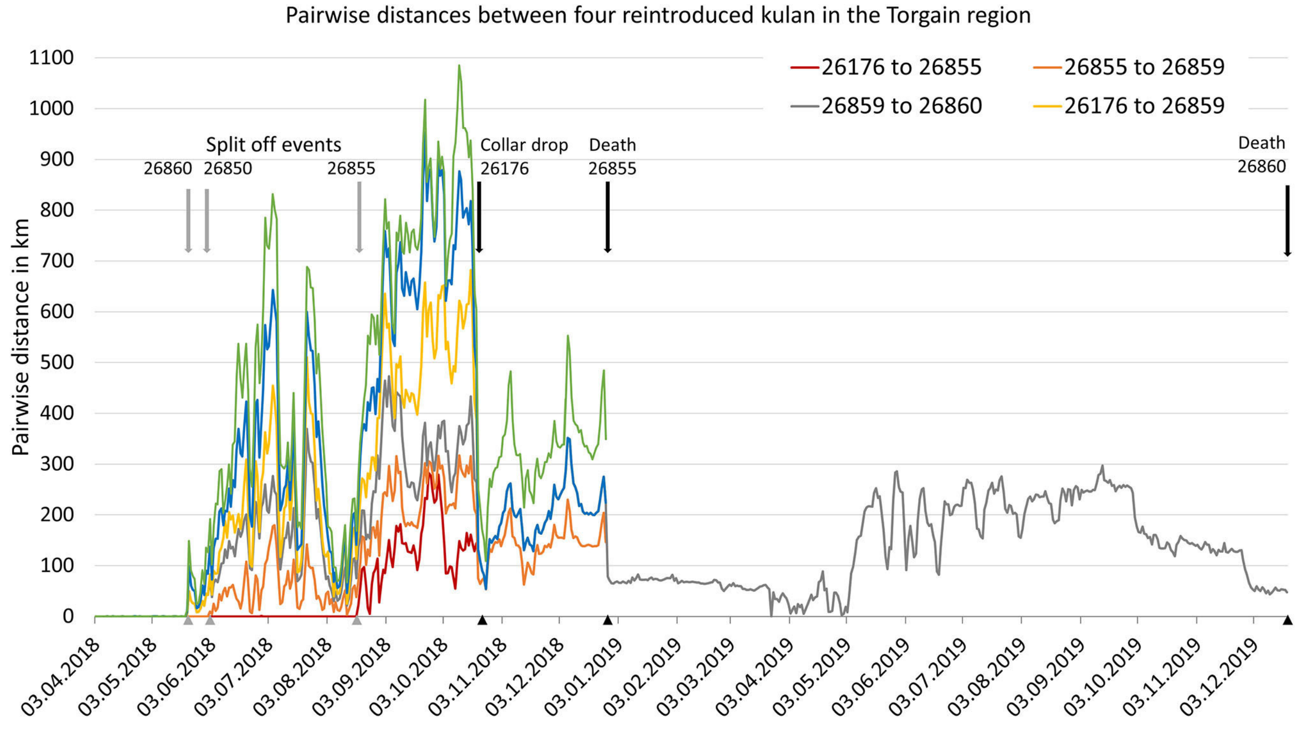

**FIGURE 3 |** Pairwise distances between reintroduced kulan in the Torgai region after release from the pre-release enclosure on 03.04.2017.

**FIGURE 4 |** Image from mare 26176's camera collar showing two yearlings feeding in the Torgai region after release and after split-up from the other three GPS collared mares.

range far separately, but also kept returning to the vicinity of the pre-release area (**Figure 5**).

## Movement Characteristics and Range Sizes

The ctmms supported a range-resident movement model for all kulan (both reintroduced and in the source populations). The best fitting model for all kulan was the general OUF model indicative of a home-range, and autocorrelated positions and velocities indicated an anisotrophic (non-circular) home range shape (**Supplementary Table 2**). The variograms for the ctmms showed an initial steep increase but reached a plateau within 1–4 months (**Supplementary Figure 2**).

Modelled daily distances travelled were 36–51 km for reintroduced kulan, which is about 2–3 times larger than for kulan in the source populations (**Table 1**). The 95% AKDEs of reintroduced kulan were huge covering 48,680–136,953 km$^2$, which is 10–100 times larger than those of kulan in the source populations (**Table 1** and **Figure 6**; **Supplementary Table 2**). The total area covered by the combined 95% AKDEs of the four kulan in the Torgai region was 152,875 km$^2$ (**Supplementary Figure 4**).

The 100% MCP covered over time by the reintroduced kulan showed a steep increase at the onset, a short temporary plateau after 15 weeks, followed by further increases. The two kulan monitored the longest reached a plateau in the summer of the second year, while the two kulan monitored over <1 year did not reach a plateau while being monitored (**Figure 7**).

Reintroduced kulan in the Torgai region did not spend the winter in the same general location and there was no evidence for a southward migration in winter. Only mare 26855 spent her first winter ca. 100 km to the south of the pre-release enclosure into the desert but was then killed by poachers. Mares 26859 and 26860 spent both winters in adjacent, non-overlapping areas ca. 100 km to the north and north-east of the pre-release enclosure in the steppe, and mare 26176 was also in this general area when her collar dropped in October 2018 (**Supplementary Figure 3**).

## Landscape Features Guiding or Restricting Movements

The ranges of reintroduced kulan overlapped almost entirely, and movements of individual kulan extended up to ca. 300 km away from the pre-release area to the southeast, ca. 200 km to the east and west, and ca. 60 km to the north (**Table 1**, **Figure 6**). In the east, mare 27176 crossed a railway twice (back and forth within 24 h), and a nearby connective road four times. In the south, mare 26860 crossed the new Zhezkazgan-Saksaulskiy railway 8 times and a nearby connecting road 11 times, but mare 26855 appeared to have "bounced off" the same railway track at two locations further to the west (**Figure 6**). All kulan crossed the Uly-Zhylanshyk river to the north of the pre-release enclosure, but none crossed the larger Torgai river further north and consequently no kulan came close to the connecting road between Torgai and Arkalyk (**Figure 6**; for 1-years animation of movements see Torgai region).

In Altyn Emel NP, the two collared kulan only used the western part of the NP and did not cross the central valley with its string of villages and irrigated agricultural land. Kulan also hardly ever went beyond the western boundary of the PA and stayed away from the steeper and higher reaches of the Sholak mountains. In the south the large Ily river and the Kapchagai

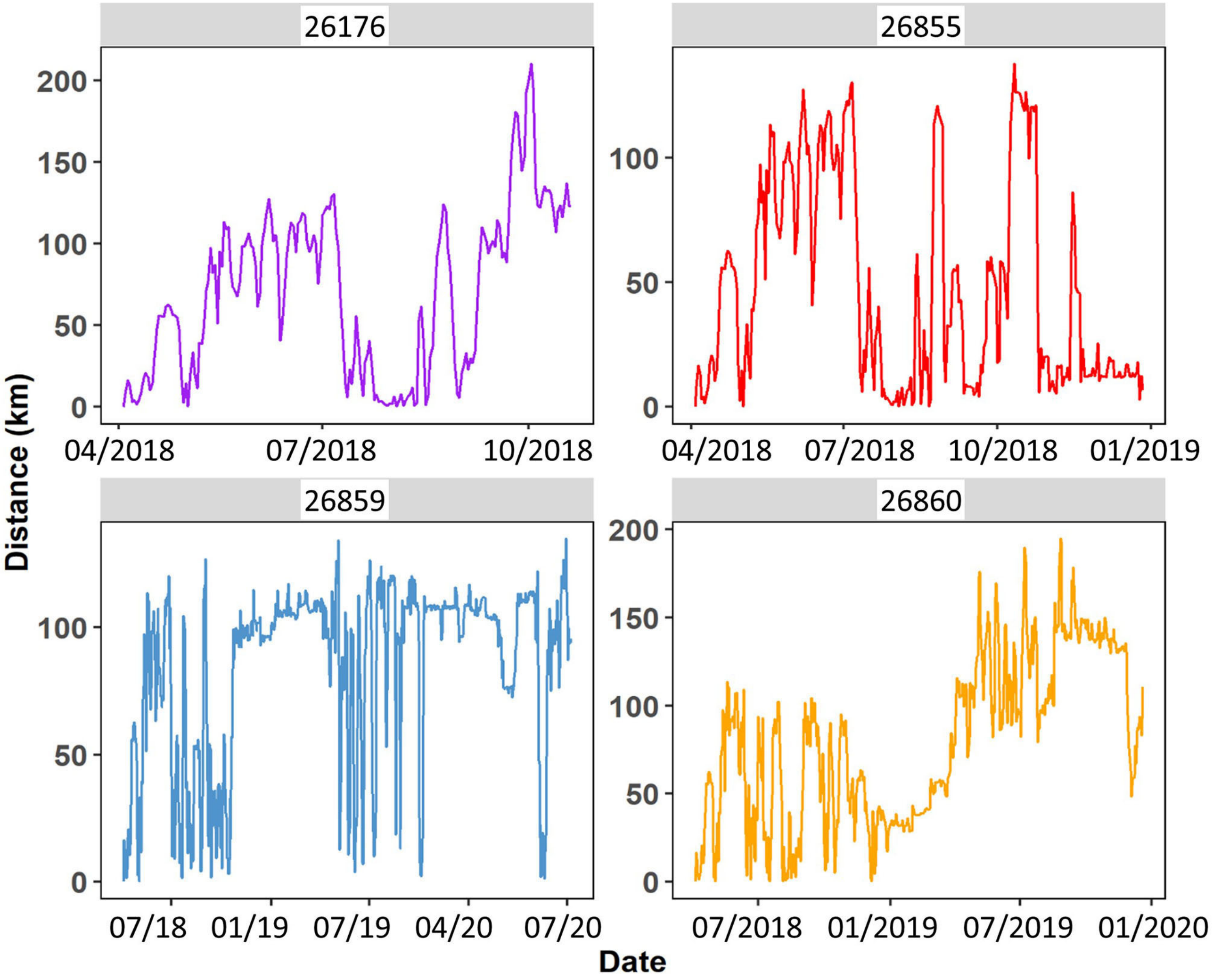

**FIGURE 5 |** Distance to pre-release enclosure by four reintroduced kulan in the Torgai region April 2018 until July 2020.

reservoir were never crossed (**Supplementary Figure 5**; for a 1-years animation of movements see Altyn Emel)

In Barsa Kelmes SNP, kulan never ventured onto the most recently exposed part of the former seabed and none of the collared kulan travelled to Barsa Kelmes island. Kulan also did not venture far beyond the eastern SNR boundary into irrigated land or land used for livestock grazing (**Supplementary Figure 6**; for a 1-years animation of movements see Barsa Kelmes).

# DISCUSSION

## Movement Coordination

The reintroduced kulan behaved like a group of horses in the pre-release enclosure, forming a tightly knit and extremely coordinated group with animals staying together virtually the entire time and with little signs of aggression (Gliga et al., 2020). After release the kulan initially stayed together and were highly synchronised in their movements, but the group broke up starting in mid-May. This point-in-time coincided with the normal birthing and mating period of kulan in the Altyn Emel source population, and the two mares which split off first had faecal oestrogen and progesterone levels which suggested that they were pregnant (Kaczensky et al., 2020). It is therefore quite possible that they left the group or stayed behind to give birth (Estep et al., 1995; Kaczensky et al., 2019).

The remaining two mares stayed together with three yearlings for another 2 months, but then also separated. We can only speculate what triggered the separation, but it could well have been the lack of a mating partner for the adult mares. Although kulan don't form stable groups, females are mostly encountered in groups and seem to profit from the combined vigilance of multiple members in the group to avoid predators (Wang et al., 2016; Buuveibaatar et al., 2017). Being alone, and especially being alone in an unknown area, is risky and this may explain why we did not observe any foals of the year in the two pregnant mares (they most likely were lost to predation) in 2017, while

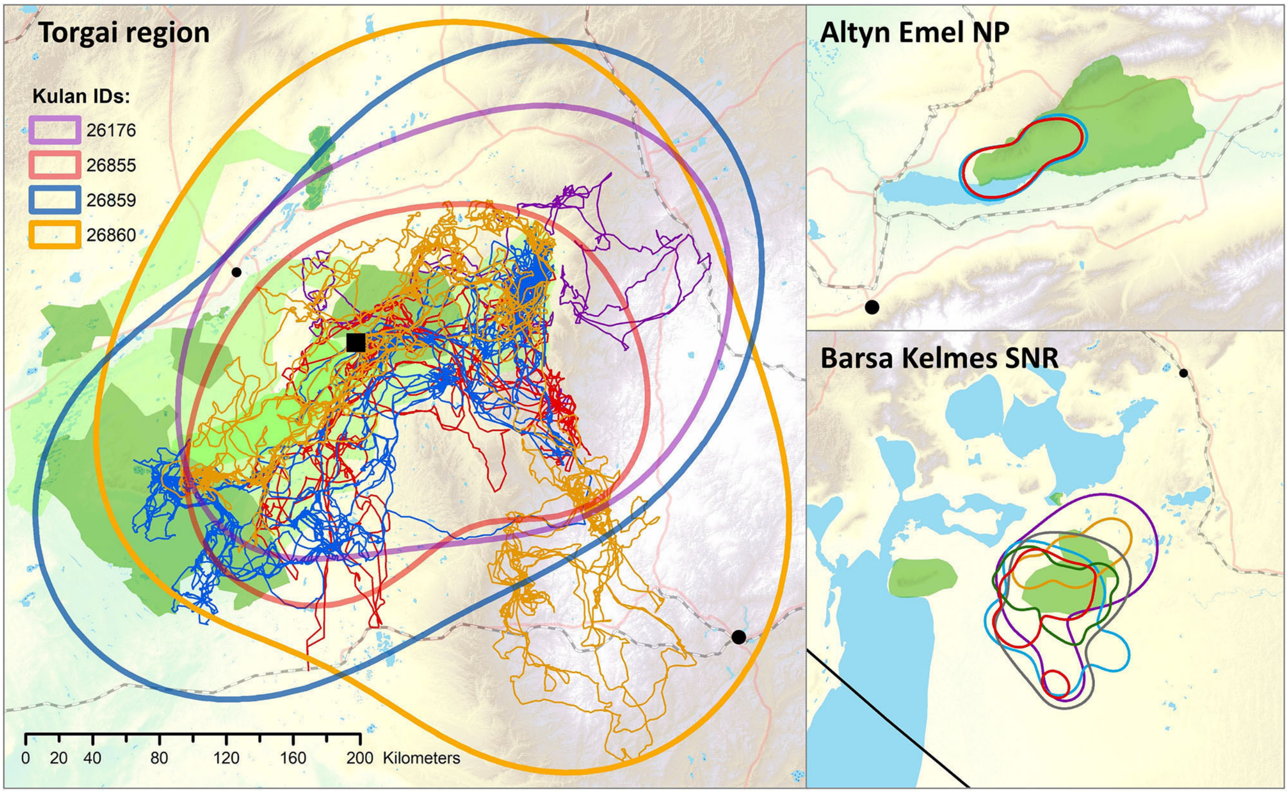

**FIGURE 6 |** Movement paths and 95% Autocorrelated Kernel Density Estimates (AKDE) of reintroduced kulan in the Torgai region (April 2018 to July 2020). The smaller panels show the 95% ADKEs of kulan in the source populations in Altyn Emel National Park (NP; October 2017–01.12.2020) and Barsa Kelmes State Nature Reserve (SNR; April 2019–01.12.2020). All maps are on the same scale and share the scalebar for the Torgai region. For an overview of the study areas and the legend of landscape features see **Figure 1**. The black line at the south-western corner in Barsa Kelmes is the international border between Kazakhstan and Uzbekistan.

the lack of a mating partner during the mating season which immediately follows the birthing season did not allow for a foal the following year. However, with only the adult mares equipped with radio collars, our ability to follow up on the fate of unmarked individuals was very limited.

Given their fission-fusion society, kulan likely do not hesitate to leave a social group, especially if they originate from a large population where overall cohesion may be lower than in smaller populations (Rubenstein et al., 2007). In Altyn Emel, ca. 3000 kulan roam over a relatively small area where water and pasture are limited and which they have known all their lives, making it easy to find conspecifics. The reintroduced kulan in the Torgai region lacked all these advantages and once separated most likely did not find each other again, pointing towards the importance of social learning in the context of reintroduction projects (Brakes et al., 2021). That kulan were seeking company became apparent from an observation of mare 26860 grazing together with a group of domestic horses in February 2019 (Kaczensky et al., 2020).

## Exploratory Movements and Soft Release

The soft release approach may not have dampened post-release exploratory behaviour, but at least kulan did stay in the vicinity of the pre-release enclosure during the first week post-release and made the first exploratory movements as a group. NHPI predicts that dispersing or translocated (basically "assisted dispersal") animals are more likely to settle in areas which are similar to their natal habitat. Translocated into novel habitats, they may embark on long-distance movements in search for familiar cues or to avoid unknown cues (Stamps and Swaisgood, 2007). We can only speculate about the motivation for the initial long-distance excursions, but we doubt they were forage, water, or predator induced. The kulan had thrived on the pasture in the pre-release enclosure and hardly touched the hay, water was abundant in the release area, and wolves were a known predator also present in Altyn Emel NP. However, what was missing were any cues of other kulan, which are plentiful in Altyn Emel NP. With the foaling and subsequent mating season coming up in a couple weeks in June, kulan may have explored the area for the presence of other kulan.

Despite showing long-distance movements, kulan seemed to have bonded with the area as all animals kept coming back to the pre-release area and their home ranges were centred around the pre-release enclosure. Unfortunately, kulan did not return at the same time to allow them to re-connect. The small number of kulan, heightened by the loss of two adult mares to poaching early in the reintroduction certainly did not help and may have resulted in too few or too faint cues for kulan to find each other. However, if kulan capture in 2018 had been successful, the presence of new kulan in the enclosure might have acted as an attraction for free ranging kulan, thus increasing the

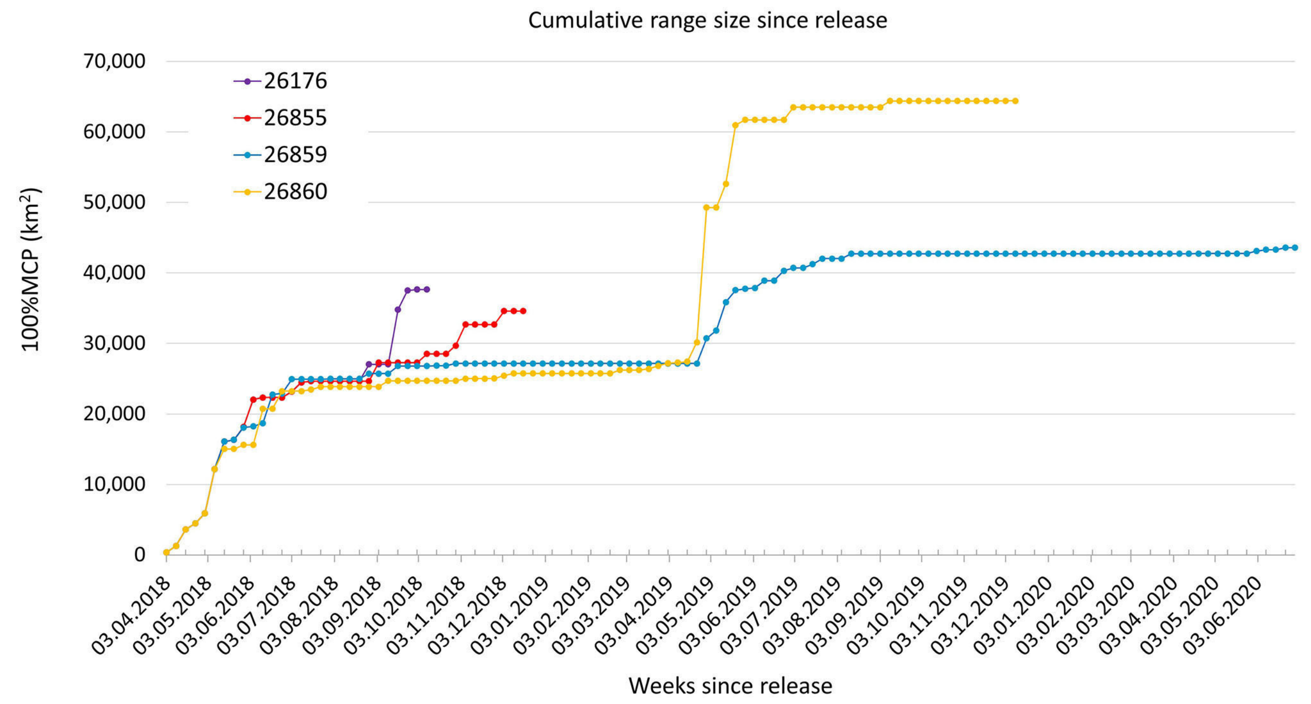

**FIGURE 7 |** Range size development of reintroduced kulan in the Torgai region since release. MCP100% were re-calculated at weekly intervals.

chance that free ranging kulan stay around and re-connect. In the Przewalski's horse reintroduction project in the Mongolian Gobi, the pre-release enclosure has continuously attracting free-ranging Przewalski's horses (mainly bachelor males), some of which even jumped the fence to join a captive group (P. Kaczensky unpubl. data).

And as proof of concept, in late May 2021, the stallion released as a subadult in 2018 (and recognisable by a blue ear tag with #12) suddenly showed up outside the pre-release enclosure, just days before the birth of a foal by mare 32671 on 02.06.2021. The stallion may well have been attracted by the upcoming post-partum estrous. This recent observation is very encouraging as it not only shows that kulan can survive in the Torgai region over multiple seasons, but they are able to re-connect with conspecifics and that the pre-release enclosure may act as a strong attraction point in a landscape otherwise largely devoid of cues of other kulan.

## Movement Characteristics and Range Sizes

Reintroduced kulan in the Torgai region were much more mobile than their respective peers with whom they were captured in Altyn Emel NP in 2017. Thus, the more productive pasture and the abundance of water did not result in lower mobility. Although initial exploratory movements were to be expected, the two reintroduced kulan which we monitored over two winters showed little indication of restricting their movements, but rather kept exploring some new areas to the south-east (mare 26860) and south-west (mare 26859). The range sizes of the reintroduced kulan in the Torgai region are in the same order of magnitude of those of kulan from Mongolia's South Gobi Region (Kaczensky et al., 2011b; Payne et al., 2020), but contrary to kulan in the Gobi, which seem to be primarily nomadic (Noonan et al., 2020), the ctmm analysis indicated a clear home-range for the reintroduced kulan.

Kulan 26860 and 26859 both returned to the same area in the second winter which further suggests the animals had settled, but also points towards a possible re-emergence of migratory behaviour as documented for a zebra population in Botswana (Bartlam-Brooks et al., 2011). However, contrary to our expectation and reports from the past (Bannikov, 1981) these two kulan spent the winter in the steppe and roamed both north and south during the reminder of the year. However, re-establishment of the most adaptive movement behaviour may take time (Jesmer et al., 2018). At least exploratory behaviour had brought all kulan in contact with the full gradient of the Torgai region from desert habitats in the south to steppe habitat in the north and this knowledge may eventually enable surviving kulan to fine-tune their movements to avoid deep snow and access the seasonally most nutritional pastures. Given our very small sample and short monitoring period relative to the potential lifespan of a kulan, which is well over 20 years (Lkhagvasuren et al., 2017), these preliminary results should not be over-interpreted.

## Landscape Features

The huge differences in daily movements and range size between the reintroduced kulan and those in the source populations in Altyn Emel NP and Barsa Kelmes SNR are puzzling. Pasture and water are more abundant in the steppe, so the question emerges as to why we see these large-scale movements of reintroduced kulan in the Torgai region. Alternatively, the question can be framed as to why we see these small-scale movements in the semi-desert of Altyn Emel NP and Barsa Kelmes SNR when kulan in the Mongolian Gobi also have huge ranges in a similar semi-desert habitat?

The movement of kulan in the Torgai region suggested that smaller rivers do not act as significant barriers, but larger ones, especially those associated with a broad band of dense vegetation probably do. The reintroduced kulan moved so far that two reached the newly constructed Zhezkazgan-Saksaulskiy railway in the south and another railway in the east and also encountered some larger connective roads. These structures have a barrier effect if traffic volume is high, but as our GPS data and experience from Mongolia showed, kulan can cross them - as long as they are not fenced (Batsaikhan et al., 2014).

In Altyn Emel NP, kulan are constrained in their movements by the Sholak mountains in the north and the Ily river and Kapchagai reservoir in the south. Movement to the west is discouraged by protected area staff with the help of a ditch dug along the western boundary and by actively chasing kulan groups back into the NP if encountered near or outside the western border (M. Sydygaliev pers. comm, 2017). This is done to protect kulan from poaching outside the NP. That kulan do not move further east may have to do with the presence of humans, livestock, and irrigated land along the central valley and the general lack of water in the eastern part of the NP. However, data from more kulan will be needed to confirm this assumption.

In Barsa Kelmes, no large infrastructure, rivers or topography restrict kulan movements. However, to the west the recently exposed seabed of the Aral sea constitutes a barrier as it has a treacherous substrate, is almost devoid of vegetation, and the remaining water in the basin is too saline to drink (Edelstein et al., 2012). Other than the Island of Barsa Kelmes, which has no drinking water, there is no suitable habitat to the west. We do not know why kulan do not expand further north, east, and south, but this may well have to do with the lack of protection. Anywhere outside the SNP where there is water and pasture there are small villages or livestock farms. Poaching also seems to be a problem and anti-poaching control is one of the main tasks of the SNR rangers (G. Satekeyev pers. comm. 2017).

It appears that in both Altyn Emel and Barsa Kelmes a combination of natural and anthropogenic factors restrict kulan movement. In contrast, in the Torgai region there are few features other than large rivers and salt lakes that restrict movement and human and livestock presence is minimal, which was one of the main reasons for selecting this area as a reintroduction site. We therefore speculate that kulan will naturally exhibit very high mobility in a landscape like the Torgai steppe when freed from anthropogenic constraints (Tucker et al., 2018). However, the downside is that there are few features which guide movements. This makes finding a highly mobile species like a kulan similar to the proverbial quest for a needle in the haystack. Even with GPS collars, rangers had a hard time to find the animals due to the kulan's high mobility, the time delay in the transmission of GPS fixes, and the lack of cell phone coverage. This difficulty to regularly check on released animals, makes them vulnerable to poaching as confirmed by the killing of two of our four GPS tagged kulan.

## Conclusions for Future Reintroductions

We believe that the main reason for the poor success of the three-year pilot phase of the kulan reintroduction to the Torgai region was the small number of kulan released, which was well below the minimum of 30 animals of past successful wild ass reintroductions (Kaczensky et al., 2016). We speculate that the fission-fusion dynamics and low movement correlation of kulan societies harbours the risk that animals released into a novel environment lose contact with each other. We believe, that this risk is particularly high if only a small number of animals is released and that it is further enhanced in steppe habitats where topographic features constraining movements are largely absent and where forage and water are more abundant and widely available than in desert-steppe or desert habitats.

Future kulan reintroductions into the Torgai region of central Kazakhstan should aim to release larger groups of kulan as originally planned. Some losses and initially lower reproductive success must be expected (Saltz and Rubenstein, 1995; Kaczensky et al., 2016) and it is therefore crucial to build up the free-ranging population as quickly as possible to reach a critical mass to increase the chance of kulan encountering conspecifics to successfully breed and increase their chance of survival.

We see the large ranges and high mobility of the reintroduced kulan as a sign of success as kulan along the steppe desert gradient should not be expected to stay only in the steppe or only in the desert habitat, but rather migrate between those two on a seasonal basis. Large ranges and high mobility are the best adaptation to highly variable climatic conditions or extreme events and can lower the risk of mass mortality due to droughts or extreme winters ("dzud") as has been shown for kulan in Mongolia (Kaczensky et al., 2011b).

The use of a pre-release enclosure seems to result in animals settling in the wider area and having kulan in the enclosure has shown to act as an attraction point for free-ranging animals, making it easier for them to re-connect with other free-ranging conspecifics. Future releases should aim to keep kulan in the pre-enclosure until after foals are born and mating has happened in the hope that this will lower the mortality risk for foals and increase the chances of new foals in the following year. However, such an approach needs to be carefully monitored (Gliga et al., 2020) as kulan held in captivity can show highly aggressive behaviour to conspecifics and infanticide is a known phenomenon in equids (Cameron et al., 2003) both of which could easily result in losses and welfare issues in the enclosure if animals are not released before things escalate.

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## ETHICS STATEMENT

The animal study was reviewed and approved by the Committee of Forestry and Wildlife of the Ministry of Ecology, Geology, and Natural Resources of Kazakhstan (permit 17-2-18/1613 dated 17.10.2017 and permit KZ28VDY00000016 dated 29.08.2019) and by the transfer agreements with Kostanay oblast (permit 17-2-18/1613 dated from 17.10.2017 and unnumbered permit dated from 07.08.2019) with Altyn Emel NP and Barsa Kelmes SNR, in 2017 and 2019, respectively and the Altyn Dala SNR. Captures, animal handling, and transport were performed in accordance with relevant guidelines and regulations. The ethic commission at the University of Veterinary Medicine Vienna was informed and provided general consent. The IUCN Equid and Reintroduction Specialist reviewed the feasibility study and provided letters of support for the reintroduction project.

## AUTHOR CONTRIBUTIONS

PK designed and supervised the work, wrote the first draft of the manuscript, and did most of the data analysis and visualisation. AS and SZ planned and organised field work in Kazakhstan and CW, TP, and NH oversaw the veterinary aspects. All authors were involved in field work and all reviewed and revised the manuscript.

## FUNDING

Main funding came from the Fondation Segré, Nürnberg Zoo, Taipei Zoo, and Association of the Friends of Nürnberg Zoo. Additional small funds came from Wroclaw Zoo and La Passerelle Conservation. Salaries for PK and JL were largely covered by the Research Council of Norway grant 251112 and those of the international veterinarians by their respective employers: LaPalmyr Zoo, University of Veterinary Medicine Vienna, Wildlife Conservation Society, Zoo Budapest, and Frankfurt Zoological garden.

## ACKNOWLEDGMENTS

Many people have committed much time and effort to driving this project forward over the last 2 years. We are particularly grateful for ACBK staff Baurzhan Iskakov, Sayat Mukhtarov, Alexandr Putillin, Roman Alexandrovich, and Renat Eskazyuly for help with all aspects of field work and to the caretakers Kishkentay Ordabayev, Kairzhan Zhusupbekov, Gani Sadvakasov, Aidar Erzhanov at Alibi for looking after the reintroduced kulan. Vitaly Levanov and rangers and personnel from the Committee of Forestry and Wildlife, Okhotzooprom, Altyn Emel NP, Barsa Kelmes SNR, Altyn Dala SNR, and the ACBK hunting reserves were instrumental for capture and monitoring. Directors Kalyk Bayadilov and Zauresh Alimbetova made work possible in Altyn Emel NP and Barsa Kelmes SNR, respectively. Endre Sos and Christina Geiger oversaw the kulan transport in 2019, Vera Voronova, Sergey Sklyarenko, Fariza Fariza Adilbekova, Dag Enke, Stephanie Ward, Michael Brombacher, and Mark Day helped steer the project, and Stephanie Kramer-Schadt provided some valuable late night R advice.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2021.703358/full#supplementary-material

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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ORIGINAL RESEARCH
published: 28 September 2021
doi: 10.3389/fcosc.2021.720202

# Movement of Rehabilitated African Elephant Calves Following Soft Release Into a Wildlife Sanctuary

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**Specialty section:**
This article was submitted to
Animal Conservation,
a section of the journal
Frontiers in Conservation Science

**Received:** 03 June 2021
**Accepted:** 23 August 2021
**Published:** 28 September 2021

**Citation:**
Goldenberg SZ, Hahn N,
Stacy-Dawes J, Chege SM,
Daballen D, Douglas-Hamilton I,
Lendira RR, Lengees MJ, Loidialo LS,
Omengo F, Pope F, Thouless C,
Wittemyer G and Owen MA (2021)
Movement of Rehabilitated African
Elephant Calves Following Soft
Release Into a Wildlife Sanctuary.
Front. Conserv. Sci. 2:720202.
doi: 10.3389/fcosc.2021.720202

The ability to locate essential resources is a critical step for wildlife translocated into novel environments. Understanding this process of exploration is highly desirable for management that seeks to resettle wildlife, particularly as translocation projects tend to be expensive and have a high potential for failure. African savannah elephants (*Loxodonta africana*) are very mobile and rely on large areas especially in arid environments, and are translocated for differing management and conservation objectives. Thus, research into how translocated elephants use the landscape when released may both guide elephant managers and be useful for translocations of other species that adjust their movement to social and ecological conditions. In this study, we investigated the movement of eight GPS tracked calves (translocated in three cohorts) following their soft release into a 107 km$^2$ fenced wildlife sanctuary in northern Kenya and compared their movement with that of five tracked wild elephants in the sanctuary. We describe their exploration of the sanctuary, discovery of water points, and activity budgets during the first seven, 14, and 20 months after release. We explored how patterns are affected by time since release, ecological conditions, and social factors. We found that calves visited new areas of the sanctuary and water points during greener periods and earlier post-release. Social context was associated with exploration, with later release and association with wild elephants predictive of visits to new areas. Wild elephants tended to use a greater number of sites per 14-day period than the released calves. Activity budgets determined from hidden Markov models (including the states directed walk, encamped, and meandering) suggested that released calves differed from wild elephants. The first two cohorts of calves spent a significantly greater proportion of time in the directed walk state and a significantly lower proportion of time in the encamped state relative to the wild elephants. Our results represent a step forward in describing the movements of elephant orphan calves released to the wild following a period of profound social disruption when they lost their natal family and were rehabilitated with other orphan calves under human care. We discuss the implications of the elephant behavior we observed for improving release procedures and for defining success benchmarks for translocation projects.

**Keywords: activity budgets, conservation behavior, conservation translocation, *Loxodonta africana*, rehabilitation and release, rewilding, social network**

## INTRODUCTION

Translocated wild animals face challenges once they are released: they must explore their new environment; learn where to find food, water, and refuge; how to find or avoid conspecifics; how to avoid or evade threats like predators (including humans); and how resources and threats may change seasonally. As they gain more knowledge about resources in the landscape and become more comfortable with their surroundings, they may adjust their movement patterns (Berger-Tal and Avgar, 2012; Berger-Tal and Saltz, 2014). Research in translocated populations has provided support for this idea. In reintroduced scimitar-horned oryx (*Oryx dammah*) in Chad, dispersal and home range establishment were correlated with time at the release site, though they were strongly influenced by past experience and seasonality (Mertes, 2019). Similarly, reintroduced ʻAlalā crows (*Corvus hawaiiensis*) in Hawaii dispersed more from supplemental feeders as the post-release period progressed (Smetzer et al., 2021). Tracking the movement of released animals as they explore can provide insights into the time it takes to discover and use vital resources and the factors that influence this resource use. This in turn may be used to guide decisions like where, when, and in what groupings to release cohorts, as well as whether and for how long to provide supplemental resources to released populations.

Exploration of release environments and how to use resources may be facilitated by social interactions, as released individuals learn from conspecifics which areas and resources to use or avoid (Owen et al., 2017). This pattern has been found across a range of taxa. For example, pine martens (*Martes martes*; a solitary mustelid) released into habitat without conspecifics took longer to settle and dispersed shorter distances than a subsequent cohort released into the same area (McNicol et al., 2020); familiarity within translocation cohorts decreased dispersal distances in the solitary and territorial Stephens' kangaroo rat (*Dipodomys stephensi*) (Shier and Swaisgood, 2012); higher pup ratios in the local population increased post-release dispersal distances in territorial and aggregating southern sea otters (*Enhydra lutris nereis*) (Becker et al., 2020); and after translocation, the Alpine ibex (*Capra ibex*) preferentially selected sites already used by residents (Scillitani et al., 2013). Thus, regardless of the social structure of a target species, investigation into an animal's exploration of a release site should account for the social context that may structure their decisions. Managers may have control over release cohort composition or release site, and an understanding of how social context influences release site exploration may be leveraged to hasten the process of exploration that may ultimately be tied to survival.

The African savannah elephant (*Loxodonta africana*) is an endangered species that is translocated for different management aims across its range, including reinforcing populations in protected areas (Slotow et al., 2005), conflict mitigation (Pinter-Wollman, 2009), and release of rescued and rehabilitated individuals (McKnight, 1995; Evans et al., 2013). Where post-release monitoring has occurred, success of translocations has been mixed, with some individuals failing to settle at release sites (Pinter-Wollman, 2009; Tiller et al., in preparation[1]). A better understanding of the exploratory behavior of translocated elephants is relevant to managers planning and implementing translocations, as it could be leveraged in decisions aimed at facilitating settlement at release sites and minimizing vulnerability that may be associated with lack of familiarity with the landscape (Pinter-Wollman et al., 2009). Exploration had a high coefficient of variation (62%) among translocated savannah elephants to the Tsavo ecosystem in Kenya (Pinter-Wollman, 2009), suggesting strong differences among individuals in exploration tendencies. Identifying predictors of exploratory behaviors that are consistent across individuals may be useful, as may identifying individuals with disproportionate impacts on group behavior. Savannah elephants are highly mobile, dependent on widespread resources, and maintain complex movement strategies that are seasonally variable and individualistic (Wall et al., 2013; Bastille-Rousseau et al., 2020). In the semi-arid regions that many savannah elephant populations inhabit, space use is strongly influenced by the use of water points (Loarie et al., 2009; Polansky et al., 2015; Bastille-Rousseau et al., 2020); knowledge of permanent water sites is particularly important for translocated elephants during the dry season (Tiller et al., in preparation)[1]. Understanding the influence of ecological conditions on translocated elephant exploration may serve to hone protocols, like timing releases with ecological conditions to maximize early exploration, ensuring that release cohorts include individuals likely to be exploratory, or setting rainfall thresholds below which translocated elephants would be supplemented with water or food if elephants have not adequately explored the resources available to them.

