WILDLIFE WELFARE

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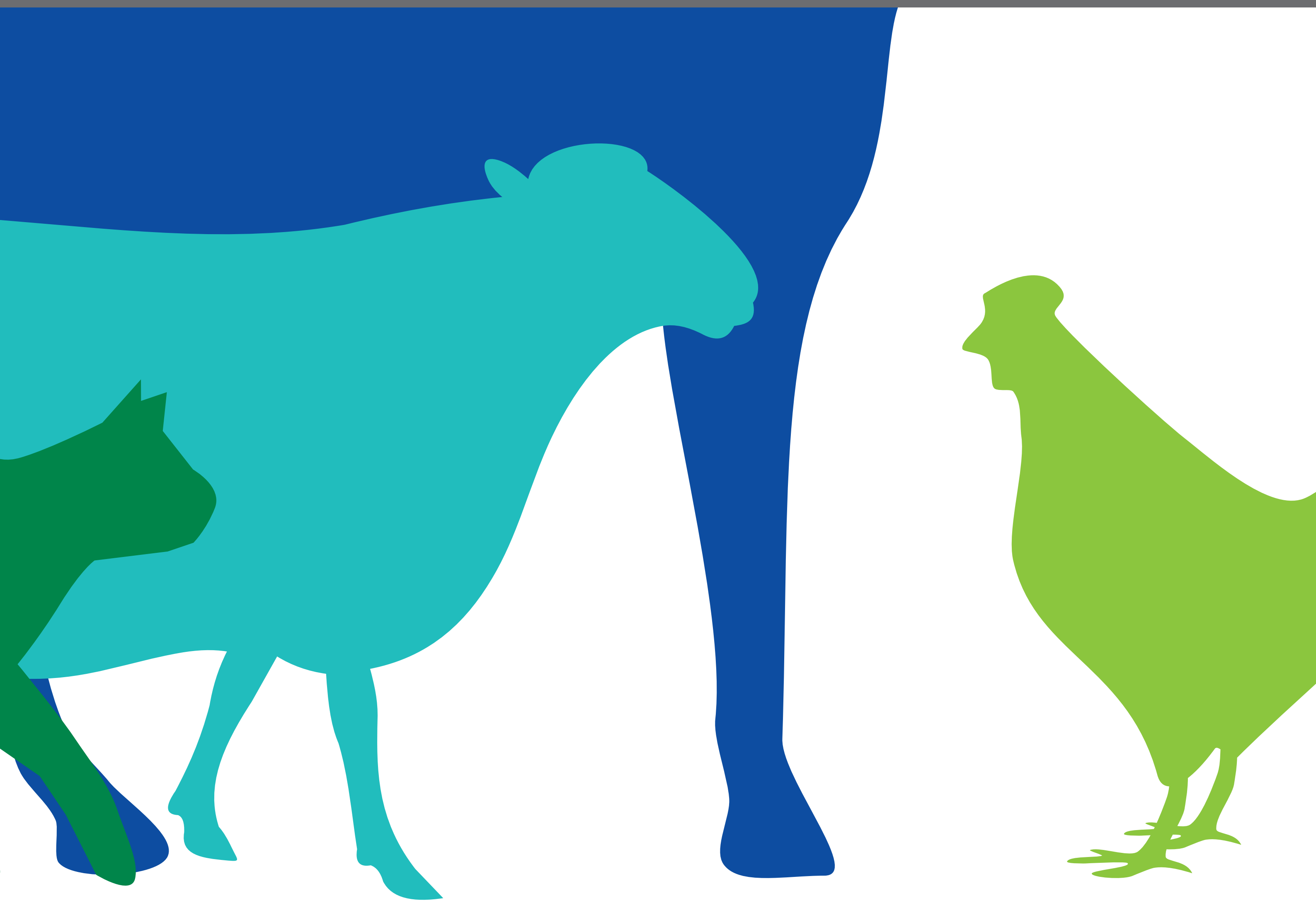

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WILDLIFE WELFARE

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EDITORIAL
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Editorial: Wildlife Welfare

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Editorial on the Research Topic

Wildlife Welfare

Animal welfare relates to the feelings, behavior, and the health status of animals. Nevertheless, animal welfare legislation rarely prescribes what animals should feel or experience, but rather what humans should do to protect the animals in their care from unnecessary suffering, and e.g., specifications to provide them with suitable housing conditions and appropriate feed to ensure a reasonably good life. This obviously applies to domesticated animals and wildlife kept in enclosures, but not to free-roaming wildlife. Wildlife welfare has received far less attention than welfare for farm or companion animals, although attempts have been made (1, 2). In recent years the extent of interest in wildlife welfare has grown, as more people have realized that humans have a substantial influence on the lives and welfare of wildlife individuals. Humans, as individuals and as a species, intentionally or unintentionally influence the welfare of wildlife in many different ways, some of which are discussed in this special issue.