In addition to ecological predictors of exploration, social context is known to influence elephant space use and likely influences exploratory behavior. How elephants move around the landscape is influenced by dominance-based spatial partitioning (Wittemyer et al., 2007) and by leveraging the ecological knowledge of family members and other social associates

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[1] Tiller, L. N., King, L. E., Ouma-Okita, B., Lala, F., Pope, F., Douglas-Hamilton, I., et al. (in preparation). The behaviour and fate of translocated bull African elephants (*Loxodonta africana*) into a novel environment.

(Foley et al., 2008). The Tsavo study of translocated elephants (Pinter-Wollman et al., 2009) found strong associations among translocated elephants and decreased segregation between translocated and resident elephants over time, which may ultimately facilitate landscape exploration as naive individuals may benefit from knowledgeable individuals. Elephants are also known to make exploratory forays with changing ecological or social conditions (Thouless, 1995; Goldenberg et al., 2018). Therefore, in order to understand exploration and establishment of translocated elephants, it is critical to understand how changing ecological and social conditions at release sites influence this process, particularly related to a translocated elephant's familiarity with other individuals at the site.

Parsing the influence of social context and seasonality on the exploratory behavior of translocated elephants may provide further insight into the range and predictability of the movement patterns that elephants exhibit post-release.

In the present study, we explore the movement tracks of eight elephant calves that were rehabilitated at an elephant orphanage and subsequently released into a fenced site in northern Kenya prior to their planned hard release onto the larger, unfenced landscape. We describe their range expansion within the fenced soft release site, first visits to water points, and activity budgets, while accounting for the influence of social, ecological, and individual factors. We relate these patterns to those of tracked wild elephants at the same site to determine whether orphan space use converged with that of wild elephants. Because elephants in semi-arid environments are known to expand their range during the wet season when they are not as constrained by limited resources (Wittemyer et al., 2007; Loarie et al., 2009), we expected visits to new sites and exploratory movements to be associated with improving ecological conditions. We expected social familiarity to facilitate spatial exploration such that calves released later and those with greater interaction with wild elephants would use more areas. Finally, we expected the activity budgets of released calves to become more similar to those of the wild elephants as time progressed, reflecting less time spent in exploratory behavior over time. We discuss our results in the context of establishing management benchmarks to guide translocation projects that progress through the stages of rehabilitation, soft release, and hard release.

# METHODS

## Study Animals and Site

The elephant calves in this study were rescued in northern Kenya following reports of distress, orphaning or abandonment. They were rehabilitated at the Reteti Elephant Sanctuary (1.11°N, 37.46°E), an elephant orphanage in the Namunyak Conservancy of the Northern Rangelands Trust. Following rescue, calves were given veterinary care, quarantined, and introduced to the other orphans. At Reteti they were fed milk from a bottle every three h, allowed to forage freely during the day, and penned at night. Between the ages of 3 and 4 years old, calves were weaned from being bottle fed and separated from the larger orphan herd in preparation for release. Ten calves were released in three cohorts ($N_{C1} = 3$, $N_{C2} = 3$, $N_{C3} = 4$) into the neighboring Sera Rhino Sanctuary within the Sera Wildlife Conservancy (1.04–1.66°N, 37.75–37.92°E) in May 2019, November 2019, and May 2020. Eight of these calves ($N_{C1} = 3$, $N_{C2} = 2$, $N_{C3} = 3$) were fitted with GPS collars prior to release and are the focus of this study.

**TABLE 1** | Summary details of tracked elephants.

| Elephant | Cohort or wild | Sex | Tracking dates analyzed |
|---|---|---|---|
| Warges | C1 | M | May 2–Oct. 10, 2019 |
| Sosian | C1 | M | May 2, 2019–Jan. 4, 2021 |
| Ilngwesi | C1 | M | May 2, 2019–Jan. 4, 2021 |
| Shaba | C2 | F | Nov. 16, 2019–Jan. 3, 2021 |
| Pokot | C2 | M | Nov. 16, 2019–Oct. 8, 2020 |
| Baawa | C3 | M | May 28–Oct. 28, 2020 |
| Nchurai | C3 | F | May 28, 2020–Jan. 4, 2021 |
| Nadosoit | C3 | F | May 28–Dec. 28, 2020 |
| Lpupo | wild | F | May 28, 2019–Jan. 4, 2021 |
| Kalama | wild | F | May 29, 2019–Jan. 4, 2021 |
| Chapulo | wild | M | May 29, 2019–Jan. 4, 2021 |
| Kaingus | wild | F | May 29–Sep. 12, 2019 |
| Serteta | wild | F | May 30–Sep. 12, 2019 |

*C1 was released May 2, 2019, C2 released November 16, 2019, and C3 was released May 28, 2020.*

The Sera Rhino Sanctuary is a fenced 107 km$^2$ wildlife sanctuary within the Sera Wildlife Conservancy which was established in 2015 to support a reintroduced population of black rhinoceros (*Diceros bicornis*), during which time a diversity of fauna, including elephants, were fenced in in the process of creating a secure habitat for rhino. The region is semi-arid savannah and is drought prone, receiving rain during two wet seasons: April–May and November–December. The vegetation is dominated by Commiphora and Acacia species. The terrain within Sera is relatively flat with granite outcrops. There are seven permanent, mostly artificial, and several naturally occurring and seasonally ephemeral water sources distributed throughout the sanctuary, which supports a population of wild elephants which ranged between ∼25–40 individuals over the course of the study as well as a range of native fauna. A complete ground count and photo-identification file was made of the wild elephants at the release site prior to the first release, from which 5 adult elephants from distinct social units ($N_{females} = 4$, $N_{males} = 1$) were selected and collared in May 2019 (**Table 1**). This was to compare their movements with the released calves to better understand any social integration that might happen with the wild elephants. Although collared released elephants were young calves and collared wild elephants were adults, we considered this a reasonable comparison because calves of this age in the wild are typically strongly cohesive with their natal groups and would therefore be expected to demonstrate similar movement patterns to those of adults. Two of these wild elephants, Serteta and Kaingus, were later driven out of the sanctuary with their families in September 2019 by the management of the Sera Rhino Sanctuary in order to reduce the local elephant density and prevent overbrowsing.

## Data Collection

Once slated for release, calves were fitted with Savannah Tracking satellite collars (http://www.savannahtracking.com/) at Reteti Elephant Sanctuary (collar deployments ranged from 2–10 weeks prior to translocation to the release site) (**Table 1**). Fittings were done while calves were bottle fed to minimize disturbance. Five wild elephants were selected for collaring. They were immobilized by a Kenya Wildlife Service veterinarian following standard procedures (Kenya Wildlife Service, 2018). Collars were set to collect GPS points every 30 min, with wild elephant collars switched to an hourly schedule midway through the study to extend battery life. Collars died and failed to collect subsequent GPS coordinates on different dates over the course of the study period (**Table 1**).

We collected vehicle-based observations of elephant aggregations as a part of a larger post-release monitoring program. When elephants were encountered when driving along the road network, observers recorded as many individuals as could be identified using individual characteristics like body and tusk shape and ear tears; an estimated group size; and whether the group was an orphan group, a bull group, a cow/calf group, or a group comprised of orphans and any resident elephants, whether females, calves, or bulls ("mixed"). Overflights were also used to locate the orphans and adults and their proximity to each other on occasion. Vehicle-based and aerial observations spanned May 2020–April 2021.

## Data Analysis

We filtered tracking datasets for points outside of the fenced sanctuary, points taken prior to each cohort's release date, and biologically implausible speeds >7 km/h. We divided the study into 14-day periods, assigned GPS locations to these periods, and assessed movement metrics within each period. In order to investigate calf discovery of critical resources, range expansion, and convergence with wild elephant space use, movement metrics calculated per time period included visits to permanent water points, visits to 1 km$^2$ grid cells, and time spent in discrete activity budget states. Periods were calculated relative to the first cohort's release (May 2, 2019) and ran through the end of the study period for a total of 48 periods.

We used ArcPro 2.7.3 (ESRI, Redlands, CA, USA) to create a grid consisting of 1 km$^2$ cells, which we then clipped to the extent of the fenced sanctuary. Each grid square was then assigned a number and overlaid with the points from the GPS collars.

We mapped permanent water sources using ArcPro, which were verified by field observers. We focused on permanent water sources because knowledge and use of permanent water points is critical to translocated elephants during dry periods (Tiller et al., in preparation)[1]. We then digitized the boundary of each mapped water source based on aerial imagery and drew a 150-m buffer around each polygon. The points from GPS collars that fell within the buffer were extracted and considered a visit to that water point. For water points and grid squares, we extracted both the total number used and the number of unique sites used per 14-day time period. Total numbers of water points and grid squares used per time period were compared between released calves and wild elephants using Wilcoxon rank sum tests, treating all released calves pooled in one grouping compared to the five wild elephants pooled.

To test our expectations that improving ecological conditions and social familiarity would influence released calf exploration of the sanctuary, we conducted two generalized linear mixed effects models with the number of new grid squares visited in a 14-day period and the number of new water points visited in a 14-day period as the response variables, respectively. Response variables were modeled with a negative binomial distribution. We included a random effect for calf identity. Covariates in each of these models reflected our expectations that exploration would be influenced by time, season, and social context: the number of 14-day time periods since the calf was released ("time since release"); which of the three cohorts the calf belonged to ("cohort"); the mean normalized difference vegetation index (NDVI) over the 14-day period derived from MOD13Q1 satellite imagery at 250 m resolution (https://lpdaac.usgs.gov/products/mod13q1v006/) and averaged across the fenced sanctuary as a proxy for ecological conditions, which were extracted using the MODISTools (Tuck et al., 2014) and raster (Hijmans and van Etten, 2012) packages in R v.4.0.4 (R Core Team, 2018); the proportion of vehicle-based observations during which the calf was observed with resident elephants (Range $N_{obs/calf} = 41–86$), similar to that used in another African elephant translocation study (Pinter-Wollman et al., 2009) ("co-occurrence"); and calf sex ("sex"). Models were conducted in the glmmTMB package (Magnusson et al., 2017) after standardizing non-binary predictor variables. We checked model residual diagnostics using 1,000 simulated residuals in the DHARMa package to ensure models were properly specified (Hartig, 2021).

To assess whether activity budgets changed over time and converged with wild elephants, we segmented movement tracks by behavioral classifications. For each individual movement path *k*, we used hidden Markov models (Morales et al., 2004) to estimate the latent behavioral state mode $b_{i,t,k}$ for each observation *i* at time *t* using log speed and turning angle parameters. Polansky et al. (2015) identified three distinct states in elephant movement based on these two metrics, which we adapted for our dataset: S1—"Encamped" characterized by slow speeds and high tortuosity associated with localized foraging and resting, S2—"meandering" characterized by moderate speeds and meandering directions associated with active foraging, and S3—"directed walk" characterized by high speeds and directional travel associated with dispersal behaviors. Speed and turning angle are calculated from successive GPS fixes, so that accurate estimates of the latent states requires temporally regular GPS fixes (McClintock et al., 2012). To ensure a regular fix rate, we sampled fixes at a standard hourly fix rate across all collars and set a threshold to exclude individuals with >5% missing fixes, though none of the tracking datasets met that threshold necessitating exclusion. Model fitting and evaluation was implemented using the momentuHMM package for R, which uses maximum likelihood estimation of the transition matrix (McClintock and Michelot, 2018). Proportion of time in each of the three states summed to one, as all GPS points were assigned to one of the three states.

Following model fitting, we used the Viterbi algorithm to estimate a behavioral state for each GPS location. Behavioral state estimates were used to construct state-level activity time budgets, defined as the percentage of fixtures in a behavioral state over time, for the full dataset and for each 14-day period. To compare activity between each release cohort and the wild elephants, we conducted generalized linear models with the activity budgets for each 14-day period as the response variable. A separate model was fitted for each state, using the cohort ID (including wild elephants as a distinct cohort) and 14-day period as covariates. We set the wild elephants as the cohort reference level for each model to assess differences relative to them.

## RESULTS

All release cohorts continued to discover new permanent water points and access new grid squares throughout the study period, though there were distinct differences among cohorts (**Figure 1**). By the end of the study period, only the first cohort had visited all seven water points, and the third cohort had visited the fewest. The first cohort took longer to visit more than one water site than the subsequent two cohorts, a pattern that was also apparent in the grid analysis (**Figure 2**). In contrast, the second cohort, and to a lesser extent the third cohort, visited more water sites and areas earlier after being released.

The median (IQR) number of grid squares used per 14-day period differed by cohort: C1 = 9 (8–12); C2 = 10 (9–11); C3 = 8 (6–10); wild = 11 (10–12), with release cohorts tending to use a smaller number of grid squares per time period than wild elephants (Wilcoxon rank-sum test: W = 7859, $p < 0.05$), though interquartile ranges overlapped (**Figure 3**). Similarly, release cohorts used fewer of the seven permanent water points per 14-day period relative to wild, with some overlap in interquartile ranges: C1 = 1 (1–2); C2 = 1 (1–1); C3 = 1 (1–2); wild = 2 (1–4) (Wilcoxon rank-sum test: $W = 7205.5$, $p < 0.05$).

Predictor variables in models showed wide variation, with mean NDVI per time period ranging between 0.197–0.618 and the proportion of observations during which released calves were recorded with wild elephants ranging across calves from 0.063–0.978. Examination of residual diagnostics for generalized linear models investigating the number of new grid squares or new water sites visited by calves per 14-day period indicated that models were correctly specified (grid: $p_{KS\_test} = 0.27$; $p_{dispersion\_test} = 0.82$; $p_{outlier\_test} = 1$; water: $p_{KS\_test} = 0.42$; $p_{dispersion\_test} = 0.21$; $p_{outlier\_test} = 1$). Models revealed NDVI and time since release to be strong predictors of both response variables, with calves visiting more new squares and water sites during greener periods ($\beta_{\mathrm{NDVI\_grid}} = 0.41$, 95% CI[0.31, 0.50]; $\beta_{NDVI\_water} = 0.39$, 95% CI[0.06, 0.71]) and earlier post-release ($\beta_{time\_grid} = -0.85$, 95% CI[−1.00, −0.69]; $\beta_{time\_water} = -0.54$, 95% CI[−1.01, −0.07]) (**Figure 4**). Additionally, more first visits to grid squares were associated with social facilitation, with later cohorts ($\beta_{cohort\_grid} = 0.51$, 95% CI[0.21, 0.81]) and higher proportions of observations co-occurring with wild elephants ($\beta_{co-occurrence\_grid} = 0.40$, 95% CI[0.14, 0.66]) significantly predictive of more new grid squares visited.

From the hidden Markov model, we classified behavioral states and constructed activity budgets from 123,054 GPS locations. C1 and C2 spent more overall time in directed walk movements compared to C3 and less time in encamped movements, while C3 had the most similar activity to the wild group (**Figure 5**). Directed walk movements appeared to be used for accessing water points and exploratory movements around the sanctuary, which helps explain why C1 and C2 had similar activity budgets but explored the sanctuary at different rates (**Figure 2**; **Supplementary Material Video 1**). Over time, models investigating the relationship between released and wild elephant activity across the 14-day periods indicated small trends in overlap of state-level activity (**Figures 5**, **6**). C1 and C2 spent less time in encamped movements than the wild elephants ($\beta_{C1} = -0.05$, 95% CI[−0.08, −0.03]; $\beta_{C2} = -0.05$, 95% CI[−0.08, −0.02]), and more time in directed walk ($\beta_{C1} = 0.07$, 95% CI[0.02, 0.11]; $\beta_{C2} = 0.07$, 95% CI[0.02, 0.12]). In contrast, C3 spent significantly less time in directed walk movements than the wild elephants ($\beta_{C3}$ =-0.08, 95% CI[−0.14, −0.02]), which was similarly reflected in their slower exploration of new grid squares.

## DISCUSSION

Understanding the exploration patterns of translocated wildlife following release into a novel environment may provide managers with information to define project milestones, cohort release composition and timing, and resource supplementation, among other management options. Elephants have been a particularly challenging taxon to translocate, and thus investigation into their exploration patterns in novel environments post-release may provide insight that improves conservation resource allocation (Pinter-Wollman, 2009; Fernando et al., 2012; Tiller et al., in preparation[1]). Our analysis of the movement patterns of eight elephant calves that were soft released into a large fenced wildlife sanctuary paired with the movement of five wild elephants in the site provides new insight into elephant space use following translocation. We found ecological and social conditions to be strongly predictive of released calf exploration of a novel landscape, and did not find support for convergence in activity budgets between translocated and resident elephants over the time period examined (up to 20 months post-release). Additionally, we found substantial differences among release cohorts in movement behavior.

Ecological conditions were strongly predictive of exploration of the soft release site, both for initial visits to permanent water points and area (1 $km^2$ grid squares). This is consistent with studies of wild savannah elephants indicating that home ranges expand during the wet season when proximity to permanent water is no longer limiting (Redfern et al., 2003; Young et al., 2009; Wall et al., 2021). To date, elephant translocations into Sera Wildlife Conservancy have been timed to coincide with rains and favorable ecological conditions. Our results highlight the importance of those favorable periods in facilitating landscape exploration while primary productivity is high and water is not limiting. If there is a lag in cohort exploration, as was the case for the first cohort released, discovery of new areas and water sources may not occur until subsequent wet seasons when elephants are more likely to make exploratory forays or associate in larger aggregations that may facilitate exploration of new areas. This may translate to greater concentrations of

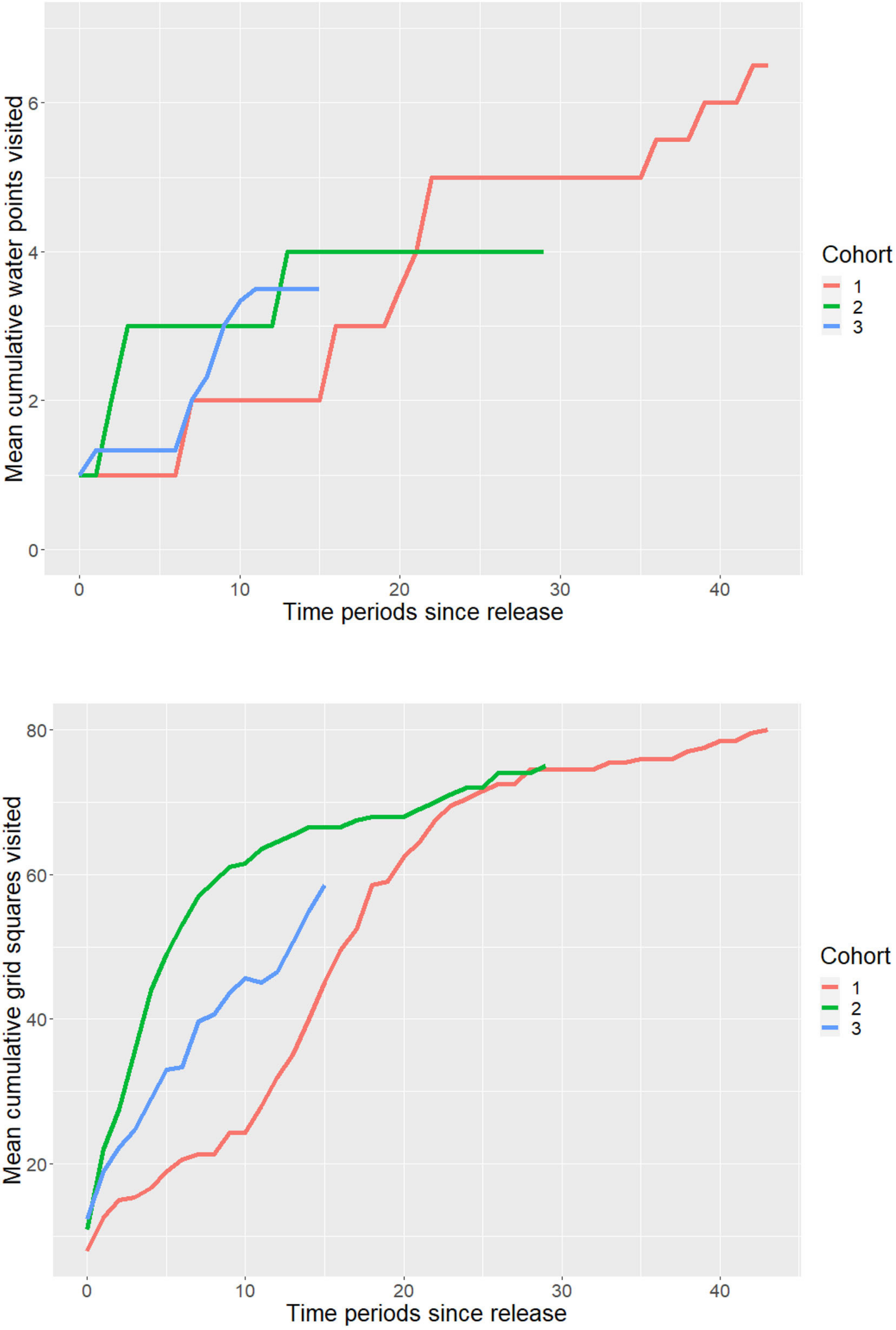

**FIGURE 1 |** Within-cohort mean number of cumulative water points (top) and grid squares (bottom) accessed by released calves. Means were calculated for each 14-day time period post-release.

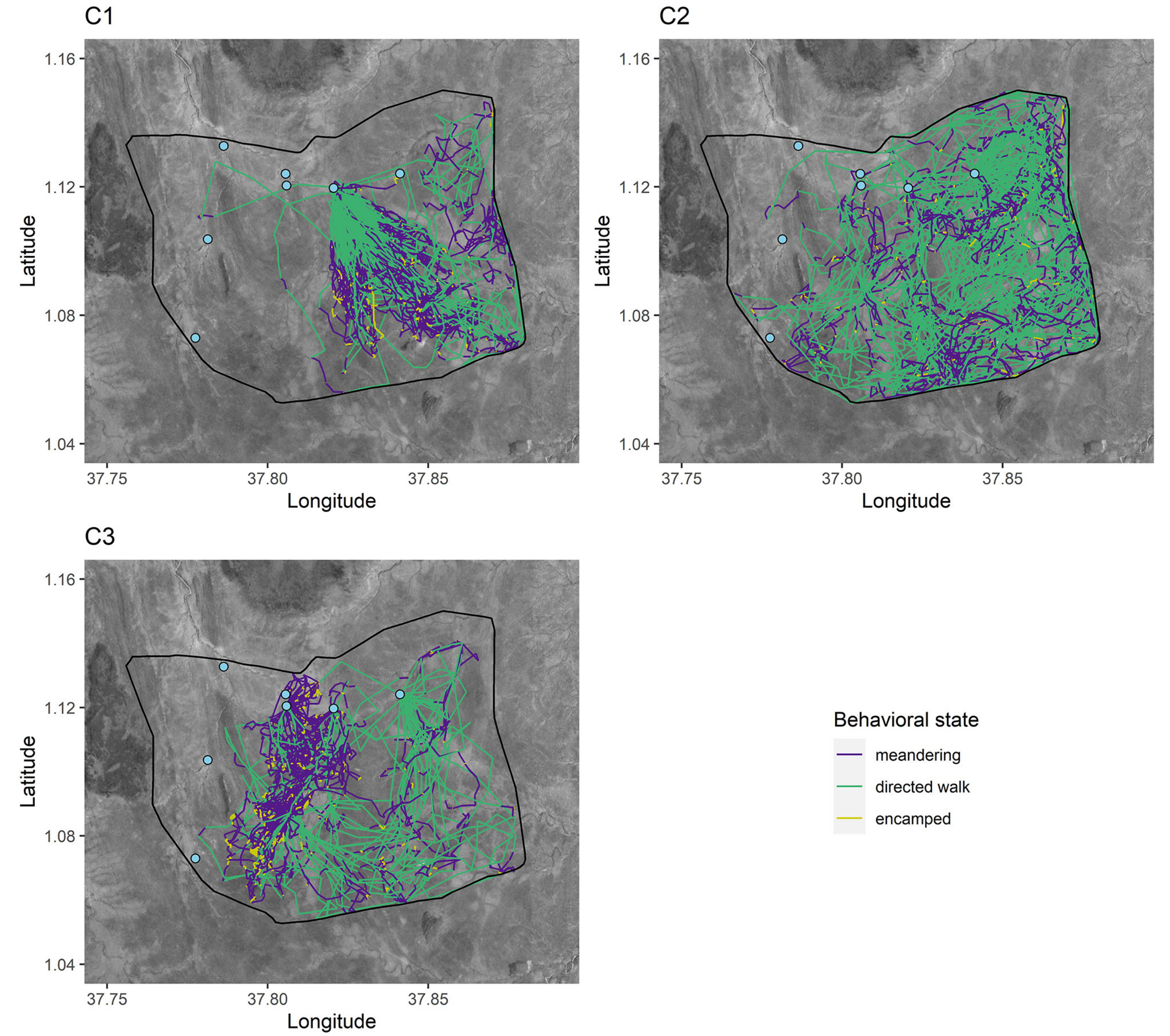

**FIGURE 2 |** GPS tracks for the first 6 months post-release for a representative member of each release cohort. Tracks are categorized by behavioral state. The fenced soft release site is outlined in black and permanent water points are represented as light blue points.

translocated elephants around the release site through at least the first dry season, with implications for the forage available to elephants and other fauna. Additionally, acquiring knowledge of permanent water sources early on post-release is particularly important for translocated elephants in arid environments. In a study comparing the tracks of translocated and resident elephant bulls in the Tsavo ecosystem in southern Kenya, Tiller et al. (in preparation)$^1$ documented the challenges for naive individuals during the dry season when familiar seasonal water points dried up. Thus, management that facilitates elephant discovery of permanent water points in semiarid systems earlier post-release should be prioritized in these systems (e.g., releasing elephants near concentrations of permanent water). In turn, as data are collected post-release they may be used to gauge the degree of success that individuals have shown in accessing key resources. For example, evidence of updated behavior (Berger-Tal and Saltz, 2014; Smetzer et al., 2021) like exploration pulses following initial adjustment periods may reflect learning and integration of new spatial information (e.g., steeper slopes in cumulative area plots; **Figure 1**), and changes in movement that track changes in ecological conditions may indicate greater exploitation of dynamic landscapes (e.g., the significance of variables related to rainfall or vegetation predicting exploration behavior; **Figure 4**). This may be particularly informative for determining when to transition animals from soft to hard release as soft release sites may function as "training grounds" that allow released animals to

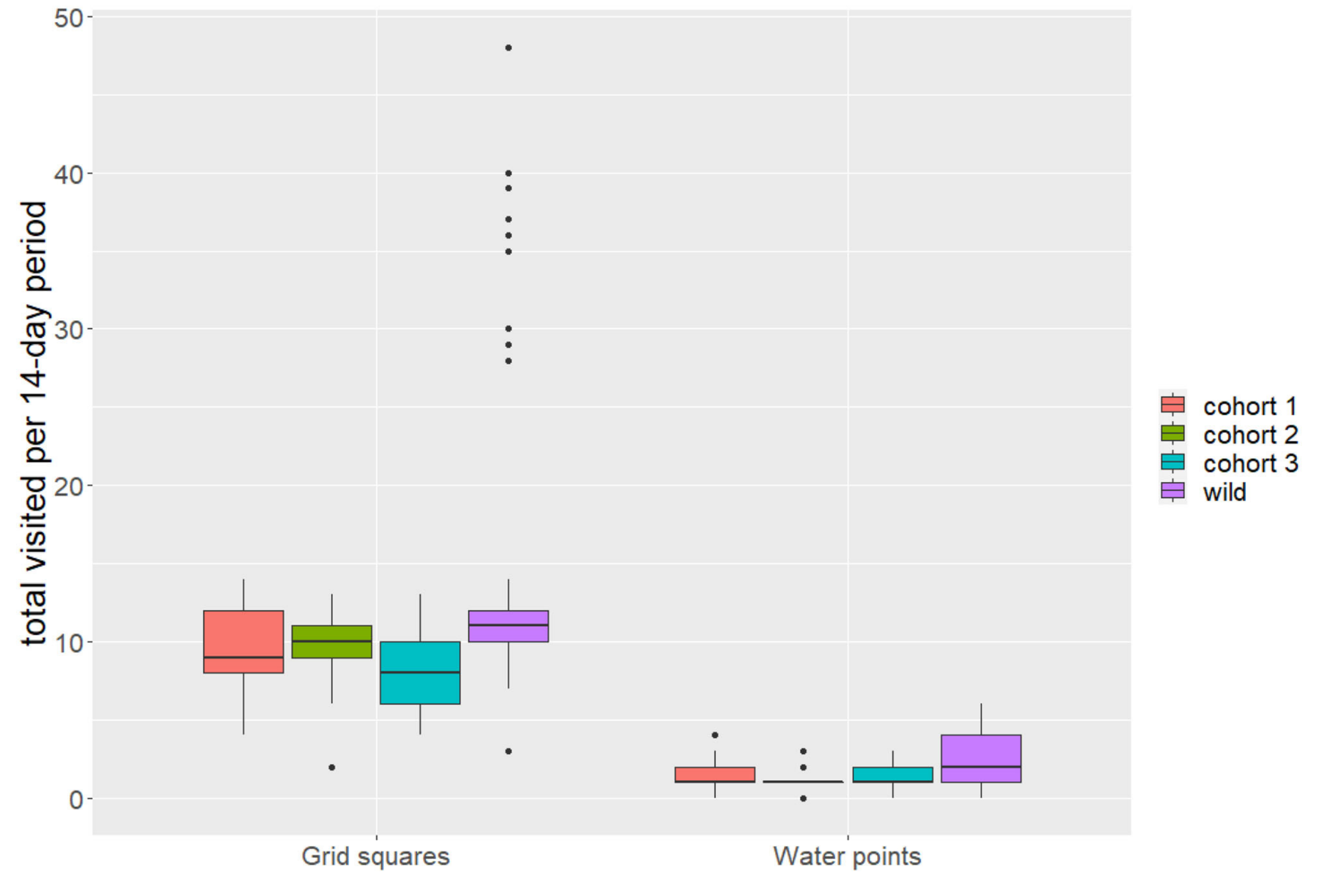

**FIGURE 3 |** Distribution of total 1 km$^2$ grid squares and water points used per 14-day period. Bold horizontal lines represent median values, boxes represent interquartile ranges, vertical lines extend to the highest and lowest points within 1.5 times the interquartile range, and points represent outliers.

gain local knowledge and to develop the necessary skills to search for resources effectively.

As expected, social familiarity was correlated with more new grid squares visited per 14-day period. Calves that associated more with wild elephants and those released later ranged into more new areas. This pattern suggests an important role for social context in facilitating and hastening landscape exploration. Movement in elephants is known to be related to established social relationships (Wittemyer et al., 2007; Foley et al., 2008) and it should therefore be expected that the social relationships of translocated elephants or lack thereof may influence the extent to which they explore their new surroundings (Goldenberg et al., 2019). There were clear distinctions in social context among the cohorts released: the first cohort was completely unfamiliar with any elephants at the soft release site, whereas the second and third cohorts were familiar with all individuals previously resident to the Reteti Elephant Sanctuary during their rehabilitation period. Thus, learning about the novel landscape from existing relationships with knowledgeable individuals was not an option for the first cohort until they established relationships with residents, a process that may take time in elephants (Goldenberg and Wittemyer, 2017). This distinction among cohorts may explain the relatively slow speed at which the first cohort visited new sites when compared to subsequent cohorts. Subsequent cohorts had the advantage of familiarity with knowledgeable individuals (Goldenberg et al., in revision)[2], which may have facilitated their earlier exploration of the sanctuary.

There is also evidence that not only familiarity, but close bonding between individuals in distinct cohorts, may be leveraged when determining cohort composition to achieve management aims, which we investigate in depth elsewhere (Goldenberg et al., in revision)[2]. Many translocation studies, including those of elephants (Pinter-Wollman, 2009; Fernando et al., 2012) and other taxa (Flanagan et al., 2016; Berger-Tal et al., 2020), have documented long range linear movements and cases where animals reject the release sites, by leaving and sometimes attempting to return to their original location. While the fencing at the soft release site in this study precludes homing, fencing may not be possible or practical in other locations. Our results suggest that familiarity and bonding with knowledgeable individuals at release sites is one way of encouraging site exploration, rather than site rejection. While

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[2] Goldenberg, S. Z., Chege, S. M., Mwangi, N., Craig, I., Daballen, D., Douglas-Hamilton, I., et al. (in revision). Social integration of translocated wildlife: a case study of rehabilitated and released elephant calves in northern Kenya. *Mamm. Biol.*

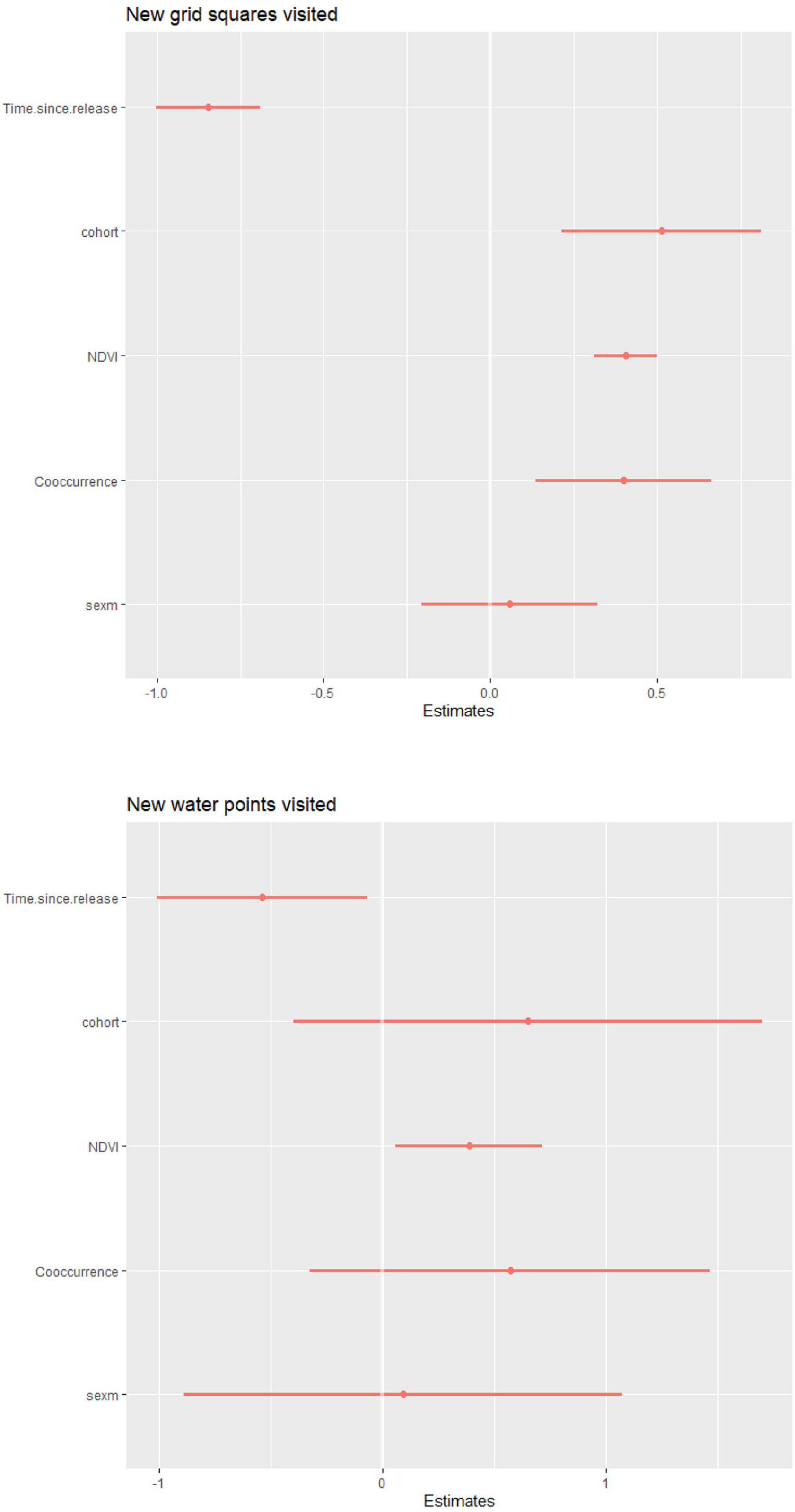

**FIGURE 4 |** Results for negative binomial models predicting new grid squares visited by 14-day time period (top) and new water points visited by 14-day period (bottom). Earlier time periods post-release, being in a later cohort, higher mean NDVI, and higher proportions of observations sighted with wild elephants were the covariates associated with a greater number of grid squares visited. Earlier time periods post-release and higher mean NDVI were associated with a greater number of water points visited.