The growing global human population is impacting wildlife habitats, and causing disturbance or destruction of nature, be it for infrastructure projects such as roads, city expansion or beach resorts, or to gain access to natural resources such as oil, timber or minerals. The expanding human population requires more food. Livestock and feed production are among the greatest threats to biodiversity and key drivers in land-use change. Forests and savannahs are being converted into agricultural land for crop and animal production while oceans are unsustainably trawled for fish. This will inevitably decrease the potential for wildlife to find suitable areas for breeding, foraging, staging during migration or hiding from predators. In this volume, Stephen and Wade present lamprey on Vancouver Island as an aquatic example of how to work with shared priorities for social expectations, conservation obligations and species recovery at the population level of welfare.

By introducing domestic livestock to an area, humans will not only compete for space, but may also contribute to the spread of various infectious diseases from livestock to wild species (and, of course, also the other way around) or from wildlife to humans (3). There is also the obvious threat, not only to the survival of certain species but also to the welfare of individual animals, caused when humans, intentionally or by accident, introduce invasive species to a new region, resulting in predation or inter-species competition for resources such as nesting sites or food. If humans then decide to eradicate such invasive species, the eradication process may in turn involve negative effects on the welfare of the individuals of the invasive species.

Unregulated hunting, poaching and unsustainable fishing by humans can, over time, reduce the number of wild animal individuals to a level where they can no longer proliferate and will become extinct. Such activities can also directly lead to animals being hit or caught, struck and lost, injured but not killed—causing considerable suffering if the animal cannot immediately be located and humanely killed. Furthermore, hunting and fishing activities may impact animals other than the

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intended prey, through disturbance, by-catch or entanglement. The entanglement of cetaceans is addressed by Dolman and Brakes, where the authors discuss the animal welfare consequences of incidental capture of marine wildlife in commercial fishing gear.

It should be acknowledged that tourism activities, even when carried out by wildlife enthusiasts, who may aim to support wildlife in the wild, may have unintended negative side effects on wild animal welfare. Wildlife encounters, such as whale-watching, seal-spotting, bird-watching, or tiger-tracking, may involve elements of disturbance or improper feeding of the target animals. The paper by Nunny and Simmonds brings up the need for strengthened legislation and guidelines to protect wild-living solitary sociable dolphins in relation to interactions with people.

In the area of wildlife conservation projects, a large range of activities from habitat restoration and head-starting programmes to translocation, captive breeding and the keeping of so-called “parallel populations” can be identified. When the focus is on species conservation, the welfare of the individual animals has historically often been given a lower priority. This has, however, changed during recent years, and scientists and others have raised questions about ethical aspects of such interventions and the potential to improve the welfare of animals involved in such projects (4–6). This aspect is highlighted in the paper by Beausoleil et al., which describes how cross-disciplinary information-sharing and collaborative research and practice in conservation can be applied in captive breeding projects, to facilitate the incorporation of both “fitness” and “feelings” to improve understanding of the welfare state of the animals.

Is there a difference between wildlife research and wildlife management regarding welfare aspects? In many countries, the legislative requirements differ depending on if the interventions are classified as research rather than management, although the actual handling of the animals may be identical. Lindsjö et al. argue for a more developed legislation about welfare matters in relation to these aspects.

Whilst aiming to improve conservation and indirectly improve the welfare status of animals, wildlife research, as well as captive breeding programmes for restoration of wild animal populations, can involve animal welfare risks (**Figure 1**). An increased interest in animal welfare can relate to various aspects of capture methods, the design of enclosures for breeding animals or head-started animals, preparation of captive-bred animals for a life in the wild, preparation of release-sites to improve the survival chances of newly-released animals, and proper post-release monitoring. In their paper, Greggor et al. highlight several of these aspects, emphasizing the need for an evidence-based approach to evaluate practices in conservation breeding facilities from an animal welfare perspective, while still meeting conservation goals. Thulin and Röcklinsberg analyse ethical considerations for wildlife reintroductions and rewilding projects, and Robins et al. discuss how telemetry can be used to improve post-release monitoring of apes. Arnemo et al. discusses long-term safety in bears equipped with radio transmitters, and Robins et al. do so in relation to orang-utans. The paper by de Jong addresses how, in accordance with the 3R principles, to avoid redundant handling and interventions. The 3R principles are commonly used when designing studies involving traditional laboratory animals for research. In wildlife research, this approach is yet to be further developed. Huber et al. focus on the possibility of using leukocyte coping capacity to quantify and evaluate stress in wildlife in captivity or when otherwise being handled by humans, and the strengths and weaknesses of this immunological approach.