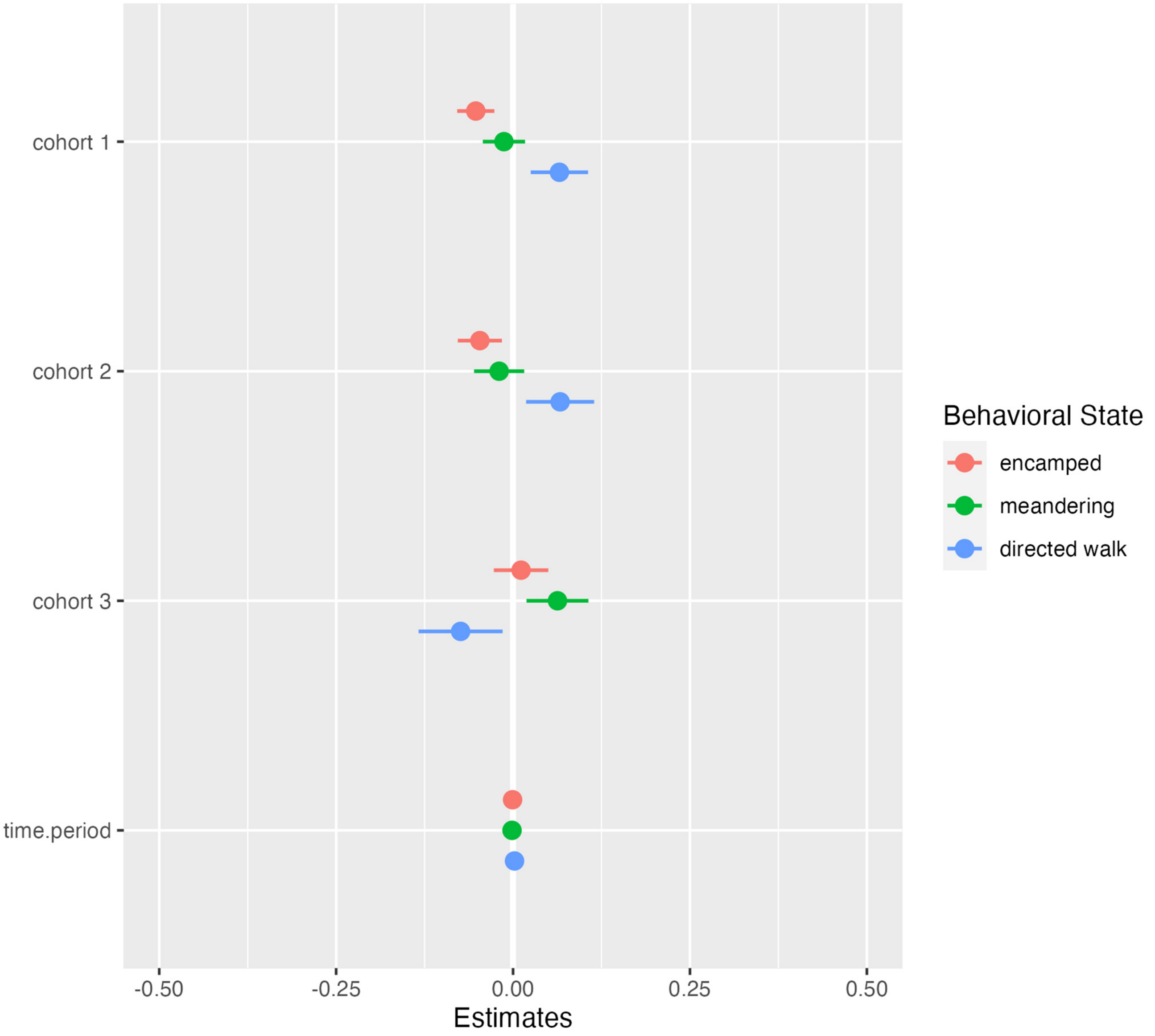

**FIGURE 5 |** Results for linear regression models predicting difference in state-level activity budgets for each cohort compared to the wild elephants over time. Color corresponds to the behavioral state (pink = encamped, green = meandering, blue = directed walk). Negative estimates indicate less time spent in a state compared to the wild elephants, and positive estimates indicate more time spent compared to the wild elephants. Bars indicate 95% confidence intervals and are significant when they do not overlap zero.

the significance of these results for elephant translocation projects is clear, we note that established social relationships across a diverse range of taxa may improve conservation translocation outcomes (Shier, 2006; Shier and Swaisgood, 2012).

In our analysis, sex was not predictive of exploration behavior in released cohorts. In their study of bull elephants translocated into the Tsavo ecosystem, Tiller et al. (in preparation)[1] suggested that younger bulls may be more successful in adjusting to release sites because younger bulls naturally undergo periods of exploration as they disperse from their families and learn their place within bull society. Studies of wild orphaned elephants suggest variability among individuals in their ability to integrate with new groups, with some females demonstrating dispersal behavior more typically associated with males (Goldenberg et al., 2016; Goldenberg and Wittemyer, 2017; Parker et al., 2021). The sample size represented in the present study is small; it will be worthwhile to revisit whether males are more exploratory post-release than females in future work and how released male calf behavior compares with that of young, dispersing wild bulls, of which only one was collared in this study. Additionally, the released population in this study is unique

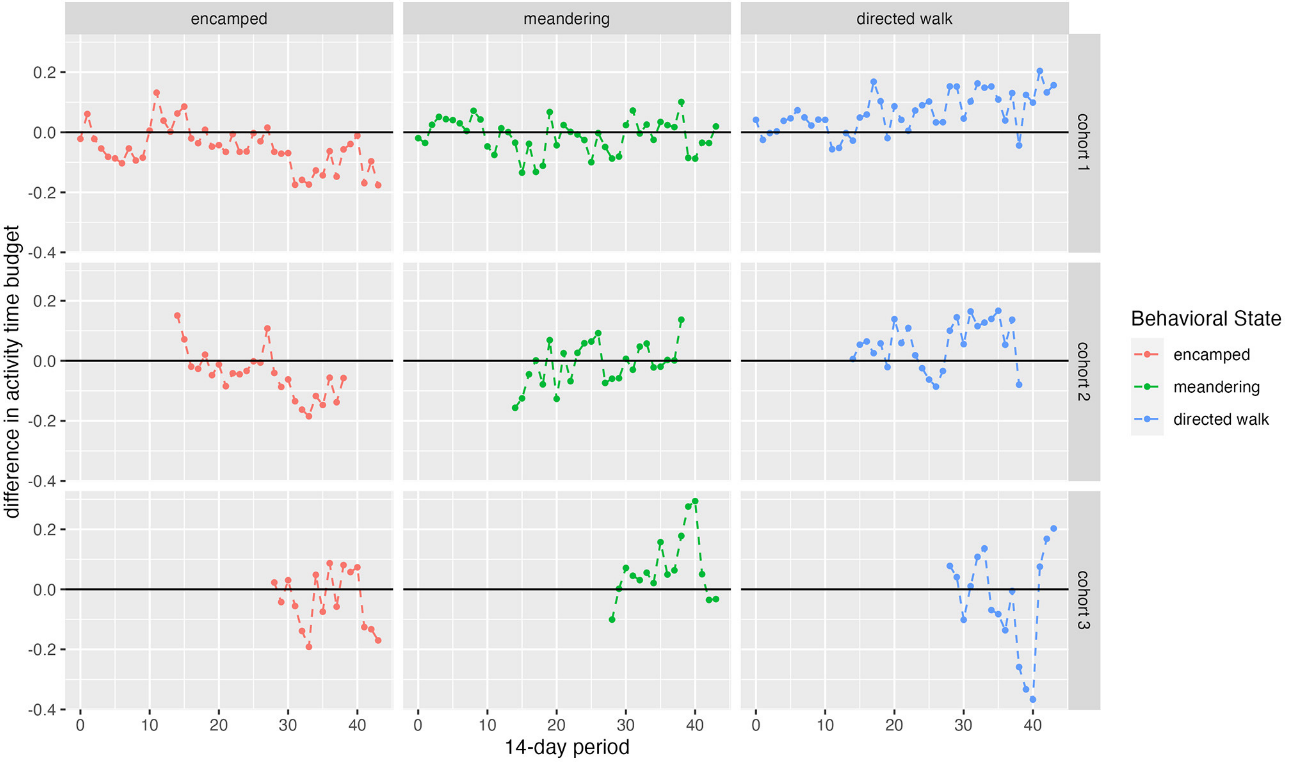

**FIGURE 6 |** Difference in activity budget plots by cohort/wild. Points closer to the bold line indicate more overlap with wild elephants.

among the literature on elephant translocations in that calves are young (~four years old) when they are translocated to the soft release site. Whether or not being released at a young age affects integration into wild herds and subsequent landscape exploration and convergence with wild elephant movement behavior warrants further study. Other individual characteristics in addition to age and sex that may be measured pre-release and potentially tied to exploratory movement post-release, like leadership and curiosity, may be worth investigating in the future.

Comparison of wild and translocated elephant movement revealed distinct differences, suggesting that released calves had not yet converged with wild elephant movement patterns over the time period analyzed. Wild elephants on average used more grid squares and more permanent water points per 14-day period than calves in release cohorts (**Figure 3**), and activity budgets suggested differences between the translocated and wild groups in the proportion of time allocated to each movement state (**Figure 6**). These results contrast with Pinter-Wollman et al. (2009), who found activity budgets between translocated and resident elephants based on observational data to converge over <one year post-release. This difference across studies may be attributable to the different pre-release experiences of the populations under study. Whereas Pinter-Wollman et al. (2009) studied wild elephant families and bulls that were translocated from one region to another, this study involves calves that were rescued and rehabilitated under human care and thus had limited experience in wild landscapes or moving at night. This highlights the additional challenges faced by orphaned wildlife raised partly under human care prior to release, and underscores the importance of extended learning periods prior to hard release. Regardless of the specific circumstances of translocated individuals, convergence in activity budgets with wild elephants (e.g., differences between activity proportions in released and wild animals trending toward zero; **Figure 6**) may serve as benchmarks to gauge individual competency post-release.

Despite the general mismatch between resident and released calf activity budgets, there were notable differences across cohorts, indicating different degrees of exploration. The first and second cohorts spent less time encamped and meandering (corresponding approximately to resting and foraging) and more time in directed walk than the third cohort and the wild residents (**Figure 5**). The directed walk state is often associated with targeted movement toward water points or prospecting behavior (**Figure 2**). This distinction among cohorts therefore suggests that the third cohort has not yet exhibited the same extent of exploration as the first and second cohorts. Translocations of other species have documented delays in exploration behavior. For example, reintroduced ʻAlalā crows made longer exploratory movements as time post-release progressed (Smetzer et al., 2021), and reintroduced European bison (*Bison bonasus*) took approximately 10 days to exhibit exploratory behavior following release (Schmitz et al., 2015). Drivers of such behavior, and particularly differences between cohorts, remain unknown.

Conservation translocations are high risk endeavors with the potential for significant conservation benefits. Understanding how individuals navigate post-release environments to obtain the resources necessary to survive and contribute to wild populations is critical to support such endeavors. The exploratory behavior of released savannah elephant calves investigated here provides insight into the strong influence of seasonality and social familiarity on resource use post-release, and the extended period over which managers should expect released calves to demonstrate activity budgets similar to wild elephants. Further, analyses like these may be useful as guides to gauge benchmarks of individual competency, like periods characterized by pulses in exploration, movement that tracks changing ecological conditions, and convergence of activity budgets with wild elephants, which may be a particularly important focus for animals that have spent time under human care. Whether or not such benchmarks correlate with the long-term survival and success of calves is yet to be determined. As noted throughout the literature on conservation translocations (IUCN/SSC, 2013; Berger-Tal et al., 2020), sustained monitoring over several years in an adaptive framework is needed to best guide the challenging decisions translocation managers are tasked with making to maximize conservation benefit and welfare. Our study contributes to this important literature to elucidate the post-release behavior of rehabilitated young orphans in a highly mobile and social species.

## DATA AVAILABILITY STATEMENT

The datasets presented in this article are not readily available because elephant tracking data are sensitive due to high rates of illegal killing of elephants in the region, and the data are therefore not archived. Requests to access the datasets should be directed to sgoldenberg@sdzwa.org.

## ETHICS STATEMENT

The animal study was reviewed and approved by San Diego Zoo Wildlife Alliance IACUC committee.

## AUTHOR CONTRIBUTIONS

SG wrote the first draft of the manuscript. SG, NH, and JS-D performed the statistical analyses. NH and JS-D wrote sections of the manuscript. SC, DD, ID-H, RL, ML, LL, FO, and FP contributed to acquisition/maintenance of the data. ID-H, FP, CT, GW, and MO revised the manuscript. All authors contributed to conception, design of the study, contributed to the article, and approved the submitted version.

## FUNDING

Donors to Save the Elephants and San Diego Zoo Wildlife Alliance funded this work.

## ACKNOWLEDGMENTS

We thank the Office of the President of Kenya for permission to conduct this work, and to the Sera Wildlife Conservancy for facilitating this research. We thank the staff at the Reteti Elephant Sanctuary, Katie Rowe, and Jeremy Bastard for elephant care and support of pre-release collaring. We are indebted to Save the Elephants for the ground identification and air surveys, and to KWS for veterinary oversight on the immobilization operations. We are grateful to Jenna Parker and Nelson Mwangi for field support and data management, and Toby Dunn for piloting the helicopter for immobilization.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2021.720202/full#supplementary-material

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Conservation Science

ORIGINAL RESEARCH
published: 30 September 2021
doi: 10.3389/fcosc.2021.703906

# Individual Variation in Temporal Dynamics of Post-release Habitat Selection

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Translocated animals undergo a phase of behavioral adjustment after being released in a novel environment, initially prioritizing exploration and gradually shifting toward resource exploitation. This transition has been termed post-release behavioral modification. Post-release behavioral modification may also manifest as changes in habitat selection through time, and these temporal dynamics may differ between individuals. We aimed to evaluate how post-release behavioral modification is reflected in temporal dynamics of habitat selection and its variability across individuals using a population of translocated female greater sage-grouse as a case study. Sage-grouse were translocated from Wyoming to North Dakota (USA) during the summers of 2018–2020. We analyzed individual habitat selection as a function of sagebrush cover, herbaceous cover, slope, and distance to roads. Herbaceous cover is a key foraging resource for sage-grouse during summer; thus, we expected a shift from exploration to exploitation to manifest as temporally-varying selection for herbaceous cover. For each individual sage-grouse ($N = 26$), we tested two competing models: a null model with no time-dependence and a model with time-dependent selection for herbaceous cover. We performed model selection at the individual level using an information-theoretic approach. Time-dependence was supported for five individuals, unsupported for seven, and the two models were indistinguishable based on $AIC_c$ for the remaining fourteen. We found no association between the top-ranked model and individual reproductive status (brood-rearing or not). We showed that temporal dynamics of post-release habitat selection may emerge in some individuals but not in others, and that failing to account for time-dependence may hinder the detection of steady-state habitat selection patterns. These findings demonstrate the need to consider both temporal dynamics and individual variability in habitat selection when conducting post-release monitoring to inform translocation protocols.

**Keywords: resource selection, post-release behavioral modification, individual behavior, individual heterogeneity, translocation, greater sage-grouse**

**Edited by:**
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**Specialty section:**
*This article was submitted to Animal Conservation, a section of the journal Frontiers in Conservation Science*

**Received:** *01 May 2021*
**Accepted:** *06 September 2021*
**Published:** *30 September 2021*

**Citation:**
*Picardi S, Ranc N, Smith BJ, Coates PS, Mathews SR and Dahlgren DK (2021) Individual Variation in Temporal Dynamics of Post-release Habitat Selection. Front. Conserv. Sci. 2:703906. doi: 10.3389/fcosc.2021.703906*

## INTRODUCTION

Most animals select for areas that have been previously visited – their familiar space (Wolf et al., 2009; Avgar et al., 2015; Ranc et al., 2020b). This behavioral process has been shown to provide benefits in terms of resource acquisition (Merkle et al., 2014; Ranc et al., 2021) and reduction of predation risk (Gehr et al., 2020). Translocated animals experience an unfamiliar landscape and therefore often undergo a phase of behavioral adjustment after being released in a novel environment (Berger-Tal and Saltz, 2014; Berger-Tal et al., 2020). During this initial phase, translocated individuals learn information about their new environment and may undertake exploratory movements to build a cognitive map of their surroundings (Berger-Tal and Saltz, 2014). Exploration and resource exploitation are at opposite ends of a behavioral gradient that translocated animals exhibit after release (Berger-Tal et al., 2014). Initially, the trade-off leans toward exploration; then, individuals gradually shift their behavior toward exploitation as they become more familiar with their new environmental context – a process that underlies the emergence of stable home ranges (Ranc et al., 2020a). The transition from exploration to exploitation has been termed post-release behavioral modification (PRBM; Berger-Tal and Saltz, 2014).

Post-release monitoring is important for understanding the success of translocation efforts (Bubac et al., 2019). Typically, the goal of monitoring is to assess individual behavior (such as habitat selection) and vital rates (such as survival or reproductive success) post-translocation (Armstrong and Seddon, 2008; Parker et al., 2013). This information helps to fine-tune translocation protocols within the context of an adaptive management framework, for example, by adjusting the choice of release sites or individuals to translocate (Letty et al., 2007; Osborne and Seddon, 2012).

When monitoring post-release behavior – for example, using telemetry devices fitted on translocated individuals – not accounting for PRBM may bias or confound estimates of habitat selection. An animal's habitat selection changes depending on current motivation and internal state (Nathan et al., 2008; Roever et al., 2014), and motivation is fundamentally different when animals are focused on exploration vs. exploitation. This issue is frequently ignored, or sometimes dealt with by discarding data for the first few days or weeks after release (e.g., Mondal et al., 2013; Werdel et al., 2021), during which behavior is assumed not to be representative of a steady state. In the latter case, the choice of the temporal cut-off to use is arbitrary and relies on the assumption that every individual in the population behaves similarly.

Evidence is increasing that individual behavioral responses to stimuli are idiosyncratic in wild populations (Cote et al., 2010; Bonnot et al., 2015; Merrick and Koprowski, 2017). Individuals with different temperaments may react differently when exposed to novel environments (Germano et al., 2017; de Azevedo and Young, 2021). Individual differences may manifest, for example, in the degree of risk-aversion exhibited during exploration (Montagne, 2016), stress-tolerance (May et al., 2016), or dispersal distances (Richardson et al., 2017); but individuals may also differ in the time it takes for them to move along the exploration/exploitation continuum, or in how their habitat selection changes as their internal state shifts.

Explicitly modeling temporal dynamics and accounting for individual heterogeneity should improve the quality of our inference on habitat selection in translocated populations. Incorporating these elements into the analysis of post-release behavior may improve translocation protocols aimed at maximizing the probability of successful population restoration. In this study, we evaluated individual variation in temporal dynamics of habitat selection after release in a novel environment using a population of greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) translocated from Wyoming, USA, to North Dakota, USA, as a case study.

Translocation has been used as a management tool to augment declining sage-grouse populations across their range (Reese and Connelly, 1997; Baxter et al., 2008, 2013; Duvuvuei et al., 2017). Sage-grouse populations have undergone severe declines since the 1960s (Garton et al., 2011; Coates et al., 2021). In North Dakota, the extant sage-grouse population experienced a sharp decline due to habitat loss and a West Nile Virus (*Flavivirus* spp.) disease outbreak in the mid-2000s (Garton et al., 2011). Augmentation of this declining population was initiated in 2017 with translocation of individuals from a large, stable population in central Wyoming (Coates et al., 2021). Using data from this translocation, our objectives were to evaluate: (1) whether sage-grouse exhibited individual variation in habitat selection during PRBM, and (2) whether including time-dependent terms improved inference on individual habitat selection.

## MATERIALS AND METHODS

We captured female sage-grouse during summers 2018–2020 from the source population near Stewart Creek, WY at night using spotlights and dip-nets cast from all-terrain vehicles (Wakkinen et al., 1992). The captured individuals included brood-rearing females (captured in June with their young chicks, 7–40 days old; Meyerpeter et al., 2021) and non-brood-rearing females (captured in June without a brood). All individuals were translocated within 24 h post-capture (Lazenby et al., 2021). We measured and weighed individuals and equipped them with rump-mounted Global Positioning System (GPS) Platform Transmitter Terminal (PTT) ARGOS-enabled tracking devices (23 g, GeoTrak©, Inc.) scheduled to acquire six locations a day at irregular intervals. In the case of brood-rearing females, we also captured their chicks, weighed them, and equipped them with Very High Frequency (VHF) suture-style tracking devices (1.1 g, Holohil Systems©, Ltd.). During transport, females and their chicks were kept separated to prevent injury but within audio-visual contact in specialized transport boxes (Meyerpeter et al., 2021). We translocated captured sage-grouse to Bowman County, ND and released them using a soft-release method, i.e., allowing for an acclimation period (∼30–45 min) in a release pen. The source habitat in WY is part of the Wyoming Basin Sage-Grouse Management Zone, characterized by large, uninterrupted sagebrush (*Artemisia spp.*) steppe (Lazenby et al., 2021). The sage-grouse population in this area is one of the largest remaining across the species range (Coates et al., 2021). The release area in ND is part of the Great Plains Sage-Grouse Management Zone which is a grass-dominated landscape interspersed with small sagebrush patches (Lazenby et al., 2021). The sage-grouse population in this area constitutes a small remnant fragment at the northeastern periphery of the species range (Coates et al., 2021).

To quantify temporal dynamics in post-release habitat selection, we analyzed GPS-tracking data for female sage-grouse in the 60 d following their translocation to ND. Model predictors included percent sagebrush cover, percent herbaceous cover, slope, and distance to roads; based on previous literature, these variables are known to be important predictors of sage-grouse habitat selection across their range (Connelly et al., 2011; Dinkins et al., 2014) as well as specifically in the translocated ND population (Lazenby et al., 2021). We obtained percent sagebrush and herbaceous cover data at a 30-m resolution from the National Land Cover Database (NLCD 2016; https://www.mrlc.gov/national-land-cover-database-nlcd-2016). We obtained data on slope at a 30-m resolution from Landfire (https://landfire.gov/). We obtained data on roads from the USGS National Transportation Dataset (USGS 2014), including paved roads, highways, and interstates as well as gravel or dirt roads. We rasterized the roads vector layer to a 30-m resolution and calculated distance of each pixel to the nearest road. We log-transformed distance values to allow for a spatial decay in the behavioral response to roads. We scaled and centered all predictors before including them in the model.

We used integrated step selection analysis (iSSA; Avgar et al., 2016) to quantify habitat selection. Because iSSA requires data at regular time intervals, we scanned our dataset to find the most frequent regular interval between locations (i.e., 11 h) and only retained 11-h steps. An iSSA simultaneously models the habitat selection process [denoted as $w(x)$] and the movement process [denoted as $\phi(x)$] underlying an animal's space use (Avgar et al., 2016). For all models, we modeled step lengths as realizations of a gamma distribution, which accounts for the heavy-tailed distribution of movement distances typically observed in empirical data; and turning angles as realizations of a von Mises distribution, which accounts for directional persistence. Both distributions were initially parameterized with population-level data (gamma with shape = 0.72 and scale = 725.04; von Mises with mean = 0.00 and concentration = 0.10). Accordingly, our movement process model was $\phi(x) = \exp[\alpha_1 l + \alpha_2 \log(l) + \alpha_3 \cos(\theta)]$, where $l$ is the step length and $\theta$ is the turning angle. We sampled 100 available steps for each observed step using these population-level gamma and von Mises distributions.

We tested our hypothesis of temporal modification of habitat selection by fitting competing models for the habitat selection process. We used model selection to evaluate whether individuals exhibited temporal modification of habitat selection by fitting an interaction between a focal predictor and the natural logarithm of time, measured as days since translocation. Herbaceous cover is the primary driver of habitat selection for translocated sage-grouse during summer (our period of investigation) in our study area. In summer, sage-grouse – and especially females with broods – rely on grasses, forbs, and the associated insect community as the main food sources for themselves and their young (Connelly et al., 2000, 2011). In the grass-dominated ecosystem of North Dakota, where sagebrush cover is sparser than in most other areas of the species range, the availability of herbaceous cover plays a more important role than sagebrush cover at fine scales (Kaczor et al., 2011). As such, if time-dependent habitat selection were to emerge in our study system, we would expect it to manifest primarily in the response to herbaceous cover. We expected individual responses to potentially vary through time for resources but not for conditions, thus we chose not to test for time-dependent responses to slope. Sagebrush is not a limiting resource for sage-grouse during summer as much as during winter, when alternative food sources are not available (Connelly et al., 2000; Swanson et al., 2013); although it remains an important broad-scale predictor of sage-grouse habitat selection, we did not expect it to be the main driver of habitat selection at fine scales during summer. Selection for roads may potentially vary through time after release, but we did not expect individual responses to switch from selection to avoidance or vice-versa; thus, we did not test for time-dependent responses to roads.

Our two competing models of the habitat selection process for each individual were:

- Model T0 did not include any time-dependence in the habitat selection process (null model);

$$w(x) = \exp(\beta_1 S_x + \beta_2 H_x + \beta_3 L_x + \beta_4 R_x)$$

- Model T1 included time-dependent selection for herbaceous cover and no time-dependence for selection for the other predictors;

$$w(x) = \exp[\beta_1 S_x + \beta_2 H_x + \beta_3 L_x + \beta_4 R_x + \beta_5 H_x \log(T_x)]$$

In the equations above, $w(x)$ denotes the habitat selection function, $S_x$, $H_x$, $L_x$, and $R_x$ denote percent sagebrush cover, percent herbaceous cover, slope, and distance to roads at location $x$, respectively, and $T_x$ denotes days since translocation when the GPS location $x$ was taken. Because the total number of parameters in the more complex model (T1) was 8, we only fit the models to individuals with at least 80 observed steps (using a minimum of 10 steps per estimated parameter as a rule of thumb to ensure adequate power). We ranked models for each individual based on Akaike's Information Criterion corrected for small sample sizes ($\text{AIC}_c$). We grouped individuals based on their top-ranked model: group T0 had model T0 as top-ranked ($\Delta\text{AIC}_c > 2$ for model T1) and group T1 had model T1 as top-ranked ($\Delta\text{AIC}_c > 2$ for model T0). Individuals for which the second-ranked model had $\Delta\text{AIC}_c \leq 2$ were not attributed to either group. For individuals in groups T0 and T1, we evaluated mean parameter estimates at the individual level under both

**TABLE 1 |** Summary of model ranking based on $AIC_c$ for translocated female sage-grouse in North Dakota in 2018–2020.

| | T0 top-ranked | T1 top-ranked | Indistinguishable |
|---|---|---|---|
| Brood-rearing females | 6 | 5 | 8 |
| Non-brood-rearing females | 1 | 0 | 6 |

*Model T0 is a null model including sagebrush cover, herbaceous cover, slope, and distance to roads as predictors and no time-dependence terms. Model T1 includes the four predictor and also a time-dependent term for selection for herbaceous cover. Both models were fit to a set of 26 translocated sage-grouse, of which 19 were brood-rearing females and seven were non-brood-rearing females. A model was considered top-ranked when $\Delta AIC_c > 2$ for the second-ranked model. If $\Delta AIC_c \leq 2$, the models were indistinguishable.*

models. We used standard errors to calculate 95% confidence intervals around mean parameter estimates using a large-sample approximation. Then, for all individuals, we calculated mean predictions of log Relative Selection Strength (log-RSS; Avgar et al., 2017) for herbaceous cover under model T1 as a function of days since translocation. Log-RSS is the natural logarithm of the ratio of the exponential habitat selection function for two sets of predictor values (Avgar et al., 2017); we chose to evaluate selection for the 3rd quartile of herbaceous cover (52%) vs. the mean value across the dataset (46%), but because our model is linear on the log-scale, these patterns would hold for any values of herbaceous cover separated by 6%.

## RESULTS

The final dataset included 26 translocated sage-grouse. Of these, 19 were brood-rearing females and seven were non-brood-rearing females. Time-dependence in habitat selection was supported for five individuals, while the absence of time-dependence (i.e., null model T0) was best supported for seven individuals; the two models were indistinguishable based on $AIC_c$ for the remaining 14 individuals (**Table 1**; see **Supplementary Material** for individual model selection tables). We found no evidence of association between the occurrence of time-dependence in habitat selection and individual status (brood-rearing or non-brood-rearing; Fisher's exact test; $p > 0.05$). Out of seven individuals in group T0, model T0 indicated selection for herbaceous cover in four, avoidance in one, and no significant response for two; we detected no significant responses to the other three predictors (**Figure 1**). Out of five individuals in group T1, model T1 indicated initial selection for herbaceous cover with a shift toward avoidance for two and initial avoidance with a shift toward selection for three (**Figures 1**, **2**); we also detected selection and avoidance of steeper slopes for one individual, respectively (**Figure 1**). When fitting model T0 to group T1, the sign of the response to herbaceous cover was reversed with respect to model T1 for four out of five individuals (**Figure 1**). When fitting model T1 to group T0, the mean parameter estimate was estimated accurately albeit with greater uncertainty (**Figure 1**). For individuals that exhibited time-dependent habitat selection for herbaceous cover, the switch from selection to avoidance (or vice-versa) occurred within 1–3 days after release (**Figure 2**).

## DISCUSSION

Using data for translocated greater sage-grouse, we showed that temporal dynamics of post-release habitat selection may manifest in some individuals but not in others, and that not accounting for time-dependence may hinder correct interpretation of habitat selection patterns. These findings showcase the need to consider both temporal dynamics and individual variability in habitat selection when conducting post-release monitoring of translocated animals.

Five translocated sage-grouse (all brood-rearing females) exhibited a temporally varying response to herbaceous cover within the first 60 days post-release. For two of these individuals, selection for higher herbaceous cover was strongest immediately after release and gradually decreased through time, switching to avoidance (**Figure 2**). The remaining three individuals initially exhibited avoidance of higher herbaceous cover and then switched to selection (**Figure 2**). A switch from avoidance to selection for herbaceous cover during post-release behavioral modification is what we expected based on theory: translocated animals should initially prioritize exploration of their new surroundings and move through the landscape regardless of the distribution of key resources, and they should gradually shift to resource exploitation once acclimated (Berger-Tal and Saltz, 2014). The trend we observed is also compatible with natal habitat preference induction, where translocated individuals select for habitat that is most similar to their natal habitat before they gradually adjust to the new conditions (Davis and Stamps, 2004). Indeed, sage-grouse habitat at the source population consisted of contiguous sagebrush steppe, where sagebrush was the dominant vegetation type and herbaceous cover was sparse; sage-grouse were then released in a grass-dominated system. Some translocated individuals may have responded to this change by initially avoiding unfamiliar features and then gradually selecting for higher herbaceous cover as they became familiar with the release area. Individuals who initially selected and then started avoiding higher herbaceous cover may have done so because their brood fledged or died within the 60 days after release, which relaxed their dependence on herbaceous cover for foraging.

Seven sage-grouse (six brood-rearing and one non-brood-rearing female) did not exhibit time-dependent habitat selection for herbaceous cover; most of them selected for herbaceous cover, one avoided it, but their behavior did not change through time (**Figures 1**, **2**). Although our sample size did not give us statistical power to make definitive claims, we did not find a link between temporal dynamics of habitat selection exhibited by translocated individuals and their status (brood-rearing or non-brood-rearing). Rather, the individual variation we observed in temporal dynamics of post-release habitat selection may be a result of intrinsic characteristics of each individual (e.g., personality; Carere and Eens, 2005).

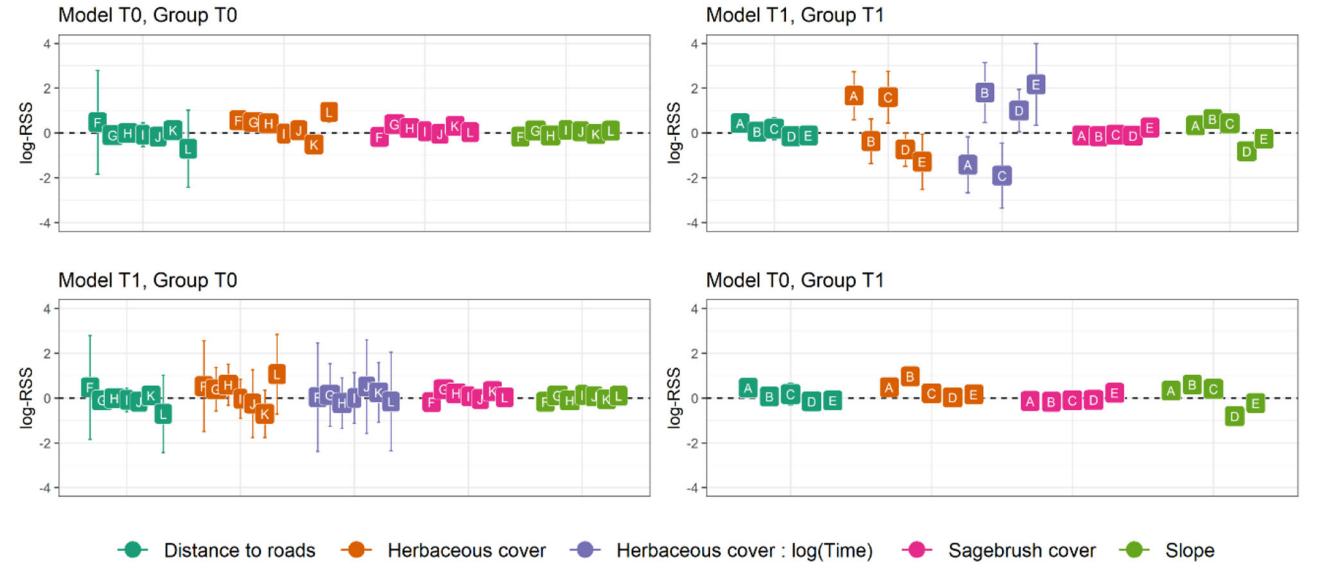

**FIGURE 1 |** Mean parameter estimates and 95% confidence intervals for habitat selection of translocated sage-grouse in North Dakota, 2018–2020, in the 60 days after release. Model T0 includes no time-dependent terms, while model T1 includes time-dependent selection for herbaceous cover, a key foraging resource during summer. Both models were fitted to each individual separately and ranked based on AICc, then individuals were grouped based on their top-ranked model. Individuals in group T0 had model T0 as top-ranked ($\Delta AIC_c > 2$ for model T1), while individuals in group T1 had model T1 as top-ranked ($\Delta AIC_c > 2$ for model T0). Parameter values express log-Relative Selection Strength (*sensu* Avgar et al., 2017), i.e., the selection coefficient for a 1-unit increase in the covariate value.

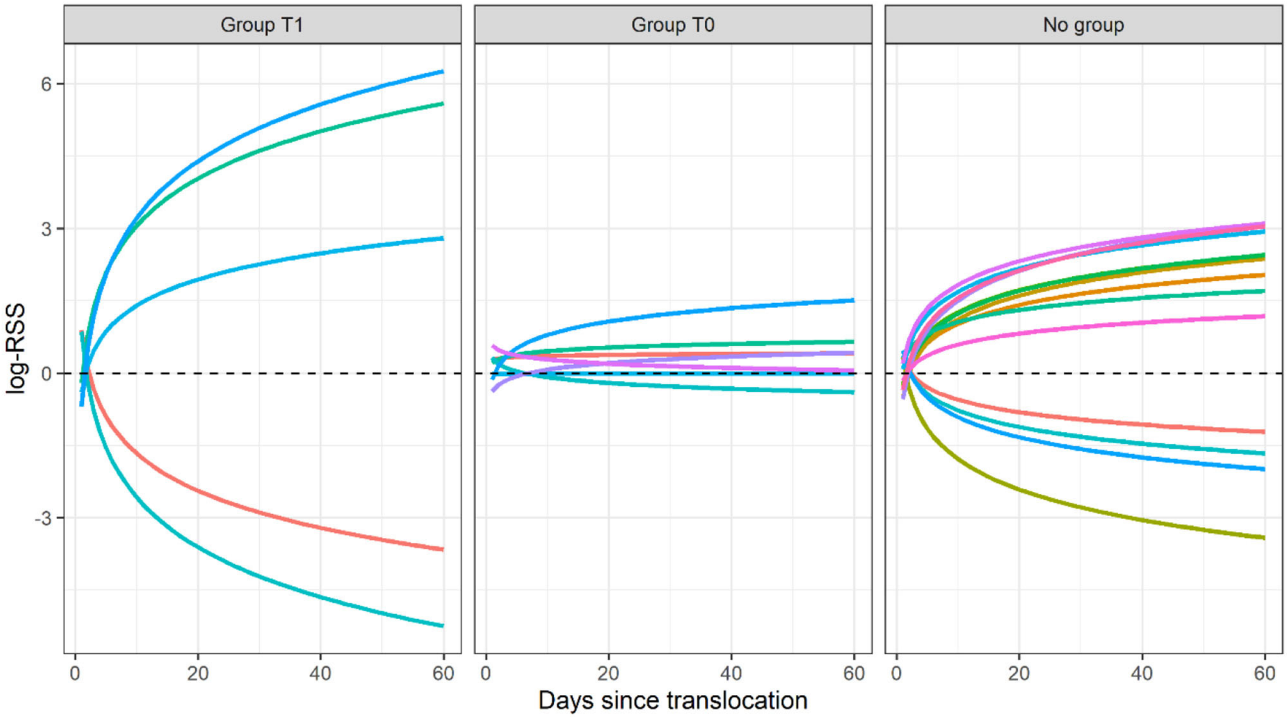

**FIGURE 2 |** Predictions of log-Relative Selection Strength from model T1 in response to herbaceous cover as a log-function of time (days since translocation) in translocated female sage-grouse in North Dakota, 2018–2020, in the 60 days after release. Predictions were evaluated using individual-level parameter estimates. Group T1 included individuals for which the model with time-dependent selection for herbaceous cover was top-ranked ($\Delta AIC_c > 2$ for model T0), group T0 included individuals for which the model without time-dependence was top-ranked ($\Delta AIC_c > 2$ for model T1), and the “no group” label denotes individuals for which the two models were indistinguishable ($\Delta AIC_c \leq 2$ for the second-ranked model).

Our results demonstrate that model formulation affects inference, reinforcing that failure to consider temporal dynamics and individual variation may substantially change the conclusions drawn about habitat selection in translocated populations. When using a model without time-dependence terms to predict habitat selection for individuals that exhibit time-dependence, our estimates of steady-state habitat selection were altered. In some cases, opposite trends canceled out – e.g., initial avoidance neutralized steady-state selection, resulting in a non-significant pattern (**Figure 1**). In others, the initial response outweighed the steady-state behavior resulting in a reversed pattern (**Figure 1**). These findings demonstrate that failing to account for time-dependent habitat selection in individuals that exhibit it is likely to lead us to inaccurate conclusions. By contrast, including time-dependence terms still resulted in accurate estimates for steady-state selection for herbaceous cover in individuals that did not exhibit temporal dynamics, albeit with greater uncertainty (**Figure 1**). All in all, these results show that the inclusion of time-dependence terms, at least during data exploration, allows for detection of temporal dynamics where they occur without compromising accuracy in estimating steady-state habitat selection.

The time-dependent model was indistinguishable from the null for the remaining 14 individuals based on $\mathrm{AIC_c}$. This is likely because the response to herbaceous cover in these individuals was too weak to outweigh the penalty from an additional model parameter. Nonetheless, our results show that fitting a model that includes time-dependent terms to individuals that do not exhibit time-dependent habitat selection increases uncertainty but does not affect the accuracy of steady-state estimates. Thus, one possible approach is to begin data exploration by fitting time-dependence models to all individuals and then further refine individual parameter estimates by removing unnecessary time-dependence terms on an individual basis.

Responses to other predictors in our models were weak, with a few exceptions: one individual selected to be near roads, four individuals selected for high sagebrush cover, one avoided steeper slopes and three selected for them (**Figure 1**). One possible explanation for selection for roads is that linear features may provide conspicuous landmarks for some individuals and help with orientation in an unknown landscape. Landmarks play an important role in spatial orientation and learning in vertebrates (Bingman and Cheng, 2005; Lewis et al., 2020), and previous studies have shown that, in some bird species, translocated individuals are able to use anthropogenic landmarks (including roads, e.g., Bélisle and St. Clair, 2002) to navigate across the landscape. Selection for high sagebrush cover and avoidance of steep slopes are typical habitat selection responses observed in sage-grouse across their range (Connelly et al., 2000, 2011). Selection for steeper slopes in some individuals was surprising, although less so when contextualized within the study area, where even the steepest slopes are only moderately steep. The fact that, overall, responses of translocated sage-grouse to key predictors were weak could be attributed to several reasons. One possible explanation is that some translocated sage-grouse were unable to behave adaptively in an environment so different from their natal habitat, at least during the first 2 months after release, and thus behaved similarly to random walkers using resources in close proportion to their availability. Another possible reason for the lack of strong responses, which is not necessarily in contradiction with the first one, is that habitat selection in translocated sage-grouse may be stronger at coarser orders of selection, but at finer scales, once settled within a general area, sage-grouse behavior becomes closer to a random walk. Finally, the release environment was rather homogeneous, and the lack of landscape heterogeneity may have resulted in weak responses.

In our study system, sage-grouse exhibited weak to moderate habitat selection responses, but accounting for temporal dynamics may be even more important in highly heterogeneous landscapes. When evaluating time-dependent habitat selection, it is beneficial to decide *a priori* on ecologically meaningful model formulations based on existing knowledge of the study species and system, especially when data availability constraints limit the complexity of the models. In this study, the size of our individual datasets did not allow us to fit time-dependent terms for multiple predictors at a time. Higher-frequency, temporally regular location data should allow researchers to include several time-dependent terms within one model and test alternative hypotheses regarding time-dependent habitat selection for multiple resources. Potentially, individuals might display time-dependent selection for different predictors and reveal new, intriguing patterns of individual heterogeneity.

Temporal dynamics in habitat selection provide insight into how long it takes for translocated individuals to reach steady-state behavior in the release area. Results from this study illustrate that (1) the time-to-steady-state may differ between individuals, (2) the acclimation phase may be shorter (or longer) than expected *a priori*, and (3) some individuals may not display any time-dependent responses. In principle, the time it takes for individuals to reach steady-state habitat selection may also differ between predictors. Often, researchers deal with post-release behavioral modification by discarding data from the first few days or weeks after release. Explicitly modeling temporal dynamics of individual behavior may inform the choice of cut-off to use when discarding data or entirely remove the need for it, because the model structure already accommodates the potential for behavioral adjustments.

Time-dependence in habitat selection could be implemented using different formulations. A shortcoming of the formulation we used is that the natural logarithm of time since release constrains the shape of the temporal-dependence curve, making it range from 0 on the first day post-release to 1 at the maximum number of days post-release (in our case, 60). At the same time, a benefit of this formulation is that our temporal dependence curve is still a linear curve that can be fit using standard software. More complex, non-linear formulation of time-dependence curves would allow for explicit estimation of individual time-dependence parameters over time-series of varying lengths. However, this implementation would require custom non-linear models, which are sometimes beyond the reach of non-statisticians; to overcome this barrier, some quantitative biologists may prefer a Bayesian solution. Custom form models would also be data-hungry due to their non-linear nature.

Temporal dynamics and individual variation in habitat selection are often viewed as a nuisance to remove; instead, we argue that they should be treated as processes on which to make inference. Our results showed that including time-dependent responses and evaluating habitat selection at the individual level may provide a detailed picture of how translocated populations respond to their new environment. Our study indicates benefits of approaches that explicitly incorporate temporal dynamics and accommodate individual variation when examining post-release habitat selection of translocated animals. Accounting for individual differences in habitat selection and post-release behavioral modification should ultimately improve population-level inference as well, by ensuring, first, that population-level analyses focus on steady-state behavior only, and second, that opposite patterns of selection between groups of individuals do not cancel each other out when analyzed collectively. Formal tests of *a priori* hypotheses on post-release behavior via appropriately designed experimental translocation have the potential to provide valuable information for adaptive management (Armstrong and Seddon, 2008). These benefits warrant high interest in future research aimed to test hypotheses on drivers of individual heterogeneity in post-release behavior.

## DATA AVAILABILITY STATEMENT

The data are available on Dryad, https://doi.org/10.5061/dryad.44j0zpcf5. The code is available on GitHub, https://github.com/picardis/picardi-et-al_2021_sage-grouse_frontiers-in-conservation.

## ETHICS STATEMENT

The animal study was reviewed and approved by Utah State University Institutional Animal Care and Use Committee.

## AUTHOR CONTRIBUTIONS

SP and NR conceived the idea. SP, NR, and BS conducted the analysis. DD and PC supervised the project and provided the data. SM curated the field data. SP wrote the initial manuscript draft. All authors contributed to manuscript editing and revision.

## FUNDING

This research was primarily funded by the North Dakota Game and Fish Department. The Wyoming Game and Fish Department also contributed funding.

## ACKNOWLEDGMENTS

We thank numerous technicians and volunteers for field data collection. We thank the U.S. Geological Survey Ecosystems Mission Area, Wyoming Game and Fish Dept., North Dakota Game and Fish Dept., the Jack Berryman Institute, Utah State University Cooperative Extension, and the Wildlife Federation for their support on this project. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2021.703906/full#supplementary-material

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Conservation Science

ORIGINAL RESEARCH
published: 12 October 2021
doi: 10.3389/fcosc.2021.733703

# Settling in: Reintroduced Persian Fallow Deer Adjust the Borders and Habitats of Their Home-Range During the First 5 Years Post Release

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Translocated animals typically find themselves in a novel environment in which they must establish a home range in a manner that will maximize their fitness. We hypothesized that the initial establishment of a home range is followed by adjustments expressed as home range shifting, and occurs as familiarity with the landscape increases, until the home range is stabilized. We studied the process of home range shifting in 42 female Persian fallow deer (*Dama mesopotamica*) reintroduced into the Galilee, Israel over a period of 2–5 years. We used changes in the degree of home range overlap between consecutive years as an indicator of stabilization. We then compared how the mean percent cover of the key vegetation types (woodland, scrubland and open pastures) differed between the areas abandoned in the first year's home range and the areas added to the last year's home range relative to the first (using a weighted paired *t*-test). We also compared the distribution (using $\chi^2$ test of independence and Levene's test for homogeneity of variance) of %cover of the 3 vegetation types between the first and last year's home range. The average home range overlap increased over the 5 years following the first release. During the first-year post release, deer avoided open pastures and preferred woodland. In later years deer increase in the % open pastures (weighted *t*-test: $p < 0.001$) and decreased the % woodland cover (weighted *t*-test: $p = 0.07$) by abandoning areas with little open pasture and steeper terrain and moving into areas with more open pasture and moderate terrain. Variance of the cover types across individuals increased with time. We conclude that the home ranges of the reintroduced deer stabilized with time. The changes in vegetation and slope are driven by time-dependent changing needs reflecting a tradeoff between safety (refuge) and foraging. Our findings suggest that using the initially established home range to determine species preferences can create a misleading picture of what the optimal home range of the species really is. Individual variation in term of preferences can take a few years to be expressed due to the initial high-risk perceived by individuals in a novel environment.

**Keywords: translocation, shift, stabilization, novel environment, habitat preference**

***Edited by:***
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***Specialty section:***
*This article was submitted to Animal Conservation, a section of the journal Frontiers in Conservation Science*

***Received:*** *30 June 2021*
***Accepted:*** *26 August 2021*
***Published:*** *12 October 2021*

***Citation:***
*Maor-Cohen M, Bar-David S, Dolev A, Berger-Tal O, Saltz D and Spiegel O (2021) Settling in: Reintroduced Persian Fallow Deer Adjust the Borders and Habitats of Their Home-Range During the First 5 Years Post Release. Front. Conserv. Sci. 2:733703. doi: 10.3389/fcosc.2021.733703*

# INTRODUCTION

Throughout much of their life, most vertebrates restrict their movements and activities to a given area in space, commonly termed home range (Burt, 1943; Powell and Mitchell, 2012). Under certain conditions, however, animals may find themselves in a completely novel environment in which they must search for an area in order to form a new home range (HR) that will maximize their relative fitness (Yiu et al., 2019). Encountering a novel environment most often occurs as a part of post-natal dispersal (Haughland and Larsen, 2004; Selonen and Hanski, 2006), but occasionally may happen because of forced abandonment of an existing HR due to natural or anthropogenically initiated disasters such as bush fires (Mao et al., 2005) or due to translocation by humans as part of management and conservation procedures. The formation of a HR in a novel environment is an important component of fitness, enabling familiarity with the landscape, so more time can be devoted to exploiting resources safely and efficiently (Berger-Tal et al., 2014). We consider this process to have two distinct phases: the search phase where an animal explores the landscape and selects a general area to settle in, followed by an establishment phase in which the newly formed home range is "fine-tuned" to best fit the animal's needs (McNicol et al., 2020). Both phases are heuristic and may take an extended amount of time (Dolev et al., 2002; Preatoni et al., 2005; Sarkar et al., 2016). In this paper we focus on the dynamics of the establishment phase.

The expected high costs of exploration for a new HR, in terms of time, risk and resource acquisition in an unfamiliar environment (Yoder et al., 2004) compared to the potential benefits of finding a better area, suggest that once established, animals are not expected to voluntarily abandon their HR (Ranc et al., 2020). Thus, the decision when to stop exploring and select an area in which to settle is a critical one which will have a long-lasting effect on the animal's fitness. However, since the exploration stage can be very costly (Berger-Tal et al., 2014), it is safe to assume that the decision to stop searching and form a HR is made before the animal is fully familiar with the landscape, its attributes, and dynamics (Saltz and Getz, under review). Thus, following the initial HR establishment, as familiarity with the HR and its surroundings increases, spatial adjustments (as opposed to complete abandonment) are expected to be made in response to the increased familiarity with the availability of resources (Ranc et al., 2020). In this context, HR establishment should not be viewed as a single event, but rather as a process that begins with the initial formation of a HR to minimize exploration costs, followed by fine-scale adjustments to perfect the HR based on increased familiarity with it and its surroundings.

The fine-scaled adjustments to a newly established HR have received little attention and may harbor important information regarding the behavioral processes in a novel environment that can contribute to enhancing translocation success (Yiu et al., 2017). These adjustments should be evident as shifts in the HR that constitute abandonment of areas that are perceived as less beneficial (or no longer beneficial/necessary) and expansion into neighboring areas that are perceived as offering relatively better opportunities (Ranc et al., 2020). Accordingly, the comparison between the landscape attributes in the newly occupied areas and those in the abandoned sections should be informative in terms of the process of HR establishment in general, and the animal's preferences, risk perceptions, and how these change over time.

Toward this end we have investigated the process of HR adjustments by Persian fallow deer (*Dama mesopotamica*) reintroduced into the Galilee, Israel, after the initial HR was formed. The reintroduction consisted of multiple releases carried out from 1996 to 2011 and was successful in establishing a wild, expanding self-sustaining population (Maor-Cohen et al., 2020). In this study we revisit a movement data set collected with long-lasting VHF platforms during the first 5 years of the reintroduction program, when tracking focused on low-resolution and long-term sampling (of up to 5 years per individual). In recent years the focus in the fallow deer project has shifted toward advanced GPS technology and fine-scale high resolution data which often limits battery life to 1–2 years of tracking (Seigle-Ferrand et al., 2021), making it less suitable for questions regarding HR establishment across years, as done here. We studied the shifting patterns of HRs from the time of the initial establishment over a period of 2–5 years. Specifically, we were interested in determining how long it took deer to stabilize their HR; the magnitude of the annual shifts in HR location; and in identifying how habitat usage changes with these shifts. We deducted the latter based on the changes that occurred in the habitat composition following the shift. We hypothesized that the establishment process will result in overall diminishing shifts in annual home ranges and that the shifts will reflect specific habitat needs.

# METHODS

## Study Site, Study Species and Release Protocol

The deer were reintroduced to Nahal Kziv Nature Reserve (35023′ S, 33033′E) in the western Galilee, northern Israel. The study area is dominated by Mediterranean vegetation, consisting of a mosaic of Mediterranean woodland characterized by dense common oak (*Quercus calliprinos*) (encompassing 30% of study area), scrubland characterized by spaced out common oak and spiny broom (*Calycotome villosa*) shrubs (encompassing 35% of study area), and open pastures containing grasses and low shrubland (encompassing 16% of study area) (Perelberg et al., 2003). The center of the reserve is a deep ravine with steep slopes in which the Kziv stream flows year-round. The surrounding landscape is dominated by moderately rolling hills.

Persian fallow deer (IUCN red list status: EN) is a medium/large sized deer of the genus *Dama* (Zidon et al., 2009). A detailed analysis of the foraging habit conducted on the European fallow deer (*Dama dama*) showed they forage predominately on grasses (encompassing 70% of their diet), sedges and rushes (Putman et al., 1993). The Persian fallow deer was considered extinct until rediscovered in Iran in the 1950's (Saltz, 2013). Captive bred populations were established from the Iranian population including in Hai Bar Carmel breeding core in Israel. In 1996 reintroductions in Israel began in Nahal

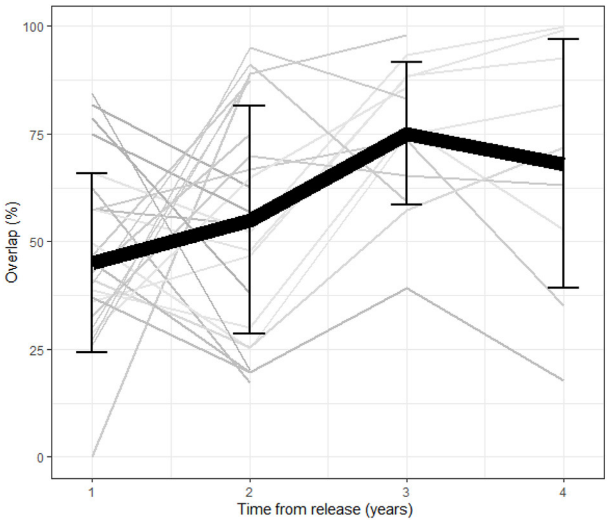

**FIGURE 1 |** Average overlap between consecutive year home ranges as a function of time from release (in years) per individual ($n = 34$). The black line represents the population mean and error bars represent the standard deviation per year. The overall overlap increases as a function of time from release reflecting a stabilization process.

Kziv Nature Reserve and continued for over a decade following procedures described by Saltz (1998).

For the first 5 years the releases were conducted semiannually and in each 6–12 individuals were released from a 11-ha habituation enclosure (Dolev et al., 2002) after spending up to three months in acclimation. Throughout the first 5 years of the study 53 individuals were released. Of these, 42 were females that were fitted with either a 1 kg (life expectancy of 5 years) or 0.5 kg (life expectancy of 2–3 years) VHF radio-collar (MOD 400 and 500 transmitters; Telonics, Mesa, Arizona, USA). The radio tracking was conducted two to three times a week with one location per animal retrieved per sampling day. Occasionally (<5%) 2 location/day were obtained and if separated by more than 6 h both were included in the database as independent measurements following the procedure detailed in Dolev et al. (2002) and the criteria provided by White and Garrott (1990). Tracking was conducted using Yagi antenna with a frequency scanning receiver. To locate the animals, the observer used triangulation from two known locations. The bearing was determined using a prismatic compass with 1° resolution. Sampling error due to animal movement was minimized by defining an *ad-hoc* minimum angle between bearing of 20° (White and Garrott, 1990), and maximum time between two bearings of 30 mins for each animal (Harris et al., 1990; Saltz, 1994; Perelberg et al., 2003). Mean triangulation error, which was calculated by randomly placing transmitters in locations unknown to the observer, was found to be 284 m (Perelberg et al., 2003) and well within the average patch size of the three habitat types relevant to this study (Bar-David et al., 2005, **Figure 1A**).

## Land Cover Estimations

Land cover estimations were done using an ortho-photos map for the upper Galilee region (produced by OFEK ltd.) with a scale of 1:3,500, pixel size of 100 × 100 m, and the software ArcView. Vegetation was classified into one of six categories: open pastures, scrubland, dense woodland, riparian habitat, cultivated orchards, and other cultivated agricultural fields. Of these the riparian habitats constitute a small fraction of the area and the cultivated lands are typically fenced and not accessible to the deer. The vegetation cover images were coupled with a roads landscape image and a built-up areas image to generate a land cover types map (Bar-David et al., 2005, **Figure 1A**). This map was exported using GIS programs [Idrisi32 (Clark Labs, Worcester, Massachusetts, USA)] and converted to a raster layer containing pixels of the different land covers where each pixel represented only one land cover type. Using ArcGIS pro each annual home range was overlayed with the land cover layer which allowed for the calculation of the total area of each vegetation type within each home range. Deer avoided built areas and roads and these were not a substantial part of any of the home ranges used in this study. Thus, although included in the landcover layer, these categories are not relevant to this study.

The elevations within the study site were translated into a contour map (using triangulation method) and from it, using the software "Idrisi," to a map of slopes across the surface (in degrees). This layer was crossed with the annual home ranges of each individual. For each individual we obtained an analysis of the home range in terms of topographical slope: the distribution of slopes in degrees, the mean and standard deviation.

## Home Range Estimation

We calculated annual home range size and spatial orientation using the 90 and 50% isopleth of the Adaptive Kernel technique (Worton, 1989) within the Home Range Extension for ArcView (Rodgers and Carr, 1998) for each year following initial release. The reintroduced fallow deer formed a home range within 6 months (Dolev et al., 2002), thus we excluded the first 6 months of data for the home range analysis and analyzed annual home ranges following this initial establishment. Using overlaying methods in GIS, we derived from each annual home range its average topographical slope and its vegetation cover composition. In this study we were mostly interested in the dominant types of vegetation cover important to the deer (which encompassed >85% of the landscapes within the home ranges): woodlands which provide better refuge, open pastures that provide the preferred forage (grasses), and scrublands that are intermediate in both respects.

## Home Range Shifting and Changes in Home Range Attributes

We characterized the temporal and spatial dynamics of HR shifting by evaluating the annual change in the spatial orientation of an individual's HR, i.e., the first-year's HR overlap with the second-year's HR, the second year's with the third and so on. The degree of overlap was calculated as the percentage of the overlapping area in the home range between two consecutive years out of the total area of home range in the second year.

We had two working hypotheses:

1. HRs stabilize over time since reintroduction. If HRs stabilize over time, we predict the degree of overlap between two consecutive years is expected to be positively correlated

with time since release. We assessed whether the HRs were becoming stabilized over time by regressing the amount of overlap between consecutive years on the number of years since each individual's reintroduction. Because the increase in overlap may be due to the increase in density with time since the onset of the project, we used the release cycle as a second predictor as a proxy for the number of animals in the study site (representing the increase in density due to the releases as well as recruitment). We tested all possible models (after testing for possible collinearity between the two predictors) and compared between them using multi-model inference and Akaiki's Information Criteria corrected for small sample size (AICc).

2. The shift in the HR reflects specific habitat needs and is an attempt to maximize fitness by modifying its spatial arrangement. The shift itself is therefore a proxy of the actual interests of the animal and is a complex outcome of the conditions/resources in the current HR and those available in the nearby landscape and how they are distributed. However, the extent of the shift in an environment that is typically patchy and irregular, is expected to poorly reflect the actual needs of the animal. Specifically, preferred or unwanted habitats are intertwined in infinite shapes and forms across the landscape, initial HR characteristics may vary between individuals, and the landscape characteristics in the neighboring areas may vary. Thus, the magnitude of the shift is the outcome of many parameters and may include large unwanted areas necessary to maintain continuity in the new HR while encompassing certain key attributes that may have a small footprint. Our attempt to explain the magnitude of the shift based on spatial and temporal changes in the landscape characteristics using multi-model inference resulted in the intercept-only being one of the leading models. Thus, while the magnitude of the shift is the key gage of the HR stabilization process, our focal interest for this hypothesis is not what determines the magnitude of the shift, but rather what is achieved by the shift. Specifically, how habitat composition has changed. Consequently, we adopted a parsimonious approach that addresses the changes in the key characteristics of the landscape known to be important to mid-sized deer: the vegetation cover and the steepness of the terrain (Nicholson et al., 1997).

For the three dominant vegetation cover types in the study area that are expected to be of value (open pastures, scrubland, dense woodland) we compared between the first and last annual HR calculated for each individual. We used the last HR because, based on our working hypothesis, later HRs are expected to be closer to what the animal is attempting to achieve. We did so by using two approaches:

(a) Looking at the distribution across all animals of the proportions of each vegetation type within the first and last HR. We determined how vegetation cover is distributed between the individual HRs by calculating the % cover of each vegetation type for each animal and counting the number of animals that fell within a certain range of cover using 10% increments as categories. We then tested for differences using a $\chi^2$ test of independence. Categories with an expected value $<5$ were merged with neighboring categories.

(b) Assessing how the average cover of each vegetation type changes between the first and last HR. We accentuated this comparison by contrasting between the area abandoned in the first HR relative to the last and the area added to the last HR relative to the first (i.e., we excluded the common area). We then tested for differences using a paired *t*-test on the arcsine transformed value weighted by the number of years that elapsed between the first and last HR. Although the woodland, scrubland, and open pasture constitute only 3 of the 6 vegetation types, these are the ones dominant within the deer home range and are therefore expected to be colinear. However, because we carried the analyses separately, errors due to zero degrees of freedom or high collinearity do not occur, yet it is important to realize that an increase in one vegetation type is directly associated with a decrease in at least one of the other two, so the findings are not independent. In both cases we carried out the comparison for both the 90 and 50% isopleths.

In addition, we performed a Levene's test for homogeneity of variance on the standard deviations of all percent vegetation cover types to examine whether there was a reduction in variance as a function of time from release. We expected that if individuals reach optimal HR characteristics by shifting their HR, variation in the populations should decrease as a function of time from release.

We recognize that other factors may affect changes in habitat preferences over time, including annual precipitation, location of water sources and presence of conspecifics. However, the area is Mediterranean with a rather constant annual precipitation in the years of the study (900–1,200 mm), rather consistent primary productivity, and moderate weather in general. We therefore consider annual variations in the environment to be relatively minor. In terms of water availability, Nahal Kziv is the main natural water source in the study area. However, cattle troughs and leaking water pipes found in agricultural fields probably supply the majority of drinking water which the deer rely on. Since we cannot quantify the availability and spatial arrangement of this resource it was not included in the analysis. In terms of conspecifics, because of collar failure as well as recruitment, our knowledge on the spatial arrangement of a significant part of the population is missing. Persian fallow deer, however, are not territorial and have loose social ties, and given that the study was carried out in the first years of the reintroduction, density dependent effects should be minor and social effects would mostly impact the rapidity of home range establishment (Sjoasen, 1997; Dolev et al., 2002).

All statistical analyses were conducted using R packages "adehabitat," "ggplot2," and "weight" for weighted *t*-test.

# RESULTS

## Home Range Overlap

A total of 42 females were tracked for 2–5 years between the years 1997 and 2001. The average HR overlap increased over the 5 years

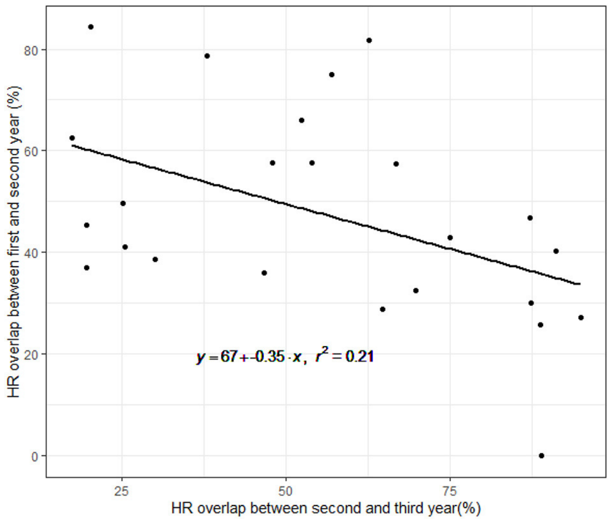

**FIGURE 2 |** Correlation between home range overlap during the first and second year, and the home range overlap between the second and third year. The black line is the expected linear relationship. The negative relationship indicates that individuals that shifted little between the first and second year, exhibited larger shifts between the second and third year.

and was 45% ± 20.8 (error here and throughout represents the standard deviation) between the first and second year, 55% ± 26.5 between the second and third year, 75% ± 16.6 between the third and fourth year and 68% ± 28.8 between the fourth and fifth year (**Figure 1**). Collinearity between the two predictors of overlap (number of years the animals were in the wild and the release cycle) was weak ($R = -0.41$, Pearsons Correlation Test). The level of overlap increased with the number of years the animals were in the wild and decreased with release cycle, with the full model having the lowest AICc and all other models trailing by delta-AICc of 6.5 or more, including the intercept only (DF = 72, coefficients: year from release = 8.5, release cycle = −1.5, year from release*release cycle = 0.5, adjusted $R^2 = 0.14$). Twenty-five females had shifted their home range over 50% at least once during the first 3 years post release. Interestingly, we found a negative correlation between the percent shift during the first and second year showing that individuals that shifted little in the first year compensated for it in the second (linear regression: $p = 0.02$, **Figure 2**).

## Home Range Attributes

During the first-year post release deer clearly selected woodland cover which made up most of their HR, both in the core and full HR (50 and 90% isopleth, **Figure 3**). The average woodland cover available in the study site is 30% and the population average of woodland cover in the HRs was 53% ±18 in the core and 51% ± 6.7 in the full HR. The deer avoided having open pastures during the first year both within the core of their HR and in the 90% isopleth, with populations average open pastures being 0.5% ± 0.8 in the core and 3.7% ± 3.5 in the full HR, even though open pastures make up 16% of the available vegetation cover within the study site (**Figure 3**). A comparison of the difference in the percentage of vegetation cover between the first and last year of tracking per female revealed an increase in the open pastures both in the core and full HR (weighted *t*-test: $p < 0.001$ for both), and a slight decrease in the woodland cover in the full home range (weighted *t*-test: $p = 0.07$). The differences in other vegetation types were not significant.

While the difference in mean percent cover was found to be significant only for open pastures, the distribution of the three cover types varied considerably, except for the woodland in the core (50% isopleth). Specifically, in the core, the distribution of percent scrubland and open pasture was different between the first and last year ($\chi^2$ test of independence: $p = 0.04$ and $p < 0.001$ respectively). In the full HR, the distribution of all vegetation types was significantly different during the first year compared to the last year ($\chi^2$: woodland: $p = 0.049$, open pasture: $p = 0.02$, scrubland: $p = 0.005$).

Our results show that in the 90% isopleth, the variation in the population was lower in the distribution of woodland and scrubland cover (Levene's test: $p = 0.001$ and $p < 0.001$ respectively) during the first-year post release compared to the last-year HR. In the core (50% isopleth) of the HR however, there was significantly lower variation in the population in distribution of open pasture (Levene's test: $p < 0.001$) and marginally significant differences in woodland cover (Levene's test: $p = 0.06$) between the first and last year.

When comparing the areas occupied during the first year and abandoned, to the areas added in the last year relative to the first, we found significant differences in the amount of open pastures added both in the core and the full HR (50% isopleth, weighted *t*-test: $p < 0.001$, 90% isopleth, weighted *t*-test: $p < 0.001$, **Figure 4**) suggesting deer abandoned areas with very low open pasture cover both within the core and their full HR and added more open areas to their HR in later years. Other tests performed on this data set came out non-significant.

Deer adjusted the slopes in the HR and selected more moderate terrain as a function of time from release. The mean slope during the first year was 15.7% ± 3.3 and during the last year 12.7% ± 3.7 a difference we found to be statistically significant (weighted *t*-test: $p < 0.0001$, **Figure 5**).

# DISCUSSION

Animals exhibit flexibility of space use within their HR and its surroundings, suggesting that they make decisions based on exploration even in a well-established HR (Creel et al., 2005; Tuqa et al., 2014). Thus, knowledge of the spatio-temporal dynamics of home ranges can further our understanding of the link between home range behavior, ecological or evolutionary processes, and their conservation-related consequences (Börger et al., 2008).

The establishment of a HR in the reintroduced Persian fallow deer population in the Kziv Reserve, Israel, appears to be a long-term process over which the HR becomes more stable. The process spans several years and is driven by instinctual behavior and time-dependent changing needs. Specifically, refuge appears to be key, but the landscape of fear (Laundré et al., 2009) evidently changes over time as a function of familiarity. The genus *Dama* tends to be more grass/roughage eaters than

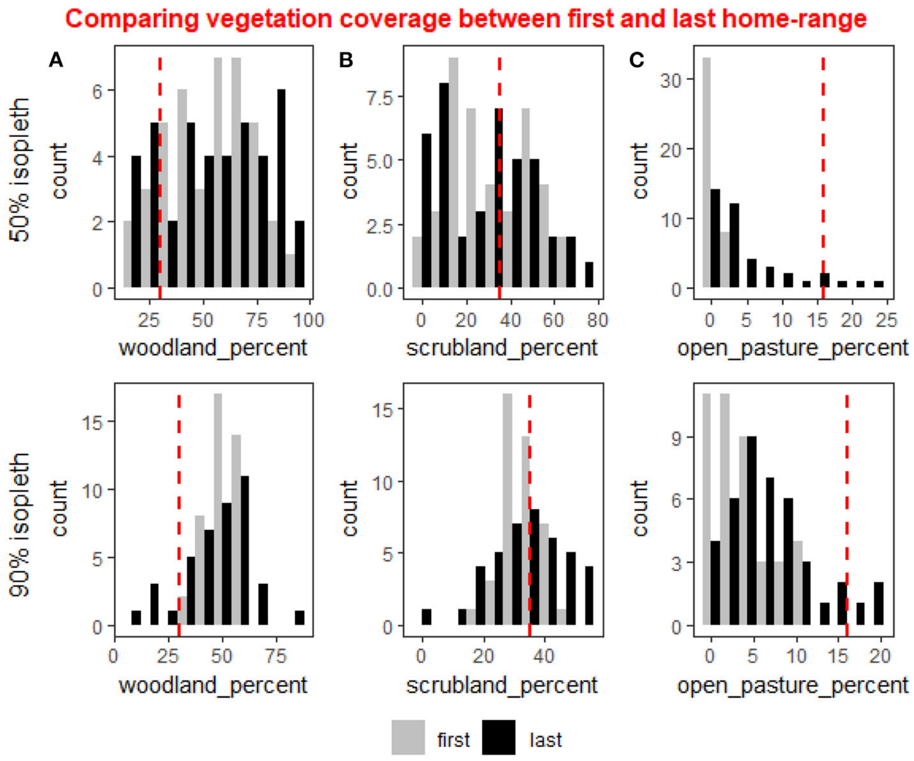

**FIGURE 3 |** The distribution of the percent coverage in individuals home ranges of three types of vegetation cover: woodland **(A)**, scrubland **(B)**, and open pasture **(C)** shown for the 50% isopleth (core of the home range, upper row) and the 90% isopleth (entire home range, lower row) in the first year after reintroduction (gray bars) and last year of tracking (black bars). In the 90% isopleth average percent woodland was reduced slightly (weighted *t*-test: $p = 0.07$) between the first and last year but the distribution was significantly wider during the last year ($\chi^2$: $p = 0.049$). In the 50% isopleth both the average percent woodland and the distribution did not vary between the first and last year. **(B)** In the 90% isopleth average percent scrubland did not change between the first and last year but the distribution was significantly wider during the first year ($\chi^2$: $p = 0.005$). In the 50% isopleth the average percent scrubland did not change but the distribution varied between the first and last year ($\chi^2$: $p = 0.04$). **(C)** In the 90% isopleth and in the 50% isopleth the deer avoided open pastures during the first and last year, but in the 90% isopleth the deer increased the amount of open pasture between the first and last year (weighted *t*-test: $p < 0.001$) and the distribution was significantly wider ($\chi^2$: $p = 0.02$). In the 50% isopleth both the average percent open pasture and the distribution differed significantly between the first and last year (weighted *t*-test: $p < 0.001$, $\chi^2$: $p < 0.001$).

browsers (Hofmann, 1989), with scrub and mixed plantations being the most beneficial for their diet during the spring and summer and open pastures during the fall and winter (Focardi et al., 1995). However, open grasslands and scrublands offer less refuge and are, therefore, riskier. Thus, fallow deer that perceive a higher risk tend to forage closer to the wooded habitat which provides cover (Pecorella et al., 2016). Familiarity is a key component of risk reduction (Gehr et al., 2020), so the perceived risk in newly translocated animals is inherently higher. The spatial behavior of the Persian fallow deer, being a prey species, is expected to be highly affected by presence of predators and/or by their perception of risk (Nicholson et al., 1997; Maor-Cohen et al., 2020). While we did not test perceived risk or predator presence directly, animals in their first-year post release are expected to be motivated by lack of knowledge and the need for safety should be prioritized. This explains the observed pattern of our deer preferring woodlands over the open and scrubland when the HR was initially established, and shifting the HR to include more open pastures over time as familiarity with the landscape increased. Predation is a key factor affecting reintroduction success (Berger-Tal et al., 2020) and in our study system, wolves are the only potential predator for the deer (Maor-Cohen et al., 2020). However, at the time of this study wolves were not present in the study area (Mendelssohn, 1983), if they were, the shift into open pasture may not have occurred.

Interestingly, a significant change in the total amount of habitat between the area added and the area abandoned as part of the shifting process was found only for the open pasture habitat, although a reciprocal process should have occurred in either the woodland, scrubland or both. This is probably due to the overall area of the open pasture being relatively small so the significance of observed decline in the woodlands would be overwhelmed by its variance. The $\chi^2$ tests demonstrate that the changes that do occur in the woodland are mostly in the outer boundaries (90% isopleth) of the home range, and such changes are also evident in the two other habitat types. Specifically, while the distribution of woodland and scrubland varied considerably among individuals and remained unchanged over time in the 50% isopleth, in the 90% isopleth there was a stronger central tendency (lower variance) in the first year that weakened later (**Figure 2**).

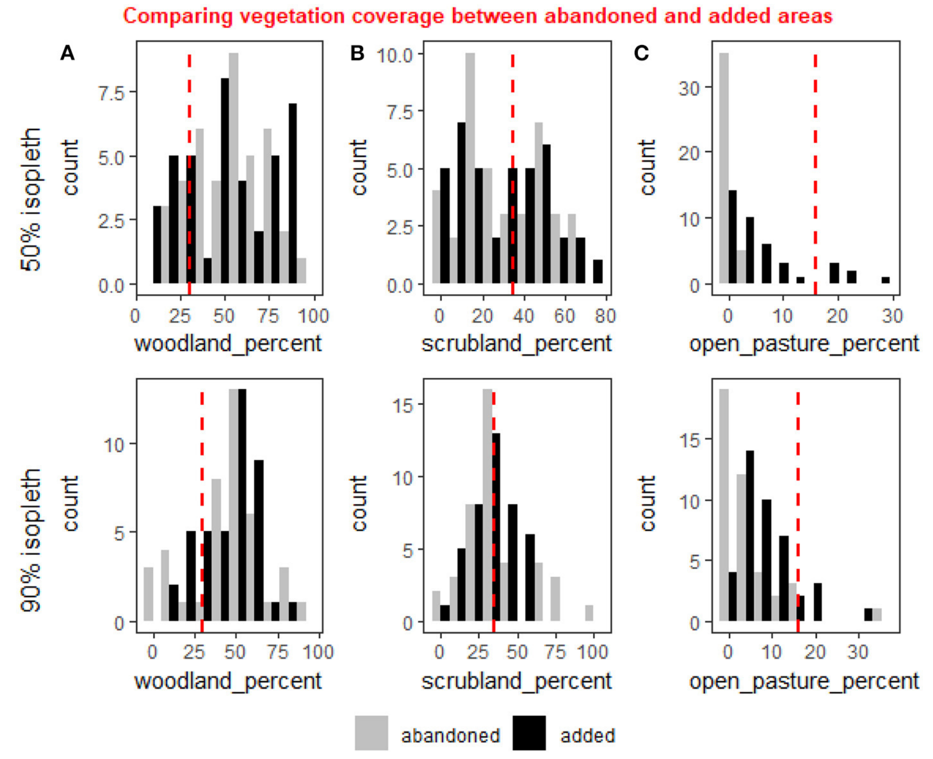

**FIGURE 4 |** A comparison of the distribution of coverage the three vegetation cover types—woodland **(A)**, scrubland **(B)** and open pasture **(C)**—between area of the first year's home range that were abandoned relative to the last (gray), and the areas added to the last year's home range relative to the first (black). The comparison is for the 50% isopleth (core of the home range—upper row) and the 90% isopleth (entire home range—lower row). The red line represents the average coverage in the study area. Percent open pasture was significantly higher in the added areas compared to the abandoned ones for both the 50 and 90% isopleths (weighted *t*-test: $p < 0.001$ for both). There were no significant changes in the woodland and scrubland, but the increase in open pastures appear to be on account of a minor (albeit non-significant) decline in the scrubland.