FIGURE 1 | Young goshawk at ringing. A short moment of close interaction between humans and the bird. Such interactions can still, if not properly carried out, involve animal welfare risks.

The ultimate aim of captive breeding programmes is often to ensure that self-sustaining, free-ranging wildlife populations can exist, and this requires suitable habitat, sufficiently large enough areas, with intact ecosystems and sustainable ecosystem services. Furthermore, the choice of breeding animals in terms of health, behavior and temperament can be highly relevant for the welfare of their offspring, once released. Should suitable groups be formed before release? This aspect of sociality, and the importance of social networks for wildlife living in groups is discussed in the paper by Brakes. In addition to the welfare impacts for the translocated animals, the welfare of animals of other species at the release site should be considered: is there competition for food or other resources? Is a novel predator being released in an area?

If a wild animal is kept in captivity, for breeding, for education or show at a zoological garden, handled in research or for management purposes, there are both legal and moral obligations related to human responsibility for the well-being of the individual animal. This special issue highlights that this responsibility extends beyond the fence.

AUTHOR CONTRIBUTIONS

CB and HL have written the draft of the editorial and it was amended and revised by the other authors. All authors have served as editors of the Research Topic.

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PERSPECTIVE
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Wildlife Population Welfare as Coherence Between Adapted Capacities and Environmental Realities: A Case Study of Threatened Lamprey on Vancouver Island

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Wildlife conservation lacks a well-accepted ethical foundation for population welfare. In this paper we propose a definition of wildlife population welfare and use a case study to suggest its value for species recovery planning. We define wildlife population welfare as coherence between the species' adapted capacities and the realities of its current environment. We present a case study of the Cowichan Lake lamprey (*Entosphenus macrostomus*), a parasitic fish species endemic to three connected lakes in British Columbia, Canada. Individual-level welfare concerns were insufficient to inspire actions to protect this threatened species. The key threats to Cowichan Lake lamprey can be linked to anthropogenic changes and global threats such as climate change. Due to prevailing uncertainties and the inability to eliminate critical threats, the species recovery plan was focussed on securing critical environmental and social assets to meet evolved adaptations of lamprey while considering the needs of other species, including people. This assets focussed approach was well suited to developing consensus for action to enable a harm reduction perspective that recognizes that many of the threats cannot be eliminated but actions could be taken to enable the population to succeed by protecting critical environmental resources. This was consistent with our population welfare perspective which focusses on assets rather than deficits to help identify shared priorities for species recovery, conservation obligations, and social expectations.

Keywords: welfare, lamprey, health, conservation, harm reduction, endangered species, resilience

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INTRODUCTION

There is little doubt that human activities are harming wild animals[1] (1). The plethora of reports of species declines and extinctions create innumerable conservation challenges. While we like to think that conservation priorities and actions are objective and science based, human attitudes and values shape our conservation behaviours (2). Which populations to protect and when to intervene is a matter of choice. Kirkwood and Sainsbury (3) identified four factors that influence our attitudes toward wildlife; (i) the extent to which we are responsible for harm to them; (ii) the extent to

[1] For the purposes of this paper wildlife refers to free ranging wild vertebrates, including amphibians, reptiles, birds, mammals, and fish

which the harmed animals are under our stewardship; (iii) the severity of the problems that harm wildlife and (iv) cultural and economic factors, including the popularity of the species involved. The authors noted the illogical but heavily weighted role popularity plays. Sociopolitical considerations, resource limitations, and ethical concerns further dictate which species can be protected and when conservation actions are implemented (4). It is increasingly accepted that conservation should not come at the expense of individual animal welfare, yet a well-accepted and applied ethical foundation for wildlife conservation that considers animal welfare is lacking (5). This is due in part to the different "value lenses" used by animal welfare and conservation scientists, with the former valuing the health, quality of life and affective