The preference of the deer to wooded areas in the early stages of translocation reflects an elevated state of stress which is linked to the translocation procedure and the novel landscape (Zidon et al., 2009). This carries two costs: reduced foraging efficiency due to reduced availability of grasses and forbs within the woodland, and the catabolic effect of the stress itself (Saltz et al., 1995). The combination of these may be the proximate factors driving reduced reproductive success that was observed post release (Bar-David et al., 2005). Thus, our results highlight the importance of ample refuge (i.e., in higher quantities than what is expected to be preferred based on any previous knowledge of the released species) in the release site.

The fine-scale details of the extent and direction of the shift are difficult to evaluate. It is safe to assume that there is a landscape perimeter surrounding the original HR which the deer are familiar with and which the deer can evaluate as potential areas for incorporation into the exiting HR. The width of this perimeter is unknown. The complexity of the landscape, namely the types of available habitat, their spatial pattern, and the characteristics of the specific patches, as well as the effects of other variables which we could not account for in our analysis (e.g., neighboring conspecifics) dictate that the decision as to which new area to incorporate into the HR and which area to abandon is a complex one, hampering our ability to provide detailed predictions as to the direction and extent of the shift.

The HR shift analysis described herein bares similarity to resource selection functions in that it is indicative of the animal's habitat preferences or needs. However, it is distinct in that resource selection functions consider the probability of use of a resource by an animal relative to current availability within the animal's HR (Boyce and McDonald, 1999; Manly et al., 2007). The HR shift analysis is a more objective measure of animal preference because it is not limited to the choices offered by the HR alone, the boundaries of which may be 'forced' upon the animal by competing neighboring conspecifics. Thus, translocations offer a unique opportunity to study animal behavior when competition is lax or absent (Sarrazin and Barbault, 1996).

Reintroduced species are often rare and threatened species for which we have limited knowledge about their specific HR requirements. Typically, one of the categories for success in the early phases of a reintroduction is the formation of a HR (Flanagan et al., 2016). Our results show that determining the preferred HR characteristics based on the first established HR can create a misleading picture of what the optimal HR of the species is. This is especially so given that some individuals performed

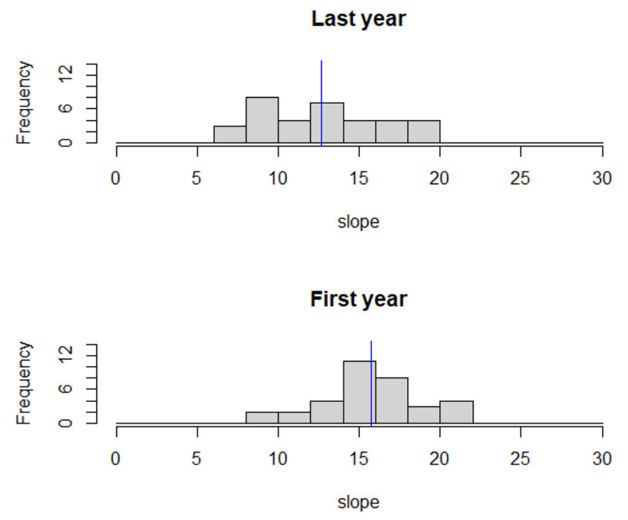

**FIGURE 5 |** The distribution of the average slope (in degrees) for the 90% isopleth of individual home ranges. The blue line represents the study area mean slope. Mean slope was significantly lower during the last year of tracking compared to the first (weighted *t*-test: $p < 0.001$).

significant shifts only in the second year after HR establishment. If the fallow deer home range preferences would have been determined based on first-year home range characteristics, it would have seemed that they do not require open pastures within the core of their home range which would disagree with the ecophysiology of the species (Hofmann, 1989). This emphasizes the importance of long-term monitoring of translocated animals, even when this monitoring is of low temporal resolution.

Initially, we suspected that the HR shifting pattern we identified was indicative of the existence of an optimal species HR structure. We predicted it takes a few years for the animals to be able to perfect their home range's composition in a way that will express the optimal HR for the species. Our results however suggest that the opposite might be true. While there are some general HR characteristics preferred by the species (i.e., woodland for safety and open pasture for foraging) we found that as time goes by, the variation within the population in terms of HR specifications increases rather than decreases. Thus, while there might be minimal HR characteristics required for the species, there is great individual variation in term of HR preferences which can take a few years to be expressed within the population due to the initial high-risk perceived by all individuals. In the first year after the initial HR was formed, individuals behaved similarly (i.e., there was lower variation in distributions) in that they all preferred refuge, while later when the animals became more familiar with their surroundings, individual variation in preferences regarding HR characteristics became more evident. That being said, it is noteworthy that while there might be a general optimal HR for the species, the animals cannot always achieve it because they are limited by what is available to them in the vicinity of the HR and that the initial formation of a HR is the outcome of a heuristic process. Thus, although a species optimum may exist, it is in most cases not attainable or detectable due the variability of the landscape and individual animal variance, respectively.

The presence of conspecifics can have a great impact on the spatial behavior of HR establishments and shifts (Seigle-Ferrand et al., 2021). Multi model inference on the overall shifting trend showed that the interaction between the time passed since release and the overall number of releases (our best proxy for density/number of individuals in the area) explained our observed pattern the best. Thus, while the time the animal spends in the environment is negatively correlated with the shifting of the HR, the density of conspecifics has an effect as well. Deer are a semi social animal which can be attracted by the presence of conspecifics (Fletcher, 2007). Thus even as density increases in the early years following reintroduction onset, it is expected that newly released females will establish a home range with little intraspecific agonistic pressures and may in fact stabilize the HR faster (by using the presence of other conspecifics as a cue) but further away due to a smaller number of available sites (Dolev et al., 2002; McNicol et al., 2020). As densities near the release site approach saturation newly released individuals will be pushed further away and will establish a HR at the edge of the newly formed population's range (Sjoasen, 1997), in an area where competition is lax enabling them a similar flexibility in HR adjustments as previously released conspecifics.

## CONCLUSIONS

Newly formed home ranges of reintroduced Persian fallow deer tend to be dynamic and continue shift for several years after initial establishment. These shifts are toward the inclusion of better foraging habitat such as open pastures in lieu of the safer woodlands. As the need for safety due to lack of familiarity of the landscape declines with time, individual variation in HR structure increases. These findings point to the importance of refuge in areas selected for reintroduction of prey species and agrees with the notion that predation is a serious obstacle to translocation success (Berger-Tal et al., 2020). The process of home range shifting provides an important insight into the interaction between translocated animals and the new landscape they confront and can help guide adaptive management protocols and conservation decision making.

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## ETHICS STATEMENT

Ethical review and approval was not required for the animal study because All reintroduced animals were handled by the Israeli Nature and Parks Authority.

## AUTHOR CONTRIBUTIONS

SB-D and AD collected the field data. MM-C analyzed the data with inputs from SB-D, OB-T, DS, and OS. MM-C led the writing together with DS and OS. All authors contributed to further drafts and approved the final version.

## FUNDING

The reintroduction programs in Israel are run and funded by the Israeli Nature and Parks Authority.

## ACKNOWLEDGMENTS

We would like to give a special thank you to Arnon Tsairi for his invaluable help with the analysis in ArcGIS. We would also like to thank Andrew Sussman, Amir Perelberg, and Roni King for their help and support in this project.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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in Conservation Science

HYPOTHESIS AND THEORY
published: 18 October 2021
doi: 10.3389/fcosc.2021.714580

# Finding a Home: Stopping Theory and Its Application to Home Range Establishment in a Novel Environment

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Familiarity with the landscape increases foraging efficiency and safety. Thus, when animals are confronted with a novel environment, either by natural dispersal or translocation, establishing a home range becomes a priority. While the search for a home range carries a cost of functioning in an unfamiliar environment, ceasing the search carries a cost of missed opportunities. Thus, when to establish a home range is essentially a weighted sum of a two-criteria cost-minimization problem. The process is predominantly heuristic, where the animal must decide how to study the environment and, consequently, when to stop searching and establish a home range in a manner that will reduce the cost and maximize or at least satisfice its fitness. These issues fall within the framework of optimal stopping theory. In this paper we review stopping theory and three stopping rules relevant to home range establishment: the *best-of-n rule*, the *threshold rule*, and the *comparative Bayes rule.* We then describe how these rules can be distinguished from movement data, hypothesize when each rule should be practiced, and speculate what and how environmental factors and animal attributes affect the stopping time. We provide a set of stopping-theory-related predictions that are testable within the context of translocation projects and discuss some management implications.

**Keywords: movement ecology, stopping rule, search theory, behavioral types, translocation, dispersal**

**Edited by:**
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*Society for the Preservation of Endangered Carnivores and Their International Ecological Study (SPECIES), United States*

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**Specialty section:**
*This article was submitted to Animal Conservation, a section of the journal Frontiers in Conservation Science*

**Received:** *25 May 2021*
**Accepted:** *10 September 2021*
**Published:** *18 October 2021*

**Citation:**
*Saltz D and Getz WM (2021) Finding a Home: Stopping Theory and Its Application to Home Range Establishment in a Novel Environment. Front. Conserv. Sci. 2:714580. doi: 10.3389/fcosc.2021.714580*

## INTRODUCTION

For mobile, sentient animals moving through an air-, sea-, or landscape with some level of predictability, knowledge is a major determinant of fitness. This knowledge pertains to where and when resources, threats, and refuges exist, promoting foraging efficiency and consequent fitness. Devoting time to learning comes at the cost of other fitness-related activities, thereby generating an exploration-exploitation dilemma (Berger-Tal et al., 2014). Familiarity with the landscape is therefore a key contributor to fitness because it reduces the necessity for searching and learning, allowing more time to be devoted to exploitation. Consequently, in most species, individuals will tend to establish residency in a given space, referred to as its home range (HR, Spencer, 2012).

Typically, animals venture into an unfamiliar environment during a post-natal dispersal phase, which in some species may be soon after hatching/birth while in others at time of sexual maturation. Occasionally, however, animals may find themselves in a novel environment due to external factors—e.g., translocation or forced abandonment of a former HR. Regardless of the cause, the animal becomes nomadic, searching for a new space in which to establish a HR. The establishment of a HR in unknown space is essentially a heuristic problem: as the animals explores the environment it accumulates information based on which, at some point, it should transition from a nomadic phase to a residential phase. During the nomadic phase a relatively high proportion of the individual's time needs to be devoted to exploration, while in a residential state a much greater proportion of its time can be devoted to resource exploitation.

The decision to switch phases should be based on information accumulated during exploration and previous past-experience. The timing of the transition between the two phases is important. On the one hand continued searching in an unknown landscape has considerable costs in terms of finding resources, exposure to risk, intra-specific competition (forgoing a potential HR that is then occupied by a conspecific), and even postponed reproduction. On the other, stopping the search and establishing a HR carries a cost of missed opportunities—i.e., missing out on a better HR had the search continued. Thus, the establishment of a HR is essentially a stopping problem (Hill, 2009), where an individual attempts to maximize or, at least, satisfice its fitness (i.e., additional HR improvements do not actually improve its fitness) by deciding how to search and when to stop searching and establish a HR.

Successful translocations offer a unique opportunity to study ecological processes such as range expansion, density dependence, and learning behavior (Sarrazin and Barbault, 1996). Specifically, translocated animals are released into a novel environment that in many instances is vacant (reintroductions) or nearly vacant (restocking) from conspecifics. The translocated individuals must then explore the landscape and eventually establish a HR. Studying the movement and behavior of these individuals can elucidate the stopping rules that are used to establish a HR and the conditions that impact the timing of stopping. These conditions include individual animal attributes, landscape characteristics, and population density effects resulting from the growth of the newly established population.

In this paper, we briefly review stopping theory and relevant rules and present a general model for the case of an animal searching for a place to establish a HR in an unknown environment. We then discuss various key factors that should, in theory, impact the stopping decision in a predictable manner and delineate potential scenarios where these predictions can be tested as a part of translocation projects.

## STOPPING THEORY

Optimal stopping theory addresses the problem of when to stop a current activity and take a particular action so that expected net rewards are maximized. As such, it underpins many animal-decision-making processes. Thus, a number of behavioral transitions in animals can be studied and explained within the framework of optimal stopping theory. Examples include HR establishment, optimal foraging and patch-use theory (when to leave a patch), mate choice (particularly females deciding when to accept a particular suitor), and predation procedures (e.g., when to give up a chase). The decisions are typically based on experience and conditions (both the animal's and the environment's) from which the expected future return is estimated and the costs and benefits of executing or forgoing the action at a given time are assessed. However, while the costs and benefits of the current activity are mostly experienced at present, the costs and benefits of stopping are a projection into the future and involve levels of uncertainty that may be reduced with additional knowledge acquired through continued search. Thus, a key issue in many stopping behaviors is the search time needed to infer a reliable assessment of the long-term cost and benefits of continuing the current activity vs. stopping and establishing a HR.

Numerous formulations of stopping theory exist (e.g., Ferguson, 2006 Chapter 1), most focused on non-ecological problems. Depending on the type of data and uncertainties, several have varying relevance to ecology and can help typify the specific case of establishing a HR in a novel environment. Common examples are:

- Marriage/secretary problem (aka best choice problem). The object of this problem is to select the best (according to an *a priori* defined criterion) of a set of *n* objects (e.g., potential spouses/interviewees). The rule is that these objects must be assessed in some arbitrary sequence, with a decision on whether to accept the object and stop the process, or to move onto the next object being required to be made after each assessment (so there is no going back). Theory demonstrates that the optimal procedure is to peruse the first $n/e$ ($\sim 0.368n$) objects and then select the first object after this that is better than every object assessed thus far. This procedure selects the best object 37% of the time, though could infrequently result in the last object being a forced selection, no matter its value. A parallel ecological example would be mate choice at a lek where a given number of males ($n$) compose the lek and a female must evaluate the males and select one to mate with. The optimum, in terms of cost (time invested in evaluation) and benefit (quality of the male) would be to evaluate a 0.368 proportion of the males and chose the next one that is better than all those previously evaluated.
- House Selling problem (aka job search problem). An owner selling a house receives one offer per unit time for all time into the future (infinite horizon). However, keeping the house on the market has a cost (advertising, mortgage repayments, lost investment opportunities). Once an offer is received a decision must be made whether to accept or keep searching. A rejected offer cannot be reconsidered. The longer one waits, the higher the cost, but the opportunity to get a better offer than the one rejected exists. If one expects the value of an offer at time $t = 0,1,2,\ldots$, denoted by $X_t$, is known to be randomly distributed on [0,1], and the cost per unit time is $c<1/2$, then the optimal solution is to choose $X_t$ the first time it exceeds $(1\text{-}(2c)^{1/2})$. In limited sense, this scenario can be applied to a sit-and-wait predator deciding whether to forgo a small prey and wait while its hunger increases for a larger prey to arrive or to consume the current prey and then set out to find a new ambush spot.

- Job Search problem. This is a generalization of the house selling problem to one that involves several factors that need to be considered each time (e.g., salary, commuting distance, work environment) where some of these parameters may not be easily quantifiable. The optimal solution to this problem varies with $n$ (Mazalov and Konovalchikova, 2015). In an ecological context, predators may confront a similar problem when deciding whether to chase a particular quarry (e.g., size of prey, speed of prey, distance to prey, features of the terrain) or continue to search for a better quarry.
- The Parking problem. An individual wants to find the closest parking spot to a particular location (i.e., the value of the spot is its proximity to this location). There are several variants of this problem, one of ecological interest being that if an individual cannot find a parking spot close the location, a revisit to those further away may reveal, with some increasing probability over time, that these previously vacant spots have now become occupied. Solutions for particular formulations of this problem are found in Tamari (1982). In ecology, this problem has similarities to post-natal dispersal in territorial species where available vacant territories are quickly occupied by conspecifics and on a first-come-first-serve basis (i.e., scramble competition).

Although not a necessity in stopping theory, in the above examples the *current activity* is a search process. Thus, stopping theory is strongly linked to search theory. However, search theory is a wider concept despite this term often being interchangeably used with stopping theory (Lippman and McCall, 2001), and even being specifically applied to the Job Search problem.

In ecology, search theory is predominantly associated with movement patterns within the context of foraging theory (Bartumeus and Catalan, 2009) and typically is not associated with stopping theory. However, although not referred to by name, stopping theory is commonly used in behavioral ecology. Patch-use, in particular, is noteworthy. Here, an individual foraging in a patch slowly exhausts available resources and the effort of finding those remaining increases with time. When the costs of continued foraging in the patch equal or exceed the benefits gained from continued foraging, individuals should cease feeding in the patch and abandon it. The resource density in the patch at this stopping point is termed the *giving-up-density* (i.e., the amount of food left in a patch at the point when the forager leaves it; Brown and Kotler, 2004; Makin et al., 2020). In this formulation of stopping theory, the search area is restricted, the number of objects ($n$) is fixed (finite horizon) but unknown, and the objects sought are removed (consumed) from the available pool, so search effort increases with time.

## THE HOME RANGE ESTABLISHMENT PROBLEM

As with the particular problems discussed above, the current activity of individuals in the HR Establishment Problem is a search process, but it differs in presenting a more complex scenario. The HR Establishment Problem is similar to the Job Search problem in that $n$ is not fixed (the animals may, in theory, keep searching indefinitely), several factors are involved, and evaluating the quality of objects is a complex and imperfect process. However, it also bares resemblance to the Parking Problem in that the competition may be on a first-come-first-served basis. Further, the search associated with HR establishment bears a high cost due to elevated risk of predation and inefficient foraging resulting from lack of familiarity with the landscape. In the case of translocations (as opposed to natal dispersal) there is another key difference. This is the lack of residence from which to carry out the search and no familiarity with the immediate surroundings, although habituation within a local enclosure prior to release may enable some familiarity. Hence, we view HR Establishment as a unique stopping problem with unique attributes, resulting hypotheses, and testable predictions. Empirical studies addressing these issues can provide insight into the process and may have management implications.

## STOPPING RULES IN HOME RANGE ESTABLISHMENT

Various rules for assessment and decision making in stopping problems have been proposed. Some may be applicable only to specific problems. Their efficacy may vary depending on the specific conditions and attributes of the decision maker and the environment in which the problem is set. The following three appear particularly relevant to HR establishment (Luttbeg, 2002):

- *Best-of-n rule*: The animal should assess $n$ options and can select the best of these. In practice this means being able to return to any of the formerly assessed options. The optimal value of $n$ depends on the cost of the search and the variance in the quality of options.
- *Threshold rule*: Based on experience (a set of $n$ previous HR assessments), the individual sets a threshold, and chooses the next encounter that exceeds this threshold. In practice this is best applied under a no return situation that precludes a best-of-$n$ rule. The *secretary problem* is a specific case of the threshold rule fixed *a priori* at $0.368n$.
- *Comparative Bayes rule*: The information obtained on each option is assumed to be incomplete and the animal, after a relatively cursory study of $n$ options, will return to gather further information on the better ones and then re-evaluate. This tactic reduces the effort involved in the initial exploration and if revisiting previously investigated options for re-evaluation is possible, is superior to the above rules (Luttbeg, 2002).

The specific stopping rule and timing for optimizing or satisficing HR establishment are expected to depend on the species characteristics, environmental conditions, and individual-animal attributes and perceptions. Two basic questions of ecological interest can be formulated regarding HR establishment: Q1. What conditions favor the use of which specific stopping rule? Q2. When to stop and establish a HR—or, more pointedly, how are varying environmental conditions, animal traits and experience expected to influence the time to HR establishment?

From these questions we formulate specific predictions that are testable in the field. We note here that we consider the stopping time as the point at which an animal sets up its initial HR and does not include partial shifts and improvements of the HR that occur after settling (Maor-Cohen et al., 2021).

## Q1. What Conditions Favor the Use of Which Specific Stopping Rule?

The future fitness associated with the various stopping rules depends largely on whether random re-encounters are possible (i.e., whether there is a finite set of options) and whether animals can resample previously encountered options (Luttbeg, 2002). These issues underpin potential differences between HR establishment under natural conditions and planned translocations. Seeking to establish a new HR under natural conditions is predominantly a phenomenon associated with post-natal dispersal and, to a lesser extent, catastrophic events such as fire. In both cases the availability of vacant HRs is expected to be limited, especially in vertebrates that tend to be "*K*-selected" and which, unless reduced by stochastic environmental conditions or heavy hunting, their population is near carrying capacity (McCullough, 1992). Thus, in contrast to the typical translocation, animals dispersing on their own initiative within relatively undisturbed populations are expected to confront a landscape nearly saturated with conspecifics and fewer opportunities for HR establishment. For example, in large territorial-predators adult survival is expected to be high, and the dynamics are dictated mostly by reproductive success and post-natal survival (Kapota and Saltz, 2018) so vacant territories are expected to be rare. Further, given that post-natal dispersal occurs within a narrow window of time, the landscape during the dispersal season will typically be flooded with individuals seeking to establish a HR (e.g., Hawlena et al., 2010). Consequently, the probability of returning to a previously evaluated area and finding that it had not yet been occupied is low. Hence, post-natal dispersers in such species are expected to rely on the *threshold rule* (e.g., Macdonald and Bacon, 1982). Although less restrictive, for individuals of non-territorial, semi-social species (such as many ungulates), establishing a permanent HR that likely overlaps with conspecifics, the conspecific saturation of the landscape during dispersal season is still expected to be a major factor.

By contrast, in "*r*-selected" species or, following a population crash, in species typified by slow growth rates, post-natal dispersers will find themselves in a relatively vacant environment where the probability is high of returning to previously explored sites and finding them still vacant. In such cases, the *best-of-n rule* or *Comparative Bayes rule* will be the better options. Further, the best of these two options will depend on whether the quality of the better sites can be reliably distinguished based on the initial exploration (thereby favoring the *best-of-n rule*) or further exploration is required (thereby favoring the *Comparative Bayes rule*).

The presence of conspecifics in sites targeted for translocation depends on the time, place, and purpose of translocations. For example, in reintroductions, individuals in the first wave of release will be confronted with a vacant environment, while later boost releases will experience an increasingly occupied landscape after successful establishment of initial releases. Thus, in reintroductions we may expect the stopping rule to shift from a *best-of-n rule* or *comparative Bayes rule* in early releases to a *threshold rule* in later releases.

Which rule is being practiced by specific individuals can be determined using high resolution movement tracks from GPS platforms. Specifically, the different rules can be distinguished by analyzing the movement trajectories of individual animals during the search phase and determining whether they revisited one or several sites before HR establishment and whether these revisits were associated with an area-restricted-search (Kapota et al., 2017). For example, individuals that: (i) settled in the last explored area without returning to any of the previous sites would be indicative of the *Threshold rule*; (ii) explored a set of potential sites and returning to the best one would be indicative of *Best-of-n* rule); (iii) settled after repeated returns to several sites would suggest the possible application of a *Comparative Bayes rule*.

Dispersal patterns will also be impacted by the starting conditions. Post-natal dispersers benefit from having a "home-base" (the maternal HR) from which to carry out pre-dispersal exploration (Debeffe et al., 2012) while benefiting from the safety offered by the maternal HR, in addition to acquiring a general understanding of the surrounding habitat characteristics from the maternal HR characteristics. This enables the animals to gain knowledge of the surrounding matrix from the safety of the maternal HR and return to it following exploratory foray in different directions—forming a start-like movement trajectory.

In translocation, animals can be released using an interim stage of adjustment by confining them to a habituation enclosure at the site of release (soft release) or released immediately on site (hard release). Soft releases enable individuals to gain some familiarity with the habitat and immediate surroundings. If soft releases provides some level of security, individuals (especially those belonging to species subject to predation) may view the release location as a safe "home-base" from which to carry out exploration forays similar to post-natal dispersal. On the other hand, hard-release individuals will not be familiar with the release site and are expected to move away immediately in search of a HR. Studies have shown that in soft-releases individuals tend to establish a HR closer to the release site (e.g., Attum and Cutshall, 2015). Regardless of the type of release, the criteria for assessing what stopping rule is being practiced still hold. Although data for determining which stopping rule is practiced clearly exist, in numerous previously reported translocation studies these ideas remain to be tested.

## Q2. When to Stop Searching and Establish a Home Range?

The optimal stopping time (i.e., the point at which the animal decides to establish a HR) is the outcome of two cost functions: (i) the cost of continuing the search (not stopping); and, (ii) the missed opportunity costs (MOC, discussed more fully below) associated with stopping the search. This holds for all three rules.

The costs associated with continued search are those resulting from movement through an unfamiliar environment, such as elevated risk, difficulty in finding resources, time devoted to learning the landscape, and forgoing breeding opportunities. Generally, these costs are expected to be constant over time, and the accumulated costs, therefore, are expected to increase linearly with time from the onset of the search.

MOC are those associated with foregone alternatives when stopping the search. MOC can only be assessed by the animal through exploring the novel landscape and forming some database of availability. As information is accumulated, the relative contribution of each additional bit of information declines so the MOC function is expected to be a positive, monotonically decreasing function of search time (e.g., a negative exponential function). These costs are also reduced with competition because the probability of realizing the benefits of the forgone alternatives declines as they become occupied by conspecifics. The optimal stopping time is, therefore, the point at which a weighted sum of search and missed-opportunity costs are minimized (**Figure 1**; the two costs have been reduced to the same units so they are given the same weightings).

The exact formulation of cost-of-search and MOC functions depends on conditions, including the expected quality of the environment and its variance in terms of food and shelter, presence of conspecifics, predation risk, and individual animal attributes such as age, body conditions, gender, and behavioral type. Based on these, numerous hypotheses can be formulated. Translocations, and specifically reintroductions, offer an opportunity to test specific hypothesis derived predictions concerning the HR Establishment problem within the stopping theory framework using comparative designs:

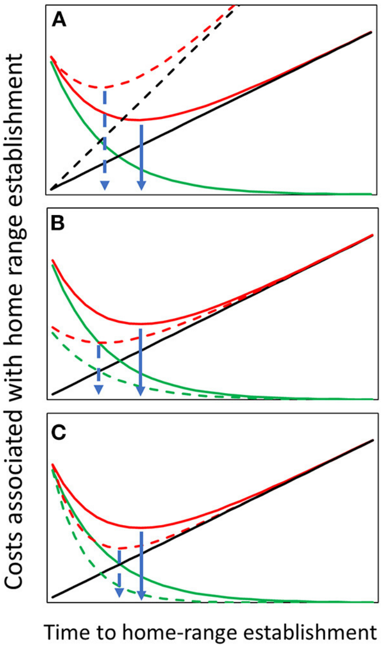

**FIGURE 1 |** The two costs involved in establishing a home range: search costs in black and missed opportunity costs (MOC) in green. Search costs increase with time. MOC increase with the variability of habitat conditions over space and decrease with time as the animal's assessment of space improves. The sum of both costs is in red, and the optimal stopping time is when this sum is minimized (indicated by the blue arrows). Each of the three sub-figures **(A–C)** compares the stopping time between two formulations of one of the cost functions. **(A)** If search costs increase (black dashed line) optimal stopping time is reduced. **(B)** If habitat variability over space is reduced (green dashed line) stopping time is reduced. **(C)** If competition is high (i.e., the better areas become unavailable) the variance in potential habitats declines reducing optimal stopping time.

- Quality of the environment and risk of predation. As quality of the environment decreases or risk of predation increases, the cost of continued search increases so the function becomes steeper, and the optimal stopping point is predicted to be earlier (**Figure 1A**). This can be tested by comparing translocations between habitat types or in the same area between seasons.
- Variance in habitat quality over space. As the variance of the quality of potential HRs over space declines, the MOC decline (**Figure 1B**) and expected stopping time is shorter.
- Presence of conspecifics. This depends on the social structure of the species. In territorial species (either solitary of group), as the presence of conspecifics increases, fewer opportunities become available, the better patches are expected to be unavailable causing the mean value of a potential HR and the variance around that mean to decline. Thus, as we see in **Figure 1C**, time to stopping shortens. Further, the probability of finding a previously visited option still unoccupied declines, so using the Threshold Rule becomes the better option. If this is combined with the decline in the variance of available HRs and lower MOC, stopping times should become particularly short. In semi-social animals that are non-territorial, the shorter stopping time may be confounded because the presence of resident conspecifics may also be used as a cue to habitat quality, potential mates, and a safer and quicker way to study the habitat by following them. Thus, in translocation projects involving multiple releases, individuals from later releases are expected to establish a HR earlier (Dolev et al., 2002). This also points to the difficulty in evaluating this response under conditions where the landscape is nearly saturated and stochastic processes in the form of the chance of finding a vacant spot overwhelm the process. As a result, few individuals may be lucky to establish a HR early on while others will have to perform a long-distance search (Lutz et al., 2015), thereby making the variance on the stopping time too large to draw any conclusions.
- Body condition. Individuals in better condition (larger/heavier) have reduced risk of starvation and depredation. They thus are expected to devote more time to search and will travel farther in an effort to find a better HR. This will result in a later stopping time (Debeffe et al., 2012). Differences will be similar to those depicted in **Figure 1A** but will be evident among individuals in the same translocation having different body condition (as determined

prior to release by one of existing indices of body condition; see Servello et al., 2005).

- Behavioral types, sex, and age. Within a species, individuals vary in their behavior according to age, sex, and behavioral types. These behavioral tendencies—whether active, bold, exploratory, sociable, or aggressive—have been shown to be relatively consistent within individuals over a given time period and in different contexts (Réale et al., 2007). There generally appears to be a linkage between these traits—more active individuals tend to be more explorative, more aggressive, and bolder. For example, in roe deer (*Capreolus capreolus*) dispersers explore more than philopatric individuals (Debeffe et al., 2013), and bold, more active amphibians tend to explore more and travel farther than their counterparts (Kelleher et al., 2018). The bolder behavioral types are expected to perceive the novel environment as less threatening and evidently assume better opportunities (i.e., greater MOC). Thus, bold individuals are expected to have a later stopping times. Younger animals with greater life expectancy also have higher MOCs, as do males in polygynous species and, thus, are also expected to have delayed stopping times.

Such studies can provide insight into HR ecology and species-specific behavioral ecology which may also have management implications. Testing these predictions can be done by determining individual-based time-to-settlement analyses using, for example, the distance from the release location (or some other movement parameters) as a function of time. This could be done using a two-segment broken stick regression function that separates the search and HR residency movements (McNicol et al., 2020). The time to establishment of an individual is determined as the point the two segments meet. The time to establishment can then be used as a dependent variable in analyses assessing the impact of the various environmental and individual animal attributes on stopping time.

## MANAGEMENT IMPLICATIONS

Translocation projects are typified by a high rate of failure, with the behavior of the released individuals being one of the key determinants of success (Berger-Tal et al., 2020). The process requires individuals to adapt rapidly to a novel environment and go through a behavior-adjustment process termed post-release behavioral modification (PRBM; Berger-Tal and Saltz, 2014). PRBM is dependent not only on objective environmental conditions and animal attributes, but also on how the animal perceives its own condition and surroundings.

The establishment of a HR is a vital step in this process because familiarity with the landscape is an important contributor to an animal's fitness. HR establishment is commonly considered an early indicator of translocation success (Yang et al., 2018; Briers-Louw et al., 2019) and is a parameter frequently assessed in reintroductions. Delayed HR establishment following the initial releases in a reintroduction delays recruitment and decreases survival of the released individuals, thereby slowing the growth of the population and subjecting it to stochasticity-related risk of elimination. Understanding the factors that influence the timing of HR establishment (i.e., stopping time) and validating the aforementioned predictions can help design translocation protocols and achieve better results. Not all factors affecting stopping time are manageable, but several can be manipulated to accelerate HR establishment. These include individual animal attributes such as behavioral types, age, and body condition. They also include release protocols such as timing and methods of release. Notwithstanding, it is important to realize that certain traits that favor early stopping time may also have negative aspects. For example, older animals are expected to show shorter stopping time due to lower MOC, but their life expectancy is shorter (hence the lower MOC). Similarly, release in the low-productivity season may reduce stopping-time; but it may impact the animal's condition and the resulting long-term dynamics of the population.

Individual personality and the tendency to disperse are correlated with bold individuals being more prone to disperse further (Cote et al., 2010), which translates into a later stopping time. More specifically, bold individuals perceive risk as being lower and MOC as being higher. Thus, translocating bolder animals may delay the establishment of a permanent resident population. This, in turn, may weaken propagule pressure and lower the probability of translocation success. Alternatively, translocating timid individuals may result in faster settlement in and around the release site, but continued releases of such individuals in the same location may cause "piling" near the release site. This would occur because the search and MOC costs are evaluated by the animals based on landscape conditions and how they vary over space. An individual released into an area that is locally saturated would be ignorant of the vacant landscape further from the release site. Near the release site the individual would experience few opportunities (vacant spots) with little variance between them (only the poorer spots remain unoccupied). With the perception of few opportunities, stopping-time would be shorter than needs be, resulting in "piling" that may well reduce population performance. It follows that some combination of both types may improve translocation results (Watters and Meehan, 2007). Specifically, varying the ratio of timid and bold individuals in subsequent releases may be optimal if early releases include a greater proportion of timid individuals than later releases. Empirical data, however, are needed to support this hypothesis.

Simulating future population performance can benefit the planning of translocations, specifically in the context of reintroductions (Saltz, 1998; Maor-Cohen et al., 2020). Incorporating animal and environmental attributes that affect the timing of HR establishment into population projection models may aid in deciding the composition of individual attributes and release methods that will maximize future population performance.

The ideas presented herein highlight the importance of post-release monitoring and new research opportunities regarding the impact of various parameters on stopping time because, as we have argued above, stopping times affect individual movement patterns with consequences for population viability. Findings from studies testing the predictions put forth in this paper can later be incorporated into meta-analyses supporting the formulation of hypotheses and the articulation of paradigms that can then be incorporated into translocation protocols.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

## AUTHOR CONTRIBUTIONS

DS and WG developed the ideas and wrote the paper. All authors contributed to the article and approved the submitted version.

## ACKNOWLEDGMENTS

We thank O. Berger-Tal and two reviewers for constructive criticism.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer DM declared a shared affiliation with one of the authors, DS, to the handling editor at the time of review.

frontiers
in Conservation Science

ORIGINAL RESEARCH
published: 03 December 2021
doi: 10.3389/fcosc.2021.718562

# Loss of Predator Discrimination by Critically Endangered Vancouver Island Marmots Within Five Generations of Breeding for Release

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Conservation translocations, which involve the intentional movement and release of organisms for conservation benefit, are increasingly required to recover species of conservation concern. In order to maximize post-release survival, and to accomplish conservation translocation objectives, animals must exhibit behaviors that facilitate survival in the wild. The Vancouver Island marmot (*Marmota vancouverensis*) is a critically endangered endemic in Canada which has been captive-bred for 24 years for reintroductions and reinforcements that have increased the wild population from ∼30 to more than 200 individuals. Despite this success many marmots are killed by predators after release and predation represents a major hurdle to full marmot recovery. To better understand if captive-bred marmots are prepared for the novel environment into which they will be released, and to determine whether such suitability changes over time, we presented taxidermy mounts of mammalian predators and non-predators to marmots that were wild-caught, and captive born for between one and five generations. We also examined mortality of offspring from marmots we tested that had been released to the wild. A minimum of 43% of offspring were killed by predators in the wild over 17 years, most by cougars. Marmots in captivity generally responded to taxidermy mounts by decreasing foraging and increasing vigilance, and overall responded more strongly to predators than non-predators, especially wolves. However, marmots in captivity for more than two generations lacked discrimination between cougars, non-predators, and controls, suggesting a rapid loss of predator recognition. This study was only possible because predator-recognition trials were initiated early in the conservation translocation program, and could then be repeated after a number of generations. The finding that changes occurred relatively rapidly (within five generations during which changes in genetic diversity were negligible) suggests that behavioral suitability may deteriorate more rapidly than genetics would suggest. Strategies addressing potential behavior loss should be considered, including sourcing additional wild individuals or pre-release training of captive-born individuals. Subsequently, post-release survival should be monitored to determine the efficacy of behavior-optimization strategies.

**Keywords: conservation translocation, reintroduction, anti-predator, behavior, vigilance, captive breeding**

**Edited by:**
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**Reviewed by:**
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**Specialty section:**
*This article was submitted to Animal Conservation, a section of the journal Frontiers in Conservation Science*

**Received:** *01 June 2021*
**Accepted:** *29 October 2021*
**Published:** *03 December 2021*

**Citation:**
*Dixon-MacCallum GP, Rich JL, Lloyd N, Blumstein DT and Moehrenschlager A (2021) Loss of Predator Discrimination by Critically Endangered Vancouver Island Marmots Within Five Generations of Breeding for Release. Front. Conserv. Sci. 2:718562. doi: 10.3389/fcosc.2021.718562*

# INTRODUCTION

With one million species at risk of extinction (IPBES, 2019), conservation interventions are critical to retain biodiversity. Conservation translocations involve intentional movement of species from one location to another to restore populations and ecosystems (IUCN/SSC, 2013) and have improved the conservation status of many species (Hoffmann et al., 2010, 2015). There is a growing realization that knowledge of behavior is important for successful conservation science (Greggor et al., 2016) which is especially true for translocations (Berger-Tal et al., 2020). In North America alone, 58% of species in conservation translocation programs have captive breeding as a component of the program (Brichieri-Colombi et al., 2018). However, captive breeding for translocation creates significant challenges associated with managing the genetics, fertility, health, behavior and reproduction of extremely small populations.

Post-release behavior can affect the fate of individuals in many ways and thus can impact the ultimate success of a translocation project (Berger-Tal et al., 2020). Mortality in the wild due to predation post-release is a major challenge (Moseby et al., 2011; Brichieri-Colombi and Moehrenschlager, 2016), and especially plagues individuals released from captive populations (Griffin et al., 2000; Harrington et al., 2013). Wild animals entering a conservation breeding program are exposed to a novel environment, one where they are typically raised in a relaxed selective environment with abundant food, no mate competition, and no natural predators where they will likely become naïve to conditions in the wild (i.e., captive selection; Frankham et al., 1986). Further, the risk of captive selection increases with the number of generations a population has remained in captivity (Swaisgood, 2010). Once captive-born individuals are released into the wild they are exposed to a novel environment as well; one where they must learn to forage and evade predators.

Many animals make tradeoffs between remaining vigilant to avoid predators and focusing attention on other fundamental aspects of life, such as foraging (Houston et al., 1993). Life in captivity will affect these tradeoffs as the frequency with which animals encounter predators influences how strongly they will respond to predators at each encounter. Individuals that are infrequently at high risk of predation will respond more strongly on those rare occasions when predators are present (i.e., the Predation Risk Allocation hypothesis; Lima and Bednekoff, 1999). Therefore, one effect of a life in captivity without predators may be that individuals increase their responses to predators over time. While increasing vigilance can be beneficial to avoid predators, it can come at a cost, as animals may need to reduce other behaviors, like foraging (Fortin et al., 2004), in order to allocate more time to vigilance. This potential shift in behavior should be of concern for any captive breeding program that plans to reintroduce animals back to the wild. Conservation breeding and reintroductions are often long-term endeavors with many programs lasting for decades [e.g., the Arabian Oryx (*Oryx leucoryx*) 40 years, (Islam et al., 2013); whooping crane (*Grus americana*) 70 years, (Barrett and Stehn, 2010); and black-footed ferret (*Mustela nigripes*) more than 30 years, (Jachowski et al., 2011)]. Given the length of these programs and the possibility of captive selection it is prudent to monitor behavior within captive and wild populations of conservation translocation programs over time.

Conservation translocations should include behavioral monitoring (IUCN/SSC, 2013). In addition to long-term monitoring, experts have been calling for increased use of rigorous experimental design and evidence-based decisions within conservation translocation science (Seddon et al., 2007). Replicating studies of endangered or threatened species is not always possible for many reasons, in part due to resource limitations and small samples sizes (Shaw et al., 2021), making those few studies that are possible even more valuable. However, studies with small sample sizes must be interpreted with caution and statistical analyses must be applied appropriately (Bissonette, 1999).

Vancouver Island marmots (*Marmota vancouverensis*; hereafter, marmots) are social, ground dwelling, rodents endemic to Vancouver Island, Canada and are listed as Critically Endangered on the IUCN Red List (Roach, 2017). In 1997 a conservation breeding program was deemed necessary to help save the species (Casimir et al., 2007), which had declined to ∼30 individuals in the wild. The wild population of marmots has increased to ∼200 individuals through reintroductions from 2003 to 2020 (Marmot Recovery Foundation, 2020) with an additional ∼100 currently in captivity. Recent studies have shown that predation is the leading cause of mortality for marmots in the wild and captive-born marmots have lower annual survival than wild-born marmots post release (Aaltonen et al., 2009; Jackson et al., 2016). Captive-born individuals may have reduced or altered predator recognition abilities or anti-predator behaviors as a result of their captive environment (McPhee, 2003; Blumstein et al., 2004). Indeed, Vancouver Island marmots remain vulnerable to predation by wolves, cougars, and golden eagles in the wild (Vancouver Island Marmot Recovery Team, 2017).

Between 2002 and 2004, Blumstein et al. (2006) tested captive marmots for their ability to discriminate between mammalian predators and non-predators. Behavioral observations indicated that wild-born and captive-born marmots were equally able to discriminate between predators and non-predators while in captivity (Blumstein et al., 2006). These findings were encouraging for the reintroduction program. However, the reduced survival of captive-born marmots relative to wild-born conspecifics (Lloyd et al., 2018) begs further research into their captive environment and behaviors. Even with higher post-release survival from a novel "stepping-stone" release approach, where individuals were released to a relatively safe and established site known for high survival, before being moved to a final release site, Lloyd et al. (2018) call for research as to how to best prepare marmots in captivity before reintroduction.

Here, we build on Blumstein et al. (2006) by repeating the previous study with new individuals including those that have been captive for additional generations. We seek to determine if there is a compounding effect on anti-predator behavior as marmots are in captivity for increasing generations. Additionally, we add a pilot study testing marmot discrimination between avian predators and non-predators. Given the marmots we test will be released to the wild or have offspring released, the way they respond to predators in captivity may, ultimately, influence species recovery. Being moved into a novel environment presents challenges for any animal, and this is particularly true when animals that have lived their whole lives in the relative safety of captivity are released into the wild. The objective of this study is to provide insight into the effect that multiple generations of captive living have on anti-predator behavior and the relationship between that behavior and potential mortality in the wild.

## MATERIALS AND METHODS

### Study Species and Location

Marmots live in polygynous colonies with one or more family groups, are semi-fossorial, and hibernate in burrows for over 200 days each year. Female marmots can breed as early as 2 years of age, but typically first reproduce when 3 or 4 years old. Marmots in the wild have been recorded living 10 years (Bryant, 2005) and in captivity marmots live up to 14 years. Marmots are found in sub-alpine meadows at high elevations (COSEWIC, 2008).

Predator discrimination trials were conducted from July–August each year, from 2016 to 2018 following Blumstein et al. (2006). Marmots were tested at the Devonian Wildlife Conservation Center (DWCC), an off-site conservation breeding facility of the Calgary Zoo located ∼30 km south of Calgary, Alberta, Canada. Marmots were housed in enclosures that had both indoor and outdoor sections. Marmots were constrained to outdoor sections of their enclosures and only one marmot was allowed into the outside section at a time so that marmots were not responding to their neighbors. The outdoor section was a yard (either 3.7 × 1.8 m or 3.6 × 3.4 m) giving the marmots a view of the surrounding area and adjacent enclosures. Each outdoor space had three hay bales; two bales on the ground with a gap between them, and a third bale on top. The gap between the two bales on the ground left a space large enough for the marmot to enter where it could hide. Barriers were placed between adjacent outdoor enclosures to ensure that each marmot was only exposed to experimental stimuli at the appropriate time. Video cameras (HikVision 3 Megapixel Ultra HD IP Camera; Bordo Security, Calgary) were installed in each outdoor enclosure to record the marmot's behavior. For smaller enclosures, one camera was mounted in the center of the roof, whereas, for larger enclosures two cameras were mounted at the top on opposite corners. All marmots that were available for testing from this captive population were included. To reduce stressors, we did not test animals that reproduced in a given year.

### Mortality in the Wild

The majority of captive-born marmots are released onto mountains within the Nanaimo Lakes and Strathcona regions on Vancouver Island with some being released into extra-liminal colonies (Jackson et al., 2016). As part of the overall recovery program for marmots, post-release survival monitoring is conducted every year by the Marmot Recovery Foundation. Marmots are tracked post-release using VHF telemetry and whenever possible, remains are recovered to determine the cause of mortality (Jackson et al., 2016; Marmot Recovery Foundation, 2020).

### Predator Discrimination

Marmots were exposed to taxidermy mounts of predators and non-predators; see Blumstein et al. (2006) for photos of mounts. Each mount was placed on a wheeled cart and rolled along a track ∼2 m from the marmots' enclosures. Blinds were placed at each end of the track which hid the taxidermy mount from the marmot's view before a trial was started and in which an observer could hide and pull the cart along the track via string and pulley reel. The track and blinds were set up at least 2 days before the trials were run to allow the marmots to acclimatize to the new equipment. Following Blumstein et al. (2006), each target marmot was exposed to four mammalian stimuli (marmot, goat, wolf, and cougar), and two procedural controls-the cart alone, and a blank where no stimulus was presented. These mammalian taxidermy mounts, cart, and tracks were the same as used in the previous study and each stimulus was presented to each marmot a single time. Starting in 2017, we also included four avian stimuli mounted in a perched position and tested the avian mounts on 10 marmots, see **Supplementary Materials** for details on avian trials.

Trials were conducted in the mornings from 07:00 h to noon, or until the temperature reached 25°C. For each trial the marmot was baited (with carrots, lettuce, or leaf-eater biscuit) to a central location in their enclosure on top of the stacked hay bales. Trials started once the marmot was calmly eating. Stimuli were pulled at a consistent rate until directly in front of the target marmot's enclosure, where they remained for 1 min. Subsequently, each stimulus was pulled into the researcher's blind and out of sight of the target marmot. The marmots were recorded on video for 1 min before each stimulus was presented, for 1 min with each stimulus in sight, and for 2 min after the stimulus was returned to a blind. The stimuli were presented to the marmots in a randomized order based on a Latin square design (Bradley, 1958). We waited at least 1 h between tests of marmots that formed a mating pair. Each marmot was exposed to a maximum of two stimuli per day, with the second stimulus being presented only after the marmot's behavior returned to a natural baseline and at least an hour had passed since the previous presentation. If the target marmot alarm called during the stimulus presentation, we waited at least 30 min before testing the next marmot to minimize possible carry-over effects. Because this study was conducted over 3 years (2016–2018) not all marmots were exposed to all stimuli in the same year.

Videos were scored by an observer that was unaware of which marmot they were watching and which stimulus was being presented. The videos were scored in JWatcher version 1.0 (Blumstein et al., 2020), and followed the same ethogram used by Blumstein et al. (2006). We focused on the proportion of time that marmots spent doing three sets of behaviors; (1) Foraging (head down ingesting food, or manipulating food with their paws); (2) Vigilant at the burrow or in the burrow (head raised, not manipulating food with their paws while standing near the burrow entrance or inside the pile of hay bales out of sight); and (3) High vigilance away from the burrow (standing on their hind legs and looking while more than one body length away from the burrow entrance).

## Data Analysis

We conducted statistical analyses in RStudio (RStudio Team, 2020) following Blumstein et al. (2006) and combined all marmots from Blumstein et al. (2006) and this study for analysis. We fitted mixed-effect models using the glmmTMB package (Brooks et al., 2017) assuming a beta distribution (logit link) for each of the three behaviors of interest (foraging, vigilance, and high vigilance). We divided marmots into three groups based on origin; wild caught, first and second generation captive born, and third, fourth, and fifth generation captive born. Furthermore, for analysis the 1 min focal period while the stimulus was present was divided into four 15 s time bins so that we could capture the immediate response and potentially track changes in response over time. We fitted models with stimulus order, generations in captivity, age, sex, stimulus type, and time bin as fixed effects, along with the interactions between origin, stimulus, age, sex, and time bin. We also included two random effects; a marmot ID which was unique to each individual and testing site which was one each of the three sites where testing was conducted. In 2002–2004 trials were conducted at all three sites, while those conducted from 2016–2018 were all conducted at the same site. We chose fixed effects, random effects, and interactions based on our knowledge of marmots and our study objective. We selected candidate models to include all fixed effects and interactions of interest. Due to our sample size we could not include a global model with all interactions and fixed effects together because such a model would not converge. Therefore, we instead selected our most highly parameterized model as the global model (Burnham and Anderson, 2002). We also fitted models with each of the fixed effects alone, and one with the intercept only. We calculated goodness of fit statistics based on our global models using the r2_nakagawa function from the Performance package (Lüdecke et al., 2021), calculated AICc values and AICc weights using the MuMIn package (Bartoń, 2020) and ranked all models by AICc values (Burnham and Anderson, 2002). We conducted model averaging using the model.avg function from the MuMIn package (Bartoń, 2020). Avian stimuli were also analyzed following the above methods (**Supplementary Materials**).

Marmots allocated no time to high vigilance away from the burrow in >90% of trials. With such high zero-inflation, models did not converge and did not produce interpretable results, therefore we did not include this behavior in further analyses.

# RESULTS

Of the 34 marmots tested (21 from 2002–2004 and 13 from 2016–2018), 17 were wild-caught (male $n = 13$; female $n = 4$), and 17 were captive born. Eleven (male $n = 7$; female $n = 4$) of 17 captive-born marmots were first or second generation in captivity, and six marmots (male $n = 4$; female $n = 2$) were third, fourth, or fifth generation in captivity. The marmots ranged in age from one to 10 years (mean 3.0 ± 2.5 SD), 10 marmots were female, and 24 were male (**Supplementary Table 1**). Ten of 34 marmots presented with the mammal taxidermy mounts were also exposed to the avian taxidermy mounts, and the cart with pedestal (see **Supplementary Materials** for avian results). The 60 s period before stimuli were presented was omitted from analysis after running an ANOVA for each response variable and finding no relationship between any behavior and the stimulus each marmot was later presented with (Foraging; DFn = 5, DFd = 165, $F = 1.059$, $p = 0.385$; Vigilance; DFn = 5, DFd = 165, $F = 1.774$, $p = 0.121$). We also omitted the second minute post stimulus presentation because we removed the mount at 60 s and this confounded interpretation.

## Mortality in the Wild

Between 2003 and 2020, 96 marmots that had at least one parent tested for predator discrimination were released and monitored in the wild using VHF telemetry. Of the 96 offspring released over 17 years, 53 marmots were confirmed dead (unpublished data, Marmot Recovery Foundation). Of these 53 marmots, 23 (43%) were killed by predators, (14 killed by cougars, five killed by eagles, and six marmots killed by an unknown predator); 14 (26%) died during hibernation, and 16 (30%) died from unknown or other causes. In addition to these 53 marmots, the fate of 40 marmots is unknown and three marmots released in 2020 are likely still alive.

Nine marmots tested between 2002 and 2004 were released to the wild, and none of the marmots tested between 2016 and 2018 have been released. Of these nine marmots, three were killed by predators (two by cougars; one by an eagle) and four died of other causes, during hibernation, or for unknown reasons. Eight of nine marmots died in the year they were released, and one survived in the wild for 8 years.

## Predator Discrimination

The global model for vigilance included interactions between generations in captivity, age, stimulus, and time, and both order and sex without interactions (DF = 149, log likelihood = 3,988.4, AICc = −7,611.7, ΔAICc = 289.5, Conditional $R^2 = 0.476$, Marginal $R^2 = 0.349$) and had random effect variances of 5.026e-09 ± 7.089e-05 SD for Site, and 0.163 ± 0.403 SD for ID. The top model for vigilance included only generations in captivity, stimulus, and the interaction between these two variables and had an AICc weight of 0.274 (**Table 1**). When the interaction between generations in captivity and stimulus was removed (Model 14; **Table 1**) the model weight decreased to 0.003 suggesting the top model is 91.3 times more likely to be the best model (0.274/0.003; Zuur et al., 2009). The global model for foraging also included interactions between generations in captivity, age, stimulus, and time, and both order and sex without interactions (DF = 149, log likelihood = 2,991.4, AICc = −5,617.7, ΔAICc = 244.4, Conditional $R^2 = 0.704$, Marginal $R^2 = 0.413$) and had random effect variances of 0.103 ± 0.322 for Site and 0.447 ± 0.668 SD for ID. The top model for foraging had a weight of 0.242 and included order, age, stimulus, and time (**Table 2**). When generations in captivity or sex were added to this top model the weights dropped to 0.181 and 0.168 respectively (**Table 2**). The interaction between generations in captivity and stimulus is not retained in any of the top models for foraging (**Table 2**) and adding generations in captivity to the top model results in a

**TABLE 1 |** Candidate models for the proportion of time marmots allocated to vigilance or time in the burrow ranked by AICc weight, with degrees of freedom (DF), log-likelihoods, AICc values, ΔAICc values, and AICc weights.

| Model number | Model | DF | Log-likelihood | AICc | ΔAICc | AICc weight |
|---|---|---|---|---|---|---|
| 1 | Vigilance ∼ gencap + stimulus + gencap:stimulus + (1\|ID) + (1\|Site) | 21 | 3,972.2 | −7,901.2 | 0.00 | 0.274 |
| 2 | Vigilance ∼ order + gencap + stimulus + gencap:stimulus + (1\|ID) + (1\|Site) | 22 | 3,973.0 | −7,900.6 | 0.55 | 0.208 |
| 3 | Vigilance ∼ age + gencap + stimulus + gencap:stimulus + (1\|ID) + (1\|Site) | 22 | 3,972.4 | −7,899.5 | 1.63 | 0.121 |
| 4 | Vigilance ∼ sex + gencap + stimulus + gencap:stimulus + (1\|ID) + (1\|Site) | 22 | 3,972.3 | −7,899.2 | 1.95 | 0.103 |
| 5 | Vigilance ∼ order + age + gencap + stimulus + gencap:stimulus + (1\|ID) + (1\|Site) | 23 | 3,973.2 | −7,899.0 | 2.19 | 0.092 |
| 6 | Vigilance ∼ order + sex + gencap + stimulus + gencap:stimulus + (1\|ID) + (1\|Site) | 23 | 3,973.0 | −7,898.7 | 2.51 | 0.078 |
| 7 | Vigilance ∼ age + sex + gencap + stimulus + gencap:stimulus + (1\|ID) + (1\|Site) | 23 | 3,972.4 | −7,897.5 | 3.71 | 0.043 |
| 8 | Vigilance ∼ order + age + sex + gencap + stimulus + gencap:stimulus + (1\|ID) + (1\|Site) | 24 | 3,973.2 | −7,896.9 | 4.28 | 0.032 |
| 9 | Vigilance ∼ time + gencap + stimulus + gencap:stimulus + (1\|ID) + (1\|Site) | 24 | 3,972.6 | −7,895.6 | 5.55 | 0.017 |
| 10 | Vigilance ∼ age + time + gencap + stimulus + gencap: stimulus + (1\|ID) + (1\|Site) | 25 | 3,972.8 | −7,894.0 | 7.19 | 0.008 |
| 11 | Vigilance ∼ sex + time + gencap + stimulus + gencap: stimulus + (1\|ID) + (1\|Site) | 25 | 3,972.7 | −7,893.7 | 7.51 | 0.006 |
| 12 | Vigilance ∼ order + age + time + gencap + stimulus + gencap: stimulus + (1\|ID) + (1\|Site) | 26 | 3,973.6 | −7,893.4 | 7.78 | 0.006 |
| 13 | Vigilance ∼ order + sex + time + gencap + stimulus + gencap: stimulus + (1\|ID) + (1\|Site) | 26 | 3,973.4 | −7,893.1 | 8.10 | 0.005 |
| 14 | Vigilance ∼ gencap + stimulus + (1\|ID) + (1\|Site) | 11 | 3,957.2 | −7,892.2 | 9.02 | 0.003 |
| 15 | Vigilance ∼ age + sex + time + gencap + stimulus + gencap:stimulus + (1\|ID) + (1\|Site) | 26 | 3,972.8 | −7,891.9 | 9.28 | 0.003 |
| 16 | Vigilance ∼ order + gencap + age + sex + stimulus + time + gencap: stimulus + (1\|ID) + (1\|Site) | 27 | 3,973.6 | −7,891.3 | 9.87 | 0.002 |

*All candidate models with AICc weight of zero included in* ***Supplementary Materials****.*

**TABLE 2 |** Candidate models for the proportion of time marmots allocated to foraging ranked by AICc weight, with degrees of freedom (DF), log-likelihoods, AICc values, ΔAICc values, and AICc weights.

| Model number | Model | DF | Log-likelihood | AICc | ΔAICc | AICc weight |
|---|---|---|---|---|---|---|
| 1 | Foraging ∼ order + age + stimulus + time + (1\|ID) + (1\|Site) | 14 | 2,945.3 | −5,862.1 | 0.00 | 0.242 |
| 2 | Foraging ∼ order + gencap + age + stimulus + time + (1\|ID) + (1\|Site) | 16 | 2,947.1 | −5,861.5 | 0.57 | 0.181 |
| 3 | Foraging ∼ order + age + sex + stimulus + time +(1\|ID) + (1\|Site) | 15 | 2,946.0 | −5,861.3 | 0.72 | 0.168 |
| 4 | Foraging ∼ order + gencap + stimulus + time + (1\|ID) + (1\|Site) | 15 | 2,945.6 | −5,860.6 | 1.43 | 0.118 |
| 5 | Foraging ∼ order + sex + stimulus + time + (1\|ID) + (1\|Site) | 14 | 2,944.5 | −5,860.5 | 1.52 | 0.113 |
| 6 | Foraging ∼ order + gencap + age + sex + stimulus + time + (1\|ID) + (1\|Site) | 17 | 2,947.4 | −5860.1 | 2.00 | 0.089 |
| 7 | Foraging ∼ order + gencap + sex + stimulus + time + (1\|ID) + (1\|Site) | 16 | 2,946.3 | −5,860.0 | 2.07 | 0.086 |
| 8 | Foraging ∼ order + age + stimulus + age:stimulus + (1\|ID) + (1\|Site) | 16 | 2,942.0 | −5,851.3 | 10.79 | 0.001 |

*All candidate models with AICc weight of zero included in* ***Supplementary Materials****.*

decrease in model weight from 0.242 to 0.181 (**Table 2**). Models for both behaviors of interest which had AICc weights <0.001 and are presented in **Supplementary Materials**.

Marmots decreased foraging and increased vigilance at the burrow or time in the burrow in response to all avian stimuli relative to the blank (**Supplementary Material**).

Marmots responded to all mammal stimuli by decreasing foraging, and responded more strongly to the wolf than any other stimulus by decreasing foraging and increasing vigilance at the burrow or time in the burrow. The greatest decrease in foraging relative to the blank was in response to the wolf, followed by the cougar, then goat, marmot, and cart (**Figure 1**; **Table 3**).

After decreasing foraging when each stimulus was presented, marmots gradually resumed foraging; relative to the first 15 s time bin of the presentation minute marmots allocated more time to foraging in the second, third, and fourth 15 s time bins (**Figure 1**; **Table 3**). Presenting stimuli to the marmots following a Latin squares design allowed us to control for the effect of presentation order and, not surprisingly, as trial number increased marmots allocated more time to foraging (**Table 3**).

Aside from decreasing foraging relative to the blank, marmots also allocated more time to vigilance at the burrow or time in the burrow (**Figure 2**). Our average mixed-effects model suggests marmots allocated significantly more time to vigilance at the burrow or time in the burrow (**Figure 2**) when presented with the wolf relative to the blank, however there were no significant differences relative to the blank for any other stimulus (**Table 3**).

## Origin and Changes Over Generations

Wild-caught marmots increased vigilance and decreased foraging relative to the blank in response to all avian stimuli and the greatest responses exhibited were to the eagle and owl.

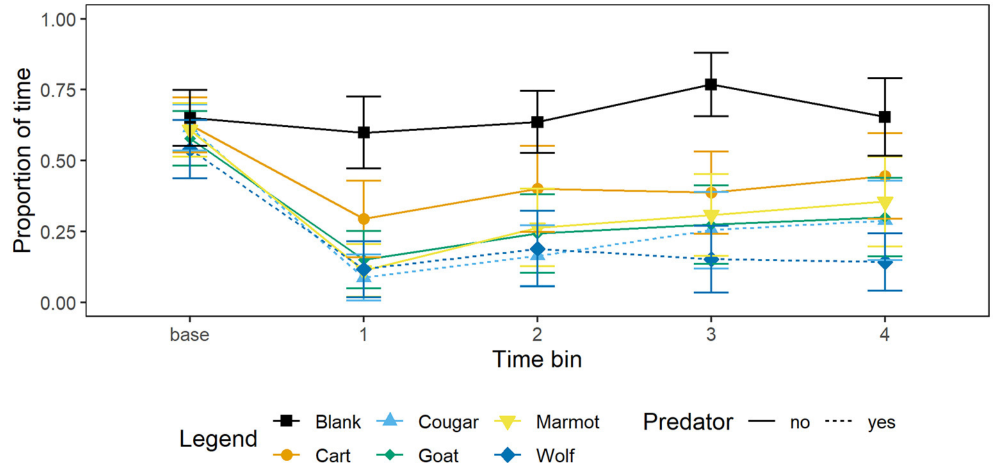

**FIGURE 1 |** Mean proportion of time and 95% CI per 15 s time bin that marmots ($n = 34$) spent foraging when presented with each of four mammal taxidermy mounts, a cart, and when a blank was scored. Baseline value represents proportion of 60 s prior to the stimulus being presented that marmots allocated to foraging.

**TABLE 3 |** Model average mixed-effects models for the proportion of time Vancouver Island marmots ($n = 34$) allocated to behaviors of interest in response to taxidermy mounts of mammals, as well as an empty cart and a blank, where no stimulus was presented.

| | | **Vigilance at burrow or in burrow** | | | | **Foraging** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Variable** | | **Estimate** | **SE** | ***z*** | ***p*** | **Estimate** | **SE** | ***z*** | ***p*** |
| Intercept | | –1.501 | 0.212 | 7.075 | <0.001 | –0.324 | 0.398 | 0.813 | 0.416 |
| Order | | 0.014 | 0.023 | 0.588 | 0.557 | 0.114 | 0.025 | 4.485 | <0.001 |
| Captive-born 1st, 2nd | | –0.028 | 0.278 | 0.100 | 0.920 | 0.164 | 0.258 | 0.636 | 0.525 |
| Captive-born 3rd, 4th, 5th | | 0.008 | 0.353 | 0.023 | 0.982 | –0.197 | 0.318 | 0.619 | 0.536 |
| Age | | –0.017 | 0.052 | 0.322 | 0.747 | 0.158 | 0.152 | 1.035 | 0.301 |
| Sex M | | 0.017 | 0.096 | 0.171 | 0.864 | –0.169 | 0.276 | 0.612 | 0.541 |
| Cart | | 0.062 | 0.208 | 0.295 | 0.768 | –0.992 | 0.156 | 6.352 | <0.001 |
| Goat | | 0.342 | 0.212 | 1.612 | 0.107 | –1.348 | 0.159 | 8.481 | <0.001 |
| Marmot | | 0.253 | 0.211 | 1.194 | 0.232 | –1.319 | 0.158 | 8.355 | <0.001 |
| Wolf | | 0.890 | 0.216 | 4.107 | <0.001 | –1.665 | 0.160 | 10.378 | <0.001 |
| Cougar | | 0.265 | 0.212 | 1.253 | 0.210 | –1.503 | 0.160 | 9.401 | <0.001 |
| Time bin 2 | | –0.002 | 0.028 | 0.058 | 0.954 | 0.277 | 0.123 | 2.257 | 0.024 |
| Time bin 3 | | –0.003 | 0.031 | 0.111 | 0.912 | 0.422 | 0.124 | 3.406 | 0.001 |
| Time bin 4 | | –0.005 | 0.034 | 0.139 | 0.889 | 0.445 | 0.125 | 3.561 | <0.001 |
| Captive-born 1st, 2nd | Cart | –0.048 | 0.332 | 0.144 | 0.886 | – | – | – | – |
| | Goat | 0.014 | 0.336 | 0.043 | 0.966 | – | – | – | – |
| | Marmot | –0.032 | 0.334 | 0.096 | 0.923 | – | – | – | – |
| | Wolf | –0.415 | 0.340 | 1.218 | 0.223 | – | – | – | – |
| | Cougar | 0.529 | 0.341 | 1.551 | 0.121 | – | – | – | – |
| Captive-born 3rd, 4th, 5th | Cart | 1.048 | 0.429 | 2.441 | 0.015 | – | – | – | – |
| | Goat | 1.623 | 0.431 | 3.766 | <0.001 | – | – | – | – |
| | Marmot | 1.403 | 0.428 | 3.277 | 0.001 | – | – | – | – |
| | Wolf | 1.410 | 0.426 | 3.307 | 0.001 | – | – | – | – |
| | Cougar | 1.307 | 0.428 | 3.048 | 0.002 | – | – | – | – |

*Full model average results, including additional parameters with estimates between 0.001 and –0.001 included in* ***Supplementary Materials****.*

However, third, fourth, and fifth generation captive-born marmots responded as strongly to the cart as they did to the predators and non-predators (**Supplementary Material**).

Wild caught, and captive-born marmots in all generations responded to mammal stimuli by increasing vigilance at the burrow or time in the burrow relative to the blank (**Figure 3**).

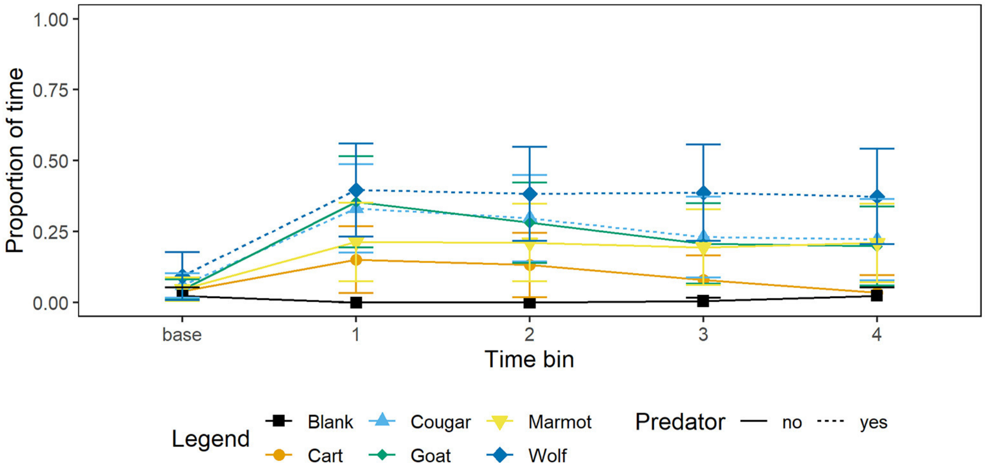

**FIGURE 2 |** Mean proportion of time and 95% CI per 15 s time bin that marmots (*n* = 34) spent vigilant at the burrow or in the burrow when presented with each of four mammal taxidermy mounts, a cart, and when a blank was scored. Baseline value represents proportion of 60 s prior to the stimulus being presented that marmots allocated to vigilance at the burrow or time in the burrow.

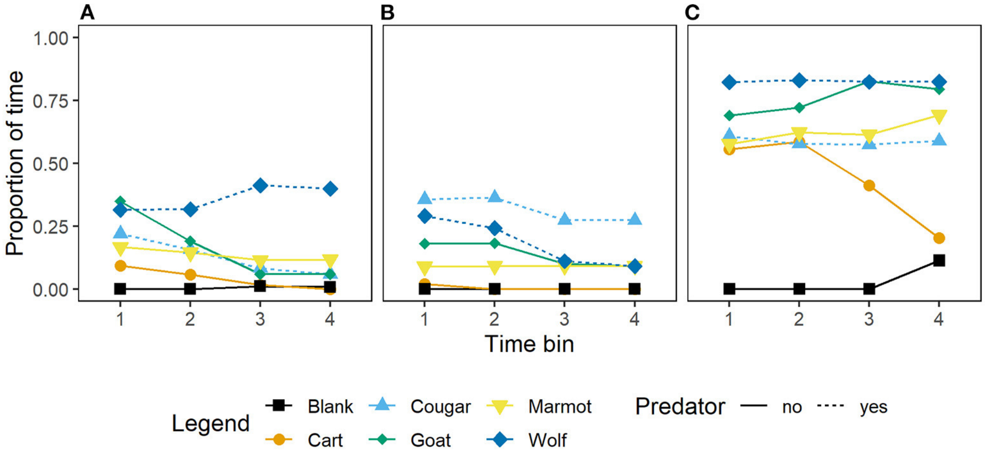

**FIGURE 3 |** Mean proportion of time per 15 s time bin that Vancouver Island marmots (*n* = 34) allocated to vigilance at the burrow or time in the burrow in response to mammal stimuli and when a blank was scored. Panels from left to right; **(A)** wild-caught (*n* = 17), **(B)** captive-born 1st and 2nd generation (*n* = 11), and **(C)** captive-born 3rd, 4th, and 5th generation (*n* = 6).

However, wild-caught and first and second generation captive-born marmots generally did not differ in the amount of time allocated to vigilance at the burrow or in the burrow (**Figures 3A,B**; **Table 3**), while third, fourth, and fifth generation captive-born marmots allocated more time to vigilance at the burrow or in the burrow in response to all stimuli (**Figure 3C**; **Table 3**). Also, wild-caught and first and second generation captive born marmots had little difference between time allocated to vigilance or in the burrow for the blank and the cart (**Figures 3A,B**), however third, fourth, and fifth generation captive born marmots increased vigilance and time in the burrow in response to the cart, the predators, and non-predators together (**Figure 3C**). Despite increasing vigilance in response to all stimuli, the proportion of time allocated in response to the cougar was similar to the proportion allocated to vigilance in response to the marmot and cart (**Figure 3C**). This suggests these marmots are equally wary of this potential predator, a conspecific, and a control stimulus.

Unlike for vigilance, models including the interaction between generations in captivity and stimulus for the proportion of time allocated to foraging carried no weight in our model set relative to the top model (**Table 2**). In addition, adding generations in captivity to the top model resulted in a decrease in model weight (**Table 2**) indicating this variable is of little importance for this response. Wild-caught marmots allocated less time to foraging in response to the predators (wolf and cougar) than to the non-predators (goat and marmot), and the cart (**Figure 4A**), and marmots that were first and second generation

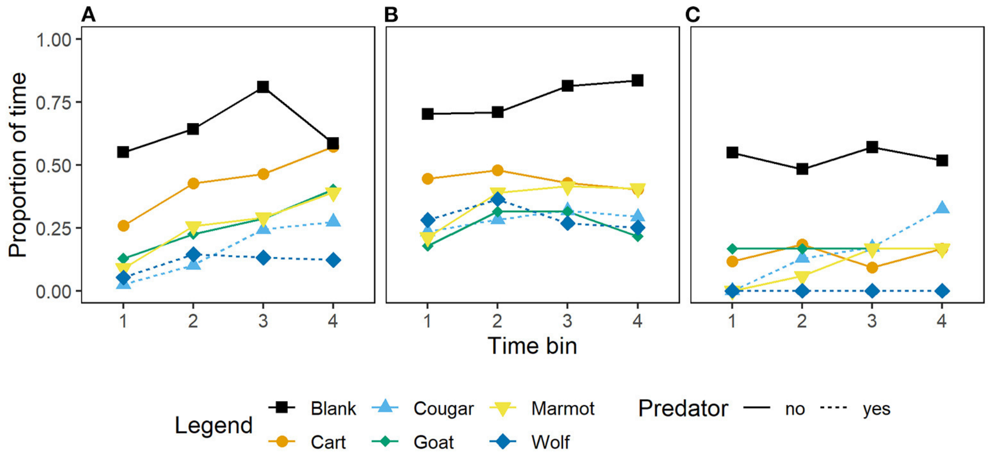

**FIGURE 4 |** Mean proportion of time by 15 s time bin that Vancouver Island marmots ($n = 34$) allocated to foraging in response to various mammal stimuli and while a blank was scored. Panels from left to right; **(A)** Wild-caught ($n = 17$), **(B)** captive-born 1st and 2nd generation ($n = 11$), and **(C)** captive born 3rd, 4th, and 5th generation ($n = 6$).

captive-born responded similarly to predators, non-predators, and the cart (**Figure 4B**). Marmots that were third, fourth and fifth generation captive-born also decreased foraging relative to the blank, however their responses to all stimuli but the wolf were similar (**Figure 4C**), suggesting these marmots may identify wolves as cause for alarm, but not cougars. However, that the interaction between generations in captivity and stimulus is not retained in any top models suggests that these differences should be interpreted with caution.

## DISCUSSION

Increasing the generations in captivity resulted in loss of predator discrimination for Vancouver Island marmots which could have implications for their survival upon release to the wild. This loss of anti-predator behavior is unsurprising because captivity eliminates, or at least lowers, the threat of predation (Geffroy et al., 2020), as has been documented in a growing body of literature. For example, 16 species of birds reduced anti-predator behavior relative to wild-caught conspecifics in one captive generation (Carrete and Tella, 2015). Marmots in this study that have been captive for more than three generations have reduced ability to discriminate between one of their most significant predators (cougar) and non-predators, or controls (goat, marmot, and cart). Marmots exhibited a similar loss of predator recognition in response to avian stimuli as well, though our avian sample size was small. Interestingly, these marmots that have been captive for three to five generations had larger responses to experimental stimuli than marmots that were wild-caught or have been in captivity for one or two generations. While an increase of vigilance or time in the burrow in response to all stimuli may seem potentially beneficial, having that increase coupled with a loss of discrimination between predators and non-predators is concerning. For example, increasing vigilance in both elk (*Cervus canadensis*) and bison (*Bison bison*) reduced food consumption (Fortin et al., 2004). Due to the risk that predators present to marmots in the wild, vigilance and fleeing to a burrow can clearly be beneficial, however, this comes at a cost of reduced time foraging, and potentially lower body condition. Given that 26% of marmots die in hibernation each year, this tradeoff could be problematic. A comparison of the loss of anti-predator behavior in response to domestication, urbanization, and captivity found that loss due to captivity occurred more slowly over time (Geffroy et al., 2020). However, it's worth noting that domesticated herbivores lost anti-predator behaviors more rapidly than omnivores or carnivores and solitary animals lost these behaviors more quickly than social ones (Geffroy et al., 2020). If the same is true for captive animals, rather than domesticated, as social herbivores, marmots may lose anti-predator behaviors at a more moderate rate.

Predation accounted for 62% of mortality where the cause was confirmed and a previous study found 61% of marmots were killed by predators (Jackson et al., 2016), with the majority of marmots being killed by cougars and eagles, followed by wolves (Aaltonen et al., 2009; Jackson et al., 2016; MRF unpublished data). Captive-born marmots have higher mortality than wild-born marmots, and cougars depredate significantly more captive-born than wild-born marmots. However, there was no significant difference in wolf predation between captive and wild-born marmots (Aaltonen et al., 2009). Marmots responded more strongly to wolves than to cougars, regardless of the number of generations they have been in captivity, whereas the marmots' ability to discriminate between cougars and non-predators seems to diminish over time. Therefore, marmots retain anti-predator responses to wolves, but lose the ability to discriminate between cougars and non-predators, despite that cougars killed more marmots than do wolves. This could be either because marmots are better able to avoid predation by wolves, or because cougars are the greater threat.

One possible explanation for marmots' retention of a predator template for wolves is that perhaps wolves were historically a more significant predator than they have been for the last century. Wolves were hunted heavily on Vancouver Island for many years in an attempt to eradicate them, and were effectively extirpated from between 1950 and 1970 (Muñoz-Fuentes et al., 2009). In the greater Yellowstone ecosystem when wolves were reintroduced and wolf and cougar activity areas overlapped, cougars began making kills at higher elevations and in more rugged areas (Bartnick et al., 2013). Cougar populations on Vancouver Island have been gradually declining since the early to mid-1990s (Hatter, 2019), but it is unclear if there is a relationship between population trends in these two species. Steindler et al. (2018) found that greater bilbies (*Macrotis lagotis*) had greatest retention of anti-predator templates in response to a predator with which they had a longest history. Perhaps marmots' retention of responses to wolves results from a longer shared history. Any predator template marmots currently have for wolves was either retained while wolves were extirpated or has developed since wolves returned to Vancouver Island. If marmots retained the template while wolves were extirpated it is not surprising that they also do so over the timeframe of this study. However, if marmots developed the ability to identify wolves as a predator since the late 1970s, it is unclear why they retain the predator template for wolves in this study but not cougars. In addition, the extirpation and reestablishment of wolves is just one way in which it is possible that the predator community into which marmots have been reestablished over the last 20 years is novel relative to the community in which they had survived in the past. For example, forestry operations have created high-elevation cut blocks which are colonized by marmots, but also draw cougars and wolves, and the construction of resource roads has increased cougar and wolf mobility in marmot habitat (Vancouver Island Marmot Recovery Team, 2017). With consistent changes to the predators that these marmots face in the wild, captive-bred individuals must be able to retain the ability to respond to the predators they would have faced historically, and adapt to the novel community of predators into which they will be released.

While the marmots in this study have not received predator awareness training (e.g., Griffin et al., 2000), they had the opportunity to view potential predators at the facility where they were housed. For example, coyotes (*Canis latrans*) can be found in the area and could potentially be observed by captive marmots from a distance. Though coyotes are absent from Vancouver Island, they may serve as a proxy for wolves. However, while marmots in this study are potentially exposed to predators, encountering potential predators when those predators pose no risk will not necessarily maintain anti-predator behavior. Therefore, it is possible that beyond five generations in captivity, and without additional intervention, marmots will lose the ability to discriminate between wolves and non-predators as well.

In order to retain or renew anti-predator behaviors in captive populations many programs develop predator avoidance training, where predator cues are paired with a stimulus that elicits a negative response in target animals (Griffin et al., 2000; Shier, 2016). Predator avoidance training in vertebrates is reported as successfully modifying behavior in 80% of studies but unsuccessful attempts may be underrepresented due to the bias toward publishing positive results (Edwards et al., 2021). Also, few studies report on survival in the wild post-release, and of those studies that did, approximately half were unsuccessful due to high mortality (Edwards et al., 2021). In some instances, captive animals were trained to avoid historical predators, only to suffer high mortality from novel sources (such as humans and dogs; Vera Cortez et al., 2015). In addition, rather than simply training target animals to recognize predators, it is important that predator avoidance training evaluates whether animals have a relevant coping strategy to predators (e.g., freezing, or fleeing; Edwards et al., 2021).

If predator avoidance training is to be undertaken as part of marmot captive breeding it should be informed by causes of mortality in the wild. Therefore, marmots should be trained to identify and respond to cougars and eagles, while efforts should be taken to retain their responses to wolves. Our results suggest that this training should be initiated in the second or third generation in captivity, if not sooner.

Studying endangered species often means having limited control over sample size and aspects of experimental design. This is of particular importance when our sample is subdivided into groups by generations in captivity. Though our sample of marmots that were 3rd, 4th, and 5th generation in captivity was particularly small ($n = 6$), the potential implications of the relationships we have observed should not be overlooked. With ca. 100 adult marmots in captivity and ca. 200 in the wild, our sample of 34 marmots represents ca. 11% of the global population. As such, the inferences we draw about the population may, ironically, be robust compared to a similar study of a non-endangered species where only a small fraction of the individuals are sampled. Because marmots that have been captive for more than three generations have only been available for study in the last few years, it is imperative to understand the impact captivity is having on behavior. In addition, our sample suffered from an imbalance of males and females. While our models did not suggest sex differences in marmot responses, it is unclear if this is due to an actual lack of differences or an imbalance in sampling. Future analyses may permit a more balanced sex ratio.

Much effort is placed in maintaining genetic diversity in captive populations (Willoughby et al., 2017) and while this is clearly important, this study suggests it is also important to include the maintenance of behavior as well. This captive population of marmots has retained genetic diversity relative to the wild population over the last three generations (Barrett et al., 2021), despite the loss of anti-predator behavior described here. Therefore, this study highlights the importance of evaluating whether individuals in captive populations change behaviors that may affect post-release fitness. Taken alone, results from Blumstein et al. (2006) suggested there was no effect of captivity on anti-predator behavior. However, including marmots born in captivity for several more generations suggests otherwise. Even for programs that include periodic training to maintain anti-predator behavior it would be beneficial to continue to monitor the effectiveness of their training.

The captive environment is novel for the wild-caught animals that establish captive breeding populations, and life in the wild is novel for captive-born individuals upon release. In addition to studying anti-predator behaviors of animals in captivity before their release to the wild, it is essential to continue studying those individuals after release as well. Given the large proportion of mortality attributed to predation in reintroduction programs (Berger-Tal et al., 2020) understanding the relationship between anti-predator behavior in captivity and mortality from predation in the wild is crucial for the success of captive breeding and reintroduction programs. We recommend that conservation translocation breeding programs conduct behavior assessments early, and continue to re-assess captive individual's behavior at regular intervals throughout a program. It is also essential that there is regular collaboration between those managing the captive and wild populations to inform how both populations are managed. Captive breeding can be a valuable tool to reestablish wildlife populations, and ensure those populations persist, however one cannot assume that an individual in captivity is prepared for life in the wild, and behavioral studies such as this are one of many pieces needed for success.

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## ETHICS STATEMENT

The animal study was reviewed and approved by the Calgary Zoo Welfare and Ethics in Research Committee, the Marmot Recovery Foundation, and the UCLA Animal Research Committee.

## AUTHOR CONTRIBUTIONS

GD-M scored videos of marmots, drafted the manuscript, and assisted in planning and conducting analysis. JR conducted statistical analyses and edited the manuscript. NL developed the project, planned the experimental trials, edited the manuscript and assisted in planning, and interpreting analysis. DB conducted the study on which this one is based, assisted in repeating the trials, planning and interpreting statistical analyses, and editing the manuscript. AM developed the project, contributed in project planning, assisted in planning and interpreting statistical analyses, and edited the manuscript. All authors contributed to the article and approved the submitted version.

## ACKNOWLEDGMENTS

We kindly thank B.D. Holland for advice and transfer of original materials. Thank you also to all who assisted with this study: C. Baird, V. Edwards, H. Elliott, J. Gellatly, L. Haines, L. Hébert, R. Kelly, A. Langill, F. LeTaro, M. Miskolczi, L. Payette-Brisson, L. Riches, C. Slade, K. Swan, K. Twamley, R. Wenman, and D. Whiteside. Thank you to the Marmot Recovery Foundation for kindly providing the post-release survival data. C. Jackson and A. Taylor for reviewing a draft of the manuscript. We also thank the reviewers, who made valuable contributions to the manuscript.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2021.718562/full#supplementary-material

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Conservation Science

ORIGINAL RESEARCH
published: 07 March 2022
doi: 10.3389/fcosc.2022.777797

# Movement Patterns of Resident and Translocated Beavers at Multiple Spatiotemporal Scales in Desert Rivers

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Wildlife translocations alter animal movement behavior, so identifying common movement patterns post-translocation will help set expectations about animal behavior in subsequent efforts. American and Eurasian beavers (*Castor canadensis; Castor fiber*) are frequently translocated for reintroductions, to mitigate human-wildlife conflict, and as an ecosystem restoration tool. However, little is known about movement behavior of translocated beavers post-release, especially in desert rivers with patchy and dynamic resources. We identified space-use patterns of beaver movement behavior after translocation. We translocated and monitored nuisance American beavers in desert river restoration sites on the Price and San Rafael Rivers, Utah, USA, and compared their space use to resident beavers after tracking both across 2 years. Resident adult (RA) beavers were detected at a mean maximum distance of 0.86 ± 0.21 river kilometers (km; ±1 SE), while resident subadult (RS) (11.00 ± 4.24 km), translocated adult (TA) (19.69 ± 3.76 km), and translocated subadult (TS) (21.09 ± 5.54 km) beavers were detected at substantially greater maximum distances. Based on coarse-scale movement models, translocated and RS beavers moved substantially farther from release sites and faster than RA beavers up to 6 months post-release. In contrast, fine-scale movement models using 5-min location intervals showed similar median distance traveled between RA and translocated beavers. Our findings suggest day-to-day activities, such as foraging and resting, were largely unaltered by translocation, but translocated beavers exhibited coarse-scale movement behavior most similar to dispersal by RSs. Coarse-scale movement rates decreased with time since release, suggesting that translocated beavers adjusted to the novel environment over time and eventually settled into a home range similar to RA beavers. Understanding translocated beaver movement behavior in response to a novel desert system can help future beaver-assisted restoration efforts to identify appropriate release sites and strategies.

**Keywords: beaver, *Castor canadensis*, translocation, movement behavior, spatial ecology, post-release movement, net displacement**

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***Specialty section:***
*This article was submitted to*
*Animal Conservation,*
*a section of the journal*
*Frontiers in Conservation Science*

***Received:*** *15 September 2021*
***Accepted:*** *28 January 2022*
***Published:*** *07 March 2022*

***Citation:***
*Doden E, Budy P, Avgar T and*
*Young JK (2022) Movement Patterns*
*of Resident and Translocated Beavers*
*at Multiple Spatiotemporal Scales in*
*Desert Rivers.*
*Front. Conserv. Sci. 3:777797.*
*doi: 10.3389/fcosc.2022.777797*

## INTRODUCTION

Animal movement behaviors, such as natal dispersal, migration, and territoriality, are important components in the life history and ecological interactions of a species (Nathan, 2008). However, when animals undergo involuntary movement such as translocation to an unfamiliar, novel area, their natural movement behavior can be substantially altered (Heidinger et al., 2009; Le Gouar et al., 2012). Some individuals may exhibit homing behavior, even when released extremely long distances from their place of origin (Dickens et al., 2010). Translocated individuals may be forced to settle in lower-quality habitats (Burns, 2005), disperse if territorial resident conspecifics already occupy high-quality habitat (McNicol et al., 2020), or move away from their release sites in search of mates (Mihoub et al., 2011). In addition, animals may be translocated in response to human–wildlife conflict, but they can again become problem individuals if released in an area that is too small to account for long-range movements or has inadequate resources (Weilenmann et al., 2010; Le Gouar et al., 2012). Difficulties with animal behavior post-translocation, primarily movement or dispersal activities, are some of the most common obstacles to translocation success (Berger-Tal et al., 2020). Therefore, identifying movement patterns post-translocation can help to set expectations and anticipate behavioral responses in future translocation efforts, and ultimately guide conservation and management.

Beaver (American beaver, *Castor canadensis*, and Eurasian beaver, *C. fiber*) translocation is a popular method of human-wildlife conflict mitigation and ecosystem restoration. Once overexploited during the fur trade of the 1700s and 1800s (Baker and Hill, 2003; Halley et al., 2021), beaver populations have now recovered in some areas and come in close contact with humans, sometimes causing unwanted flooding, damaging trees, and jeopardizing infrastructure. Translocation provides an alternative method to lethal control by removing beavers from conflict situations and allowing them the opportunity to play a critical role in restoration initiatives. American and Eurasian beavers are ecologically similar (Rosell et al., 2005), and as ecosystem engineers, both species can significantly alter the system they inhabit, primarily through dam building (Mills et al., 1993; Larsen et al., 2021). Beaver dams retain water and mitigate the effects of drought, add heterogeneity to stream channels, impact riparian vegetation, and benefit many other species (Naiman et al., 1988; Rosell et al., 2005; Pollock et al., 2014). However, retaining translocated beavers at a targeted site and encouraging the initiation of passive restoration through dam-building can be challenging, and translocated individuals may not behave similarly to naturally occurring, dam-building beavers, at least initially (Pilliod et al., 2018; Nash et al., 2021).

Beavers are central-place foragers, and dams are most commonly built by territorial colonies to create pools as cover near their lodge or burrow for predator avoidance and transport of wood; beavers rarely build dams during natal dispersal or transience (DeStefano et al., 2006; McClintic et al., 2014b; Ritter, 2018). The home range of established beavers typically covers 1.6–3.9 river kilometers (Breck et al., 2001; Herr and Rosell, 2004; Havens et al., 2013), while dispersing subadult beavers typically travel 3.5–19.8 km before settling (Beer, 1955; Sun et al., 2000; Ritter, 2018). Autonomous displacement recorded for translocated beavers ranges widely from 3.3 to 238 km, leading to variable dam-building success post-translocation (Hibbard, 1958; McKinstry and Anderson, 2002; Petro et al., 2015).

Beavers can play a vital role in desert rivers, sustaining water and increasing habitat complexity with their dams, especially because many arid systems have become imperiled by altered flow regimes and drought, habitat simplification, invasive species, and climate change (Harper, 2001; Stromberg, 2001; Mott Lacroix et al., 2017). However, the ecology of naturally occurring (hereafter, resident) beavers is understudied in desert rivers, and few translocation studies have been conducted in such systems (Gibson and Olden, 2014; Barela and Frey, 2016). Further, post-release movement behavior of translocated beavers, into a novel degraded desert river where resources may be more patchy, scarce, and unpredictable, may be different from other environments where the majority of beaver studies have occurred (Gibson and Olden, 2014; Barela and Frey, 2016).

We investigated the post-release movements of translocated American beavers (hereafter, beavers) on multiple spatiotemporal scales for 6 months post-release, using resident beavers for baseline comparison of movement behavior. We hypothesized that, at a landscape scale, translocated beavers would initially move farther and more quickly than resident adult (RA) beavers, similar to subadult beavers during dispersal. Farther and faster movement of translocated beavers was expected since they would likely be exploring their novel environment, potentially searching for a mate and a suitable site to settle, whereas RA beavers have established territories and would not need to move as far or as quickly. We also hypothesized translocated beavers would initially be more active than adult resident beavers on a fine-scale (1-h sampling sessions), continuously exploring their new environment, leading to faster movement speeds. In contrast, resident beavers using a familiar territory with set activity patterns would result in slower movement speeds. Our final hypothesis is that after establishing territories, translocated beavers would eventually settle into similar fine- and coarse-scale movement patterns that are similar to territorial adult resident beavers. A better understanding of the movement patterns of translocated beavers in this novel system can help develop an expectation framework of beaver movement behavior for future beaver-assisted restoration efforts in desert systems.

## MATERIALS AND METHODS

### Study Area

We conducted our study in desert tributaries of the Green River, along the lower stretches of the Price River and San Rafael River in east-central Utah, USA. Simplification, aggradation, dewatering, and invasive species encroachment have degraded the lower reaches of these rivers (Walker and Hudson, 2004; Bottcher, 2009). A multi-agency collaborative partnership had previously selected certain sections of these rivers for restoration, hereafter called "targeted restoration sites." On the Price River near Woodside, UT, USA, a 20.5-km stretch of river was identified as a targeted restoration site, and on the San

Rafael River near Moonshine Wash, an 8.1-km stretch of river was identified as a targeted restoration site. Invasive tamarisk removal, gravel bar additions, native tree planting, and beaver dam analog (BDA) construction had been completed at Moonshine Wash, with beaver translocations included as a passive restoration technique at both sites (Laub, 2015, 2018). Dams built by translocated beavers were intended to supplement the dam-building activity of existing resident beavers as part of the restoration efforts, with the primary objective being to create complex habitat for federally endangered and regionally sensitive endemic fish species such as the Colorado pikeminnow (*Ptychocheilus lucius*), bonytail chub (*Gila elegans*), razorback sucker (*Xyrauchen texanus*), bluehead sucker (*Catostomus discobolus*), flannelmouth sucker (*Catostomus latipinnis*), and roundtail chub (*Gila robusta*; Bottcher et al., 2013; Budy et al., 2015).

We also selected a third field site, a 1.5-km stretch near Cottonwood Wash on the San Rafael River, because it was a unique, complex stretch of river with high habitat suitability for the desert fish species listed above (Bottcher, 2009). This complex reach developed after a sediment plug in 2010 slowly formed a shallow, braided system in the otherwise simplified and degraded river (Lyster, 2018). A resident beaver colony was already established and active there, maintaining and extending complex fish habitat, so we did not translocate any beavers to this site but used it to study resident beaver movement patterns.

Both rivers flow through red rock desert, canyonlands, and desert shrubland. Willow (*Salix* spp.), Fremont cottonwood (*Populus fremontii*), common reed (*Phragmites* spp.), and non-native and invasive tamarisk (live and dead; *Tamarix ramosissima*), and Russian olive (*Elaeagnus angustifolia*) make up the majority of riparian vegetation, with cattails (*Typha* spp.) also growing at Cottonwood Wash. Typical temperatures range from 37°C in the summer to −11°C in the winter, and there is little rainfall, averaging 21 cm per year (National Oceanic Atmospheric Administration, 2021).

To determine existing resident beaver presence before translocations, we conducted sign surveys at Cottonwood and Moonshine Wash in June 2019 and along the Price River in August 2019. Surveys entailed walking, wading, or floating along the rivers and marking all lodges, burrows, dams, and fresh beaver sign such as foraging, slides, and scent mounds on a handheld GPS unit (Garmin, Chicago, Illinois, USA; Model GPSMAP 78s or 66st). We observed evidence of resident beaver activity at Cottonwood Wash and in several stretches of the Price River, but no fresh activity at Moonshine Wash.

## Capture, Quarantine, Tagging, and Release

All procedures including animal capture, handling, tagging, and monitoring were approved by Institute for Animal Care and Use Committees at Utah State University (No.10128) and USDA-National Wildlife Research Center (QA-3171). We responded to calls to capture nuisance beavers in northern, central, and eastern Utah for our translocation efforts; these beavers would have been euthanized if not captured and translocated. We captured resident beavers along the Price River and at Cottonwood Wash. We captured translocated and resident beavers from May to October of 2019 and 2020 using Hancock/Koro suitcase-style traps, Comstock box traps, and non-lethal cable restraints. To accommodate quarantine protocols (Utah Division of Wildlife Resources, 2017; Pilliod et al., 2018), we held translocated beavers for at least 3 days at the Utah State University Beaver Ecology and Relocation Center in Logan, Utah, or the field site. Beavers were provided tree cuttings, root vegetables, rodent pellets, and fresh water daily (Campbell-Palmer and Rosell, 2015). They were held an average of 4.4 ± 1.3 days (1 Standard Error) before release.

We chemically immobilized beavers with Butorphanol, Azaperone, and Medetomidine, supplemented with oxygen and isoflurane, to process translocated and resident beavers (Roug et al., 2018). During processing, we assigned an age class based on weight and body size (subadult = 1–2 years, adult >2 years; Patric and Webb, 1960) and sexed beavers using anal gland secretion (Schulte et al., 1995; Woodruff and Pollock, 2018). We categorized beavers into four state categories: RA, resident subadult (RS), translocated adult (TA), and translocated subadult (TS). Due to small sample size, we were unable to split state categories by sex. All beavers received a passive integrated transponder- (PIT-) tag (Biomark APT12 tags; Boise, Idaho, USA) inserted in the tail. We also fitted adult and subadult beavers >9 kg with tail-mounted transmitters (Rothmeyer et al., 2002; Arjo et al., 2008). Transmitters were either a remotely downloadable store on-board GPS tag (Africa Wildlife Tracking; Rietondale, Pretoria, South Africa) or a VHF modified ear-tag (Advanced Telemetry Systems, Isanti, Minnesota, USA; Model #M3530). Initially, we secured GPS- and VHF-tags with 19 mm neoprene and 19 mm steel washers, then to improve transmitter retention we increased the sizes of washers to 38.1 mm neoprene and 31.8 mm steel washers in September 2019 (Windels and Belant, 2016). Resident beavers were released at their capture sites, while translocated beavers were released at unoccupied stretches of the Price River restoration site and Moonshine Wash study site on the San Rafael River.

## Monitoring

We tracked beavers 2–7 times per week via GPS locations and radio-telemetry using homing-in or triangulation techniques from May through October in 2019 and 2020. To generate beaver locations from triangulations, we input at least three telemetry azimuths ≤30 min apart into "Location of A Signal" (LOAS, version 4.0, Ecological Software Solutions, Sacramento, CA) using Maximum Likelihood Estimation. We only included LOAS locations <200 m from the river with <10 ha error ellipse in analyses. We also used semi-permanent and submersible passive integrated antennae (PIAs; Biomark; Boise, Idaho, USA) in the rivers to passively detect PIT-tags from May 2019 through March 2021. Some beavers emigrated from the targeted restoration sites, so we scanned along the Green River monthly, conducted one aerial flight, and floated the Price and San Rafael Rivers several times to attempt to locate these individuals. We only included live detections in analyses and assumed that all PIA detections were of live beavers.

We determined transient (temporary) and permanent settlement sites of translocated beavers, which we defined as areas with ≥3 consecutive locations within 0.86 km (the mean

**TABLE 1** | Types of location data used in models of beaver movement, collected from May 2019 to March 2021 in desert rivers in east-central Utah, USA.

| Data type | Error associated with data ($\bar{x} \pm 1$ standard error) | Proportion of data in MDD modeling[a] | Proportion of data in DR modeling | Proportion of data in SL modeling[b] | Proportion of data in FS modeling |
|---|---|---|---|---|---|
| Passive integrated antennae detection | 0 $m^2$ | 0.45 | 0.60 | 0.30 | – |
| GPS location | 34.3 ± 2.3 $m^2$ | 0.03 | 0.05 | 0.09 | – |
| Telemetry—homing location | 0 $m^2$ | 0.12 | 0.14 | 0.21 | – |
| Telemetry—triangulation | 3055.8 ± 651.9 $m^2$ | 0.26 | 0.21 | 0.40 | – |
| Single azimuth intersecting river | 17.8 ± 1.5 $m^2$[c] | – | – | – | 1.00 |

[a] *An additional 14% of locations were release events.*

[b] *Data type at the end of each step.*

[c] *Based on calibration tests using stationary test transmitters.*

*The models include maximum distance detected (MDD; distance between the most upstream and downstream locations for each beaver, in river km), displacement (DR; distance from release, in river km), step length (SL; distance from one observed location to the next, in river m), and fine-scale movement rate (FS; median 5-minute step length, in river m).*

maximum river distance detected for our resident beavers), used for ≥7 days for transient sites, and ≥91 days (3 months) for permanent sites (*similar to methods in* Woodford et al., 2013; Matykiewicz et al., 2021). Time to permanent settlement was recorded as the time an individual was released subtracted from the first time an individual was encountered at its permanent settlement site.

We also conducted hour-long, fine-scale movement monitoring sessions on a weekly to bi-monthly basis per individual. First, we triangulated the location of each beaver to get a general location and position ourselves perpendicular to that point along the river. From this location, we took an azimuth every 5 min to approximate movement patterns in the river. Depending on terrain and vegetation, we were 10–320 m from the river during monitoring sessions. All data are reported as $\bar{x} \pm 1$ Standard Error.

## Coarse-Scale Movement Analysis

We used three methods to compare coarse-scale movement patterns among translocated and resident beavers and test our hypotheses. We used all locations ≥2.5 h apart for these analyses (**Table 1**). First, we used package "riverdist" in Program R for these analyses (Tyers, 2016, version 0.15.3; R Core Team, version 4.0.3, 2020). We snapped the most upstream and downstream locations for each beaver to the closest vertex (spaced 0.5 m apart) of our river network shapefile and calculate the maximum distance detected (in km) for all resident and translocated beavers. Second, we calculated the displacement for all beavers, defined as the distance of each beaver location from their release site (in kilometers), only including individuals with ≥3 locations within the first 6 months post-release, as we detected very few individuals longer than this. Third, we calculated the step length (in m) between consecutive points.

We constructed a log-linear regression model set comparing *ln(maximum distance detected)* and beaver state category (RA, RS, TA, TS) in order to analyze maximum observed river distance. For the latter two measurements (translocated beavers), we constructed two log-log linear regression mixed-model sets to assess differences in displacement from release *(distance from release ∼ time since release)* and the distance from one observed location to the next *(step length ∼ step duration)* between resident and TA and subadult beavers, and the influence of several covariates on these differences (**Table 2**). The log-log regressions are necessary to account for the theoretically expected non-linear relationship between displacement and time (*for further details see* Street et al., 2018). Individual beaver ID was included as a random effect on both the intercept and *ln(time since release)* or *ln(step duration)*. In the step-length model, we included only step lengths >0 m, step durations ≤60.8-day (2 months), and individuals with ≥2 steps.

We categorized discharge [high, medium, or low; cubic feet per second (cfs)] based on median historical average discharge (87.2 cfs) for the lower Price and San Rafael Rivers, using 66 and 84 years of data, respectively (United States Geological Survey, 2021a). We included all discharges from 0 to 30.9 cfs in the low category, discharges from 31.0 to 142.9 cfs in the medium category, and all discharges >143.0 cfs in the high category.

We used NDVI as a greenness index of standing plant biomass at beaver locations (Pettorelli et al., 2011; Neumann et al., 2015). NDVI can be used as a measure of suitable beaver habitat because tamarisk thickets and desert habitat have lower NDVI than cottonwood, willow, and riparian zones favored by beavers (Lesica and Miles, 2004; Nagler et al., 2004; Barela and Frey, 2016). Over 95% of beaver locations used in analyses had a location error <900 $m^2$, so we downloaded 30 × 30 m resolution Landsat 8 Operational Land Imager Surface Reflectance scenes with <15% cloud cover for NDVI derivation. We ordered scenes through USGS Earth Explorer (United States Geological Survey, 2021b; https://earthexplorer.usgs.gov/) and NDVI calculations from the Earth Science Processing Architecture platform (United States Geological Survey, 2017; https://espa.cr.usgs.gov/). We generated seasonal mean NDVI pixel values using the "Mosaic to New Raster" tool in ArcGIS Pro (Environmental Systems Research Institute, 2021; version 2.8.0; Redlands, CA, USA). In our rivers, discharge and NDVI typically follow seasonal patterns, so we did not include season as an additional covariate.

We fitted the maximum distance model using the "lm" function in base R (R Development Core Team, 2020; version 4.1.0), while we fitted the displacement and step length models

**TABLE 2** | Key to parameters included in four models of resident adult, resident subadult, translocated adult, and translocated subadult beaver space use.

| Parameter | Parameter code | Included in MDD modeling | Included in DR modeling | Included in SL modeling | Included in FS modeling |
|---|---|---|---|---|---|
| Maximum distance detected | MDD[a] | X | | | |
| Displacement from release site | DR[a] | | X | | |
| Step length | SL[a] | | | X | |
| Median 5 min displacement | MD[a] | | | | X |
| Individual beaver ID[b] | *i* | | X | X | X |
| State category (Resident adult) | RA | X | X | X | X |
| State category (Resident subadult) | RS | X | X | X | |
| State category (Translocated adult) | TA | X | X | X | X |
| State category (Translocated subadult) | TS | X | X | X | X |
| Step duration | SD | | | X | |
| Time since release | TR | | X | X[c] | |
| Is PIA detection | PIA | | | X | |
| River discharge (low discharge) | LD | | | X | |
| River discharge (medium discharge) | MD | | | X | |
| River discharge (high discharge) | HD | | | X | |
| Normalized Difference Vegetation Index | NDVI | | | X[c,d] | |
| Time of day (night) | N | | | | X |

*Beavers were monitored via PIT-, VHF-, and GPS-tags in desert rivers in east-central Utah, USA, from May 2019 to March 2021. Models were fitted to each of four response variables: (1) maximum distance detected (MDD; distance between the most upstream and downstream locations of each beaver, in river km; n = 53), (2) displacement (DR; distance from release, in river km; n = 1,110), (3) step length (SL; distance from one observed location to the next, in river m; n = 600), and (4) fine-scale movement rate (FS; median 5-min step length, in river m; n = 68).*

[a] *Response variable.*

[b] *Random effect.*

[c] *Scaled and centered.*

[d] *Start of step.*

using package "nlme" in program R (Pinheiro et al., 2013; version 3.1.152). We constructed models for the three coarse-scale movement metrics using several covariates (**Table 2**). We confirmed normality using diagnostic plots of the best model residuals.

## Fine-Scale Movement Analysis

We estimated the location of each beaver in the river using the "Bearing Distance to Line" and "Intersect" tools in ArcGIS Pro (Environmental Systems Research Institute, 2021; version 2.8.0; Redlands, CA, USA) from the azimuths taken during fine-scale (5 min between consecutive observations) movement monitoring sessions (**Table 1**). We assumed beavers were in the river for all locations. Using these estimated points, we calculated the step length between consecutive points in "riverdist" using the same methods as described above. Lastly, we calculated the median 5-min step length (in m) for each sampling session. We were unable to include all 5-min step lengths within all sampling sessions because our sample size was too small to include nested random effects of sampling session within individual beaver ID. In addition, we did not detect any RSs long enough to conduct these fine-scale movement monitoring sessions, and we excluded Cottonwood Wash from this analysis because we only monitored one individual at a fine-scale in this site. High median distance moved was an indicator of an active beaver, perhaps out foraging, while a low median distance moved likely indicated an inactive beaver, likely resting.

We used a log-linear regression mixed model to compare the fine-scale movement rates (median 5-min step lengths) of RA, TAs, and subadult beavers, and the influence of several covariates on these movement patterns (**Table 2**). We categorized daytime as 06:00–17:59 h and nighttime as 18:00–05:59 h. We fitted the fine-scale movement rate model using package "nlme" in program R (Pinheiro et al., 2013; version 3.1.152). We used residual diagnostic plots to confirm normality.

# RESULTS

We captured and PIT-tagged 41 translocated beavers and fit 35 translocated beavers (21 adults, 14 subadults) with radio transmitters. We PIT-tagged 16 resident beavers and fit 12 resident beavers with radio transmitters (9 adults, 3 subadults). We censored three additional resident beavers from analyses because they died from capture- or processing-related events. We released resident beavers at their capture sites, at Cottonwood Wash (2019; $n = 3$, 2 adults and 1 subadult) and in the Price River (2019 and 2020; $n = 13$, 8 adults and 5 subadults). We released 36 translocated beavers (76.5%) as family groups or as pairs formed during quarantine. We released 33 translocated beavers (16 adults and 17 subadults) in unoccupied portions of the Price River targeted restoration site both years, but only released 8 translocated beavers (5 adults and 3 subadults) near BDAs at Moonshine Wash in 2019. Drought in 2020 caused extremely low

**TABLE 3 |** Fixed effects estimates from four movement models of resident adult (RA), resident subadult (RS), translocated adult (TA), and translocated subadult (TS) beavers monitored via PIT-, VHF-, and GPS-tags in desert rivers in east-central Utah, USA, from May 2019 to March 2021.

| Parameter | Estimate | Lower 95% CI | Upper 95% CI | *p*-values |
|---|---|---|---|---|
| **Maximum distance detected** | | | | |
| RA | −0.42 | −1.18 | 0.34 | 0.29 |
| RS | 2.12 | 0.98 | 3.26 | <0.001 |
| TA | 2.56 | 2.07 | 3.05 | <0.001 |
| TS | 2.31 | 1.78 | 2.84 | <0.001 |
| **Coarse-scale displacement** | | | | |
| RA | 0.30 | −0.21 | 0.81 | 0.26 |
| RS | 0.90 | −0.22 | 2.02 | 0.12 |
| TA | 0.45 | 0.12 | 0.78 | 0.01 |
| TS | 0.59 | 0.22 | 0.96 | <0.01 |
| RA*Ln(TR) | −0.01 | −0.21 | 0.19 | 0.91 |
| RS*Ln(TR) | 0.52 | 0.01 | 1.03 | 0.05 |
| TA*Ln(TR) | 0.35 | 0.21 | 0.49 | <0.001 |
| TS*Ln(TR) | 0.46 | 0.32 | 0.60 | <0.001 |
| **Coarse-scale step length** | | | | |
| RA | 4.71 | 3.69 | 5.73 | <0.001 |
| RS | 7.73 | 5.85 | 9.61 | <0.001 |
| TA | 6.61 | 5.67 | 7.55 | <0.001 |
| TS | 6.48 | 5.36 | 7.60 | <0.001 |
| PIA | 0.42 | 0.03 | 0.81 | 0.03 |
| LD | −0.64 | −1.42 | 0.14 | 0.11 |
| HD | −0.26 | −1.16 | 0.64 | 0.57 |
| NDVI | −0.11 | −0.31 | 0.09 | 0.24 |
| RA*Ln(TR) | −0.69 | −1.06 | −0.32 | <0.001 |
| RS*Ln(TR) | 0.18 | −0.56 | 0.92 | 0.62 |
| TA*Ln(TR) | 0.08 | −0.25 | 0.41 | 0.64 |
| TS*Ln(TR) | 0.03 | −0.44 | 0.50 | 0.89 |
| RA*Ln(SD) | 0.47 | 0.12 | 0.82 | 0.01 |
| RS*Ln(SD) | −0.13 | −0.99 | 0.73 | 0.78 |
| TA*Ln(SD) | 0.61 | 0.30 | 0.92 | <0.001 |
| TS*Ln(SD) | 0.47 | 0.02 | 0.92 | 0.04 |
| **Fine-scale movement rate** | | | | |
| RA | 1.95 | 1.36 | 2.54 | <0.001 |
| TA | 1.21 | 0.35 | 2.07 | <0.01 |
| TS | 1.45 | 0.88 | 2.02 | <0.001 |
| N | 0.89 | 0.34 | 1.44 | <0.01 |

*Models were fitted to each of four response variables: (1) maximum distance detected (distance between the most upstream and downstream locations for each beaver, in river km; adjusted $R^2 = 0.78$, $n = 53$), (2) displacement (distance from release, in river km; marginal $R^2 = 0.45$, conditional $R^2 = 0.86$, $n = 1{,}110$), (3) step length (distance from one observed location to the next, in river m; marginal $R^2 = 0.30$, conditional $R^2 = 0.51$, $n = 600$), and (4) fine-scale movement rate (median 5-min step length, in river m; marginal $R^2 = 0.20$, conditional $R^2 = 0.28$, $n = 68$).*

flows in the San Rafael River, resulting in unsuitable conditions for translocation at Moonshine Wash.

We detected RS and translocated beavers over significantly longer stretches of river than RA beavers (**Table 3**; **Figure 1**). The average time passed between an individuals' most up- and down-stream locations was 54.1 ± 31.5 days for RA beavers, 35.9 ± 30.1 days for RS beavers, 38.1 ± 23.6 days for TA beavers, and 40.6 ± 12.1 days for TS beavers. We detected 41.4% of all TA and subadult beavers ($n = 17$) >20 km from their release site (**Figure 2**), and 61.4% of RS and translocated beavers were downstream of their release site at their final detection (25.0% of RS, 66.7% of TA, and 63.2% of TS). Eleven translocated beavers (four adults at the Price River, two adults at Moonshine Wash, and five subadults at the Price River) settled in transient resting sites within the targeted restoration sites for an average of 16.2 ± 2.7 days before moving to other areas. We did not observe any transient resting sites for RS beavers. Four translocated beavers (two adults, two subadults) permanently settled outside the targeted restoration sites 8.6–155.4 days after release (72.2 ± 34.6 days); three near the confluence of the Green and Price Rivers, and one subadult beaver farther downstream, near the town of Green River. We detected these beavers for an average of 134.8 ± 7.5 days with PIAs at these settlement sites.

Based on the displacement model, we observed distinct differences between RA beavers and RS or translocated beavers in the relationship between the distance traveled from their release sites and time (**Table 3**; **Figure 3**). For RAs, *ln*(*time since release*) had no detectable effect on *ln*(*distance from release*)—RA beavers did not change their displacement from their release site over time. In contrast, translocated beavers and RS beavers moved farther from their release sites during the monitoring period, albeit at a diminishing rate (**Table 3**; **Figure 3**). The random effects of Beaver ID on both the intercept and the effect of *ln*(*time since release*) substantially improved model fit [likelihood-ratio $\chi^2_{(2,\ n=1{,}110)} = 225.29$, $p < 0.001$; marginal $R^2 = 0.45$, conditional $R^2 = 0.86$].

Based on the step-length model, we observed differences between the displacement rates of RA beavers and RS or translocated beavers (**Table 3**). Passive integrated antennae detections were associated with higher displacement rates, while neither river discharge category nor NDVI value at the start of a step affected displacement rates in the model. Resident adult beavers moved more slowly than the beavers in other state categories, although the confidence intervals of all state categories overlapped to some extent (**Figure 4**). When all other covariates were held constant, RA, and translocated beavers exhibited acceleration initially, followed later by gradual deceleration in increasing step duration. Resident subadult beavers exhibited quick deceleration initially, followed later by gradual deceleration in increasing step duration (**Figure 4**). Resident subadult beavers displaced fastest over short time periods (i.e., hours and days), while translocated beavers displaced fastest over long time periods (i.e., months, **Figures 4**, **5**). Resident adult beavers moved the slowest at all temporal scales (**Figure 5**). Resident adults also reduced their speed as time since release increased, whereas the three other beaver state categories demonstrated a slight increase in speed as time since release increased (**Figure 5**). Similar to the displacement model, the random effects of Beaver ID on both the intercept and the effect of *ln*(*step duration*) substantially improved model fit [likelihood-ratio $\chi^2_{(2,\ n=600)} = 11.66$, $p < 0.01$; marginal $R^2 = 0.30$, conditional $R^2 = 0.51$].

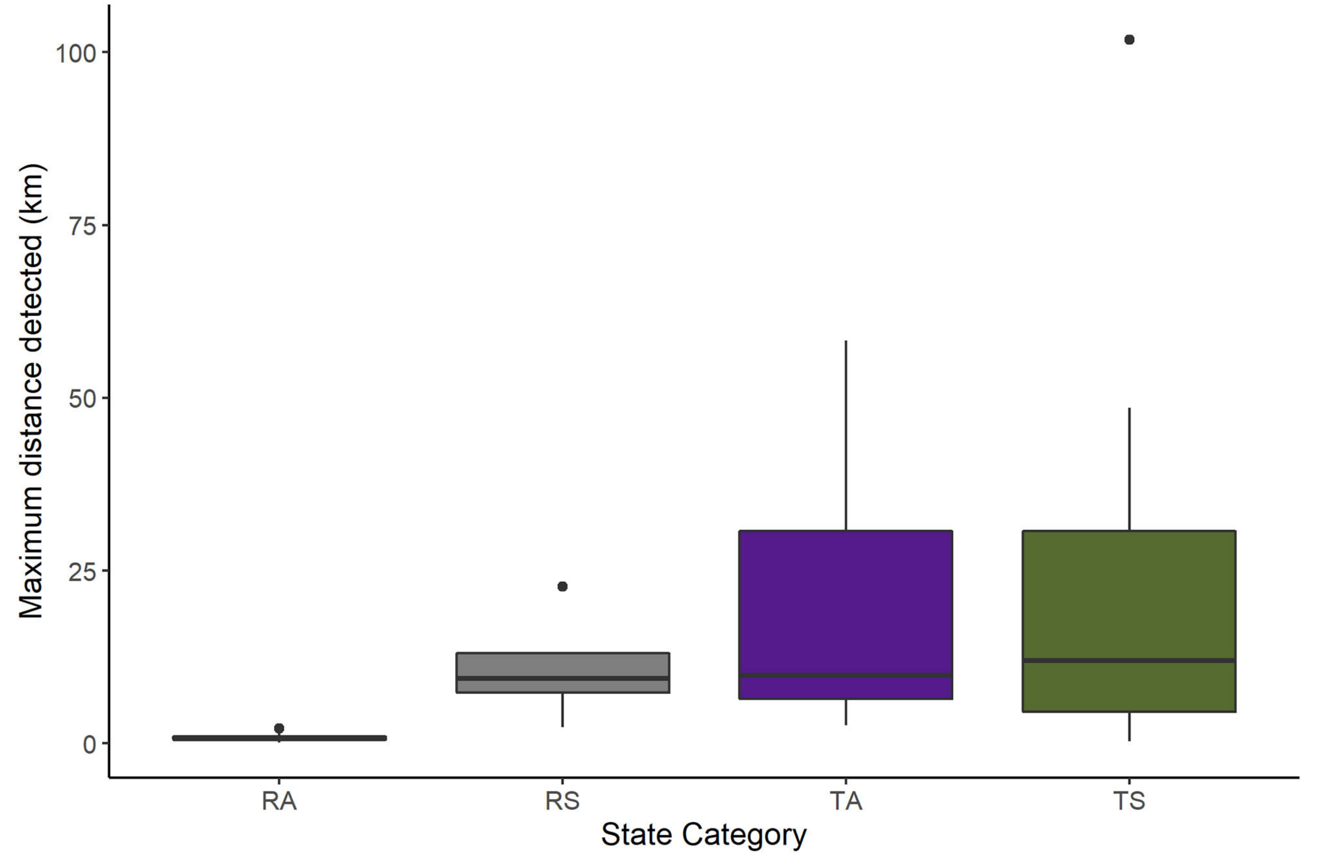

**FIGURE 1 |** The maximum distance between the most upstream and downstream locations resident adult (RA, *n* = 9), resident subadult (RS, *n* = 4), translocated adult (TA, *n* = 21), and translocated subadult (TS, *n* = 19) beavers were detected (km) in the Price, San Rafael, and Green Rivers in east-central Utah, USA. Beavers were monitored via PIT-, VHF-, and GPS-tags from May 2019 to March 2020. The boxes encompass the first through third quartiles (25–75 percentiles), while the whiskers extend to the highest or lowest values within 1.5 times the inter-quartile range (the distance between the first and third quartiles). Maximum distances detected outside of this range are outliers and plotted as points.

The fine-scale movement rates of RA and translocated beavers were similar (**Table 3**; **Figure 6**). Time of day (i.e., day vs. night) was an important parameter explaining fine-scale beaver movement patterns, with beavers being more active at night. Including a random effect of Beaver ID on the intercept in the fine-scale movement rate model did not improve model fit [likelihood ratio $\chi^2_{(1,\ n=1,110)} = 0.28$, $p = 0.6$; marginal $R^2 = 0.20$, conditional $R^2 = 0.28$], but was necessary to account for the repeated sampling events for individual beavers.

## DISCUSSION

Our findings suggest translocated beavers exhibited movement behavior similar to dispersing RS beavers, likely moving through their new environment in search of a mate and a suitable site to settle. We found that translocated beavers demonstrated movement patterns similar to RS beavers in the first 6 months post-release, with an exploratory dispersive phase following release gradually decaying into more sedentary space-use indicative of home range establishment. Translocated beavers moved substantially farther and faster than RA beavers, beavers which already had established territories and therefore likely had no need for such exploratory movement patterns. However, contrary to our fine-scale movement rate hypothesis, we observed no differences in median distance moved between translocated and RA beavers over a short time span (5 min), suggesting day-to-day activity patterns such as foraging and resting were not greatly impacted by dispersal or translocation. These results suggest that although translocated beavers typically demonstrated wide-ranging movement patterns initially, movement behavior patterns will eventually mimic RA beavers.

Resident adult beavers remained in small stretches of river throughout time, with maximum distance detected between the most upstream and downstream locations of each beaver averaging 0.86 ± 0.21, suggesting they held established home ranges and territories. The distance we observed was smaller than naturally occurring American and Eurasian beaver home ranges reported in other studies (3.6 ± 0.3 km, Graf et al., 2016b; 2.2 ± 0.5 km, Breck et al., 2001; 1.8 ± 0.3 km in smaller streams and 3.6 ± 0.5 km in larger rivers, Havens et al., 2013). Smaller

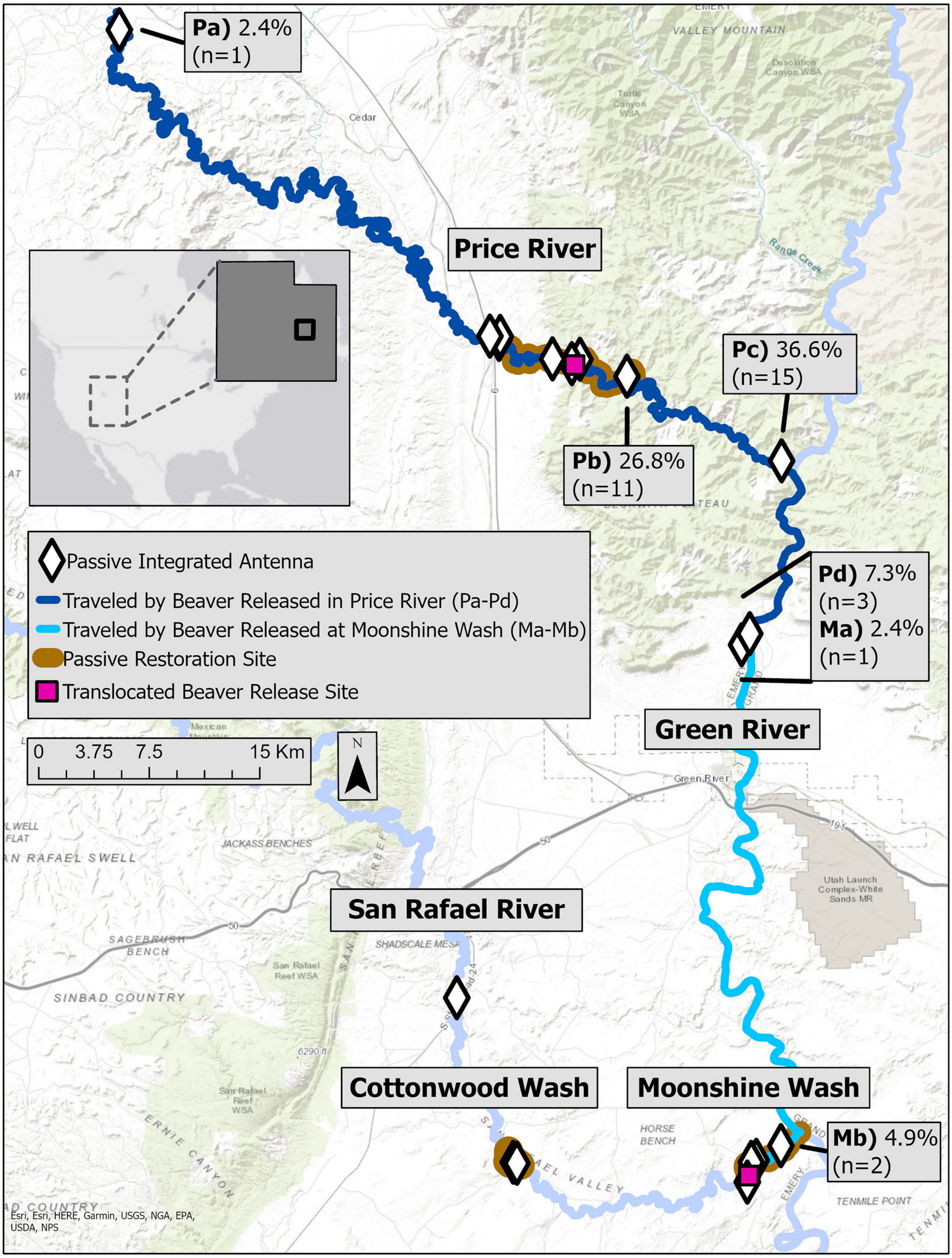

**FIGURE 2 |** Passive restoration sites and surrounding stretches of river on the Price River and the lower San Rafael River at Cottonwood Wash and Moonshine Wash in east-central Utah, USA. Inset text boxes labeled with letters represent the proportion and number of translocated beavers detected at certain passive integrated

*(Continued)*

**FIGURE 2 |** antennae (PIAs) outside of or near the end of the passive restoration sites. The color of the river line indicates which release site translocated beavers originated from (Moonshine Wash or Price River)[a]; 36.6% ($n = 15$) of translocated beavers were not detected by the labeled PIAs (Pa-Pd or Ma-Mb), and 17.1% ($n = 7$) of translocated beavers were detected at more than one of the labeled PIAs. [a]*Distance each PIA is from each release site: Pa, 101 km from Price River release site; Pb, 7 km from Price River release site; Pc, 29 km from Price River release site; Pd, 47 km from Price River release site; Ma, 58 km from Moonshine Wash release site; Mb, 5 km from Moonshine Wash release site.*

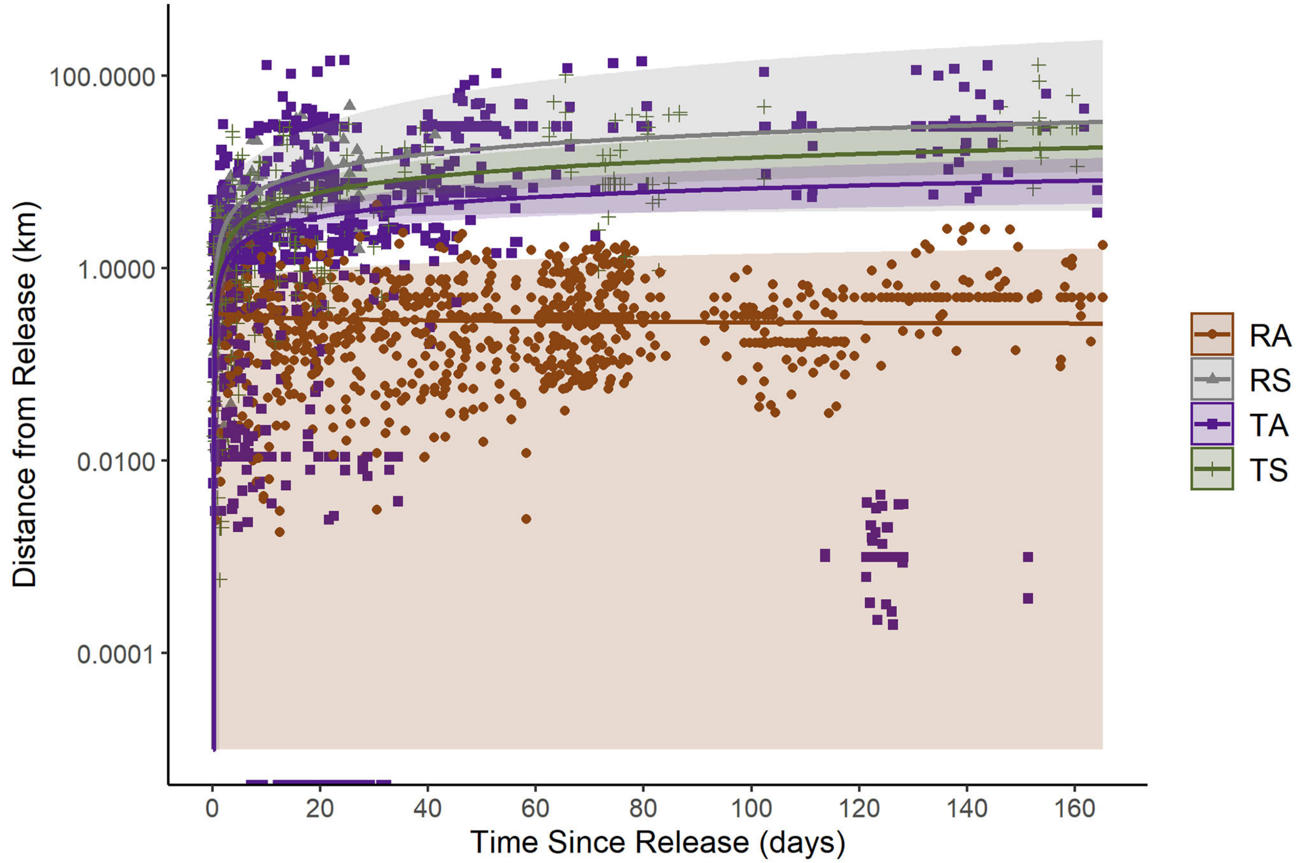

**FIGURE 3 |** Relationship between distance from release (displacement, in river km) and time since release for beavers (RA, resident adult; RS, resident subadult; TA, translocated adult; TS, translocated subadult) monitored in desert rivers, east-central Utah, USA, from May 2019 to March 2021. Lines and shaded 95% Confidence Intervals only include the fixed effects from the back-transformed predicted values of a log-log regression linear mixed model (marginal $R^2 = 0.45$, conditional $R^2 = 0.86$, $n = 1{,}110$).

home ranges may be caused by resources being less dispersed and less diverse in smaller rivers (Havens et al., 2013). Our findings are consistent with previous findings in smaller streams, such as a small creek in Oregon where mean linear home range size was 1.56 ± 0.71 km (1 SE; Maenhout, 2013). Alternatively, home ranges may have been small because seasonal resource availability affects beaver movement (Bloomquist et al., 2012; McClintic et al., 2014a; Korbelová et al., 2016), which may be intensified in a desert ecosystem. Summer temperatures in our study system were extremely high and food resources were often localized; these two factors potentially contribute to reduced movements. In addition, we tracked many beavers during drought periods when river discharges were low, increasing the difficulty for beaver to evade predators when far from the safety of a burrow or lodge.

The maximum distances we detected between the most upstream and downstream locations for each RS were similar to or larger than movement patterns recorded in other studies. In Montana, mean dispersal-settlement distance for subadult American beavers was 10.9 ± 3.1 km (Ritter, 2018), and in Oregon, it was 16.2 ± 9.3 km (Maenhout, 2013), yet mean dispersal distance of Eurasian beavers in Norway was 4.5 ± 5.4 km (Mayer et al., 2017). The four RS beavers in our study dispersed following release; three moved >9.0 km. One beaver only moved 2.38 km from its natal colony to another colony, an indication of successful dispersal (Sun et al., 2000). While it is possible that capture, quarantine, and handling could have induced these dispersal events (e.g., Kukalová et al., 2013), a study in Norway demonstrated no change in short-term Eurasian beaver space use post-capture and post-tagging,

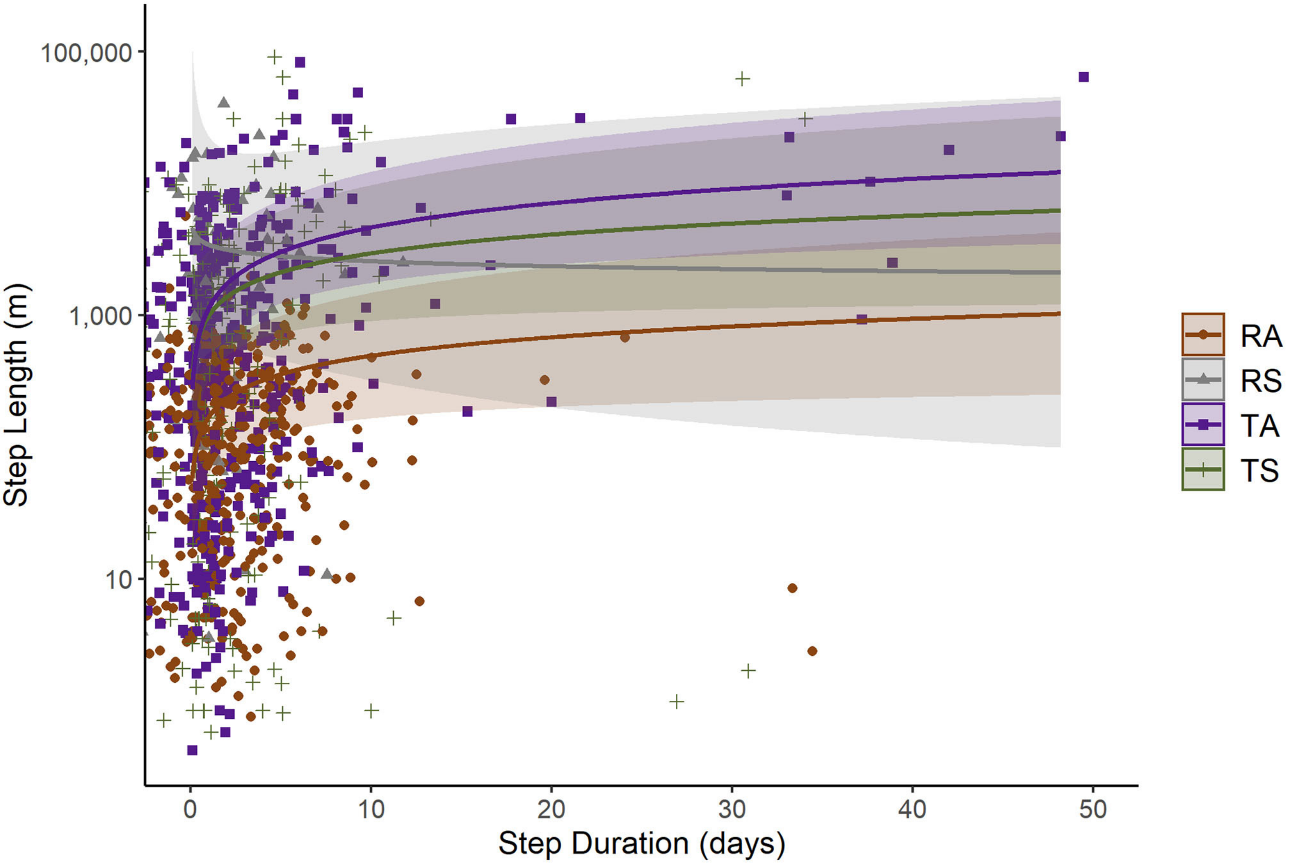

**FIGURE 4 |** Relationship between step length (in river m) and step duration (in days) for beavers (RA, resident adult; RS, resident subadult; TA, translocated adult; TS, translocated subadult) monitored in desert rivers, east-central Utah, USA, from May 2019 to March 2021. Lines and shaded 95% Confidence Intervals only include the fixed effects from the back-transformed predicted values of a log-log regression linear mixed model (marginal $R^2 = 0.30$, conditional $R^2 = 0.51$, $n = 600$). We held all other covariates included in the model constant for visualization purposes (medium river discharge category only, PIA detections only, mean NDVI value, and mean time since release).

although only dominant adults were included in their study (Graf et al., 2016a).

Similar to other studies, translocated beavers were detected to have moved similar maximum distances as RS beavers. The mean distances moved for beavers translocated in North Dakota was 14.6 ± 2.1 km (Hibbard, 1958), 7.4 straight-line km for beavers translocated to streams in Wisconsin (Knudsen and Hale, 1965), and >10 km from their release sites for 51% of translocated beavers in Wyoming (McKinstry and Anderson, 2002). Conversely, translocated beavers only moved a mean distance of 3.3 ± 0.2 km from their release sites in Oregon, indicating their model-based method of release-site selection may have identified high-quality vacant habitat, encouraging beavers to stay (Petro et al., 2015). Translocated individuals may also roam much farther than naturally dispersing individuals. Along with our study, where translocated beavers moved up to 101.8 km, beavers have been reported to move 238 km in North Dakota (Hibbard, 1958) and 76.2 km in Wisconsin (Knudsen and Hale, 1965).

Results of our displacement model showed that RS and translocated beavers moved farther from their release sites than RA beavers. Spatiotemporal autocorrelation may exist due to our use of sequential observations in this model and despite accounting for repeated observations using random effects. Nonetheless, our results serve as an effective demonstration of the considerably larger distances traveled by dispersing subadult and translocated beavers compared to RA beavers, even soon after release. Final detections for 61.4% of our translocated and RS beavers were downstream of their release sites, similar to previous studies of dispersing subadult beavers that reported that the predominant direction of travel is downstream (Leege, 1968; Sun et al., 2000). Beavers likely exert less energy while covering longer distances when traveling with the current. Results from our displacement model show TA beavers demonstrated lower displacement from release than resident and TS beavers, potentially indicating these individuals settled more quickly, although this result should be interpreted with some caution because the confidence intervals overlapped. Most adult translocated beavers likely

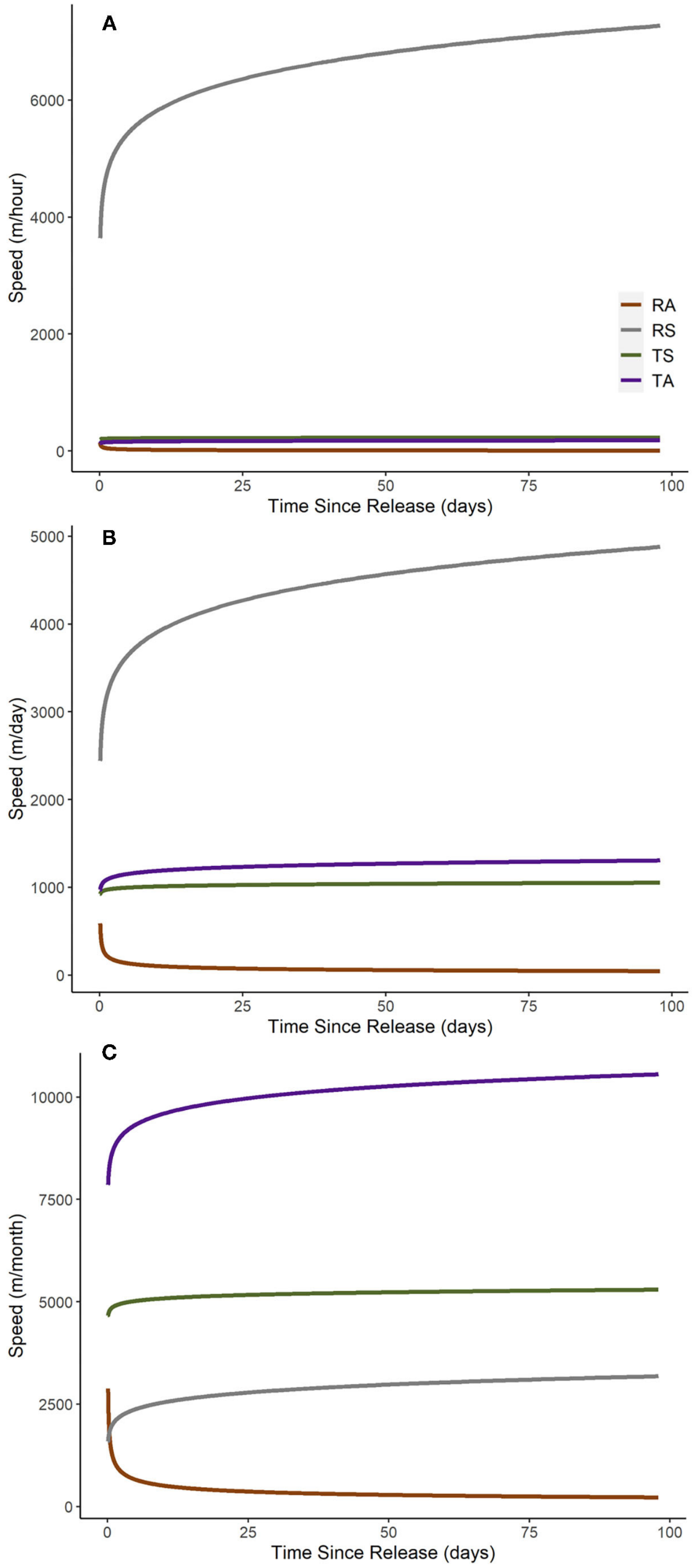

**FIGURE 5 |** Predicted relationship between speed (step length/step duration) at multiple temporal scales [**(A)**, m/hour; **(B)**, m/day; **(C)**, m/month] and time since release for resident adult (RA), resident subadult (RS), translocated adult (TA), and translocated subadult (TS) beavers monitored in the Price, San Rafael, and Green Rivers, Utah, USA, from May 2019 through March 2021. Relationships are based on a log-log regression linear mixed model. All other covariates included in this model were held constant for visualization purposes (medium river discharge category only, PIA detections only, and mean NDVI value).

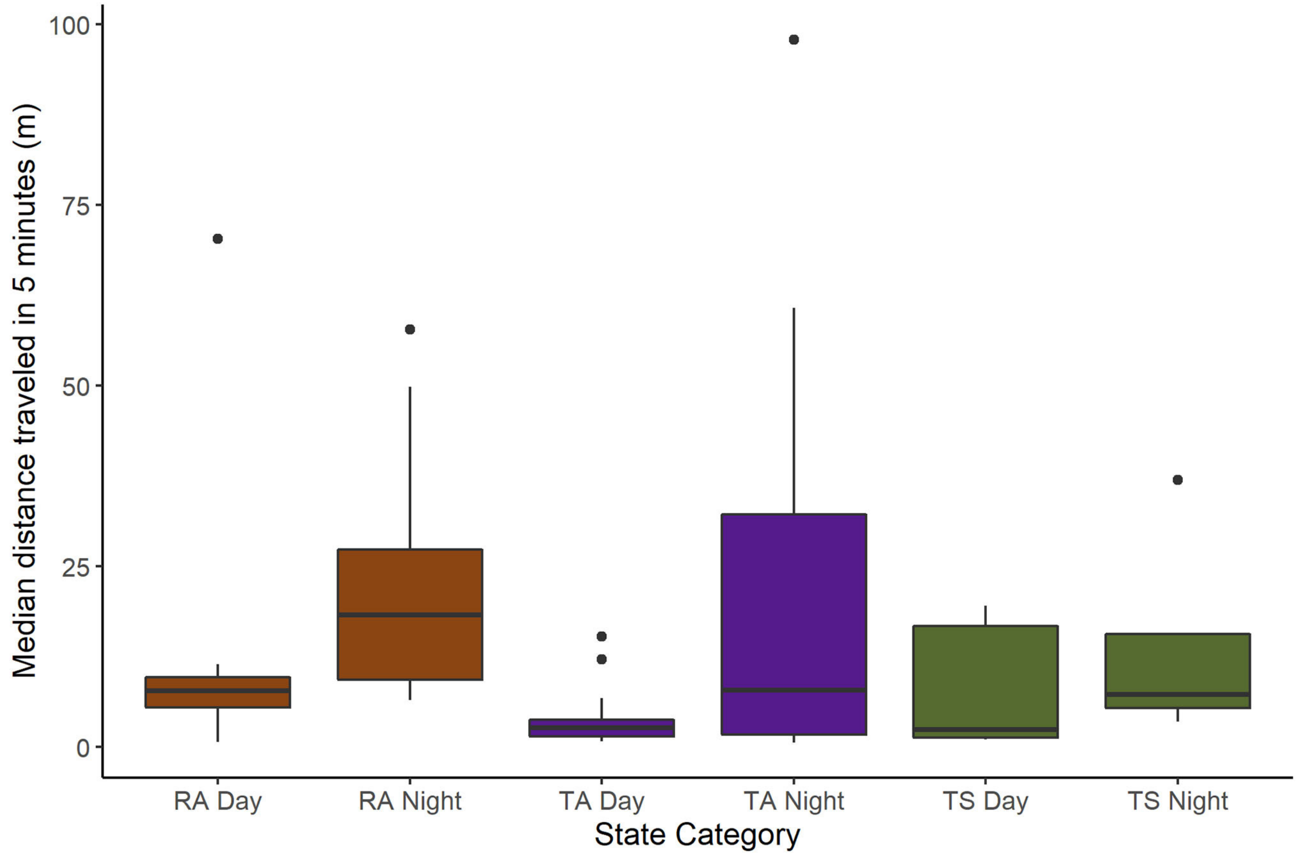

**FIGURE 6 |** Median distance traveled in 5-min intervals during 60-min sampling sessions for beavers monitored in the Price, San Rafael, and Green Rivers, Utah, USA, from May 2019 through October 2020. Observations are separated by time of sampling session (day or night) per beaver state category (RA, resident adult; TA, translocated adult; TS, translocated subadult). The boxes encompass the first through third quartiles (25–75 percentiles), while the whiskers extend to the highest or lowest values within 1.5 times the inter-quartile range (the distance between the first and third quartiles). Median distances traveled in 5 min outside of this range are outliers and plotted as points.

already experienced natal dispersal through an unfamiliar environment and territory establishment in their lifetime (Baker and Hill, 2003). Perhaps this previous experience led them to more quickly settle in the closest suitable site, find a mate, and defend their new territory from subordinate subadult beavers, who may not have dispersed before. Knowledge on previous experience by beavers slated for translocations may be difficult to obtain but could improve which individuals would exhibit philopatry and should be considered in future research.

Dispersing beavers may need to travel longer distances to find an area to settle with sufficient resources for survival in desert rivers because they have patchier and more unpredictable resources (Gibson and Olden, 2014; Barela and Frey, 2016). Rivers in our study had low existing beaver densities (Macfarlane et al., 2017). This may have allowed RS and translocated beavers to be choosier about selecting high-quality sites for settlement because there was reduced “social resistance” effects (Armansin et al., 2020) with more unoccupied territories and less potential for aggressive encounters with conspecifics (DeStefano et al., 2006). Some of our translocated beavers used temporary settlement sites centered around a discovered burrow or hiding place as a known safety refuge from which to conduct exploratory movements; this has been documented in dispersing subadult beavers (Sun et al., 2000; McNew and Woolf, 2005; Ritter, 2018).

When existing resident populations are low, as is common in conservation translocation or reintroduction efforts (Seddon et al., 2014), translocated individuals may have to travel farther to find a mate. One week post-release we observed no translocated beavers who were released as a pair or family group in close proximity to each other, indicating that translocated beavers were likely unable to find their original release groups and instead were searching for new mates. This group fission is similar to a study in Kazakhstan in which translocated kulan (*Equus hemionus kulan*) had difficulty reconnecting with other translocated individuals once breaking from the group, negatively impacting reproduction in the reintroduced herd (Kaczensky et al., 2021). These findings emphasize the importance of translocating large numbers of individuals or releasing individuals near existing populations to increase conspecific encounter rates and increase recruitment, a key to conservation translocation success.

Our results also demonstrated RS and translocated beavers move more quickly than RA beavers, although there was some overlap in confidence intervals. Resident adult beavers were likely already settled in the best quality habitat, spending more time in concentrated areas of high resource availability with a known place of safety nearby, therefore moving more slowly to reduce their encounter rates with predators (Prokopenko et al., 2017; Dickie et al., 2020). Conversely, the fact that RS and translocated beavers were in an unfamiliar, novel environment may have heightened their perceived predation risk, causing them to move faster. Beavers moved faster the farther they were from their lodge to minimize increased predation risk from alligators in less familiar areas of Alabama (McClintic et al., 2014b).

Fine-scale movement behavior did not differ among categories of beaver, suggesting environmental factors had a larger effect on median distance moved over short time periods (5 min intervals). In general, beavers exhibit crepuscular or nocturnal activity patterns, a common predator avoidance strategy (Swinnen et al., 2015). Translocation or dispersal did not alter this behavior; all beavers moved less during the day, likely resting in burrows or lodges to insulate against the extreme desert temperatures (Buech et al., 1989). During dispersal or translocation, beavers must still forage and rest to survive, and our fine-scale movement patterns suggest that these short-term behaviors remained similar to RA beavers. We note that there is likely some error in our estimation of the true location of beavers during fine-scale monitoring. We used single azimuths to estimate locations, but the error remained generally the same at various sampling distances from the river based on calibration tests using stationary test transmitters, and among different beaver state categories. As such this bias was fairly uniform across sampling sessions and should not affect relative comparisons.

Inference from our results are somewhat limited due to sample size once individuals were classified among the beaver categories. For example, we did not include sex because it was confounded with other parameters in the models: both male and female beavers are territorial and disperse, so we did not expect sex to have a strong effect on movement as compared to beaver category (Baker and Hill, 2003). Results for RS beavers demonstrated the largest variation and widest confidence intervals of the four beaver categories, likely due to the small sample size of this state category ($n = 4$). In future studies, the use of more detailed habitat covariates or conducting a habitat selection analysis may reveal more about the external drivers of coarse-scale movement behavior in desert systems (e.g., Wang et al., 2019; Ritter et al., 2020). Despite our unsurprisingly low small sample size and thus limited inferential power, the patterns we observed were clear and supported most of our original hypotheses.

In terms of displacement, though translocated beavers tended to move more similarly to dispersing RS beavers overall, we observed a gradual leveling-off of differences among beaver categories, suggesting these individuals will eventually establish a home range similar to RA beavers and may subsequently build dams which contribute to restoration. Logistical challenges limited our monitoring period to 6 months post-release, or shorter periods for some individuals due to transmitter failure (Doden, 2021), so confirming settlement site establishment was challenging. However, we observed four translocated beavers permanently settle outside of the targeted restoration sites 8.6–155.4 days post-release, supporting our expectation that translocated beavers will eventually settle and behave similarly to RA beavers in regard to movement. Indeed, translocated individuals of any species must adjust to their novel environment to survive but need time to learn and explore their new surroundings in order to make appropriate changes to their behavior. For example, translocated "alalā" (*Corvus hawaiiensis*) in Hawaii learned to be more vigilant over time to limit predation at supplemental feeding sites (Lee et al., 2021), and swift foxes (*Vulpes velox*) translocated in Canada exhibited distinct post-release movement stages (initial acclimation, establishment, final settlement) as they adjusted to their new surroundings over time (Moehrenschlager and Macdonald, 2003).

The comparative technique we used here to monitor naturally occurring resident individuals to translocated individuals should inform translocation expectations and outcomes for the conservation of beavers as well as other species. Results from a concurrent study demonstrated that 40.4% of translocated beavers included in this study were detected outside of targeted restoration sites, while no RA beavers were detected outside of the targeted restoration sites (Doden, 2021). Despite the variable site fidelity of translocated beavers, 22 dams were constructed by resident and translocated beavers in the targeted restoration sites during the study, suggesting that translocations had some success in supplementing resident beaver dam-building and contributing to restoration objectives. Identifying ways to improve the proportion of translocated beavers that settle within targeted restoration sites is an important next step. Previous studies have observed increases in beaver dams near structural features such as BDAs installed in rivers, and these structures create deep pools which may help improve translocation success (Bouwes et al., 2016; Pollock et al., 2018). However, this approach has yet to be studied simultaneously with translocations in desert systems. In addition, even beavers that settled outside of targeted restoration sites should be considered to contribute to restoration success at a more riverscape scale. These desert tributaries have, in some cases 50–100 km of very degraded habitat, and native fishes are challenged by this flow-related habitat simplification at very large scales (Budy et al., 2015; Pennock et al., 2021). Our study presents novel research critical to informing future beaver translocation efforts in desert rivers, because this study is the first to compare naturally occurring resident beaver movement behavior to translocated beaver movement behavior in the same system and is one of few studies of beaver movement ecology in desert systems (Gibson and Olden, 2014).

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation or at Dryad, doi: 10.3389/fcosc.2022.777797

## ETHICS STATEMENT

All procedures in this study including animal capture, handling, tagging, and monitoring were approved the Institute for Animal Care and Use Committees at Utah State University (No. 10128) and USDA-National Wildlife Research Center (QA-3171).

## AUTHOR CONTRIBUTIONS

ED participated in methodology, data collection, data analysis, writing of the original manuscript draft, and review and editing. PB took part in conceptualization, funding and resource acquisition, supervision, and review and editing. TA participated in methodology, data analysis, and review and editing. JY engaged in conceptualization, methodology, funding, resource acquisition, supervision, and review and editing. All authors contributed to the article and approved the submitted version.

## FUNDING

Funding for this study was provided by the U.S. Bureau of Land Management (Agreement L18AC00121), the Utah Division of Wildlife Resources (in-kind), the U.S. Bureau of Reclamation (Agreement R19AC00153), the Ecology Center at Utah State University, the Utah Chapter of the Wildlife Society, the U.S. Department of Agriculture-National Wildlife Research Center, and the U.S. Geological Survey, Utah Cooperative Fish and Wildlife Unit (in-kind).

## ACKNOWLEDGMENTS

The authors thank all of the collaborating organizations and involved personnel from those organizations for funding and logistical support. In particular, we are grateful to Gary Thiede (USU, Fish Ecology Lab) for logistical support and to Peter MacKinnon (USU, Biomark Inc.) and Daniel Keller (UDWR) for equipment support during field studies. Special thanks to Annette Roug (UDWR) and the USU Beaver Ecology and Relocation Center, particularly Nate Norman, for their hard work capturing and processing beavers. Thanks to the landowners who granted access to their property for our study and the many volunteers and technicians who assisted in the field. The findings and conclusions in this publication have not been formally disseminated by the U.S. Department of Agriculture and should not be construed to represent any agency determination or policy. This research was approved by the Institute for Animal Use and Care Committees at USDA-National Wildlife Research Center (QA-3171) and Utah State University (#10128). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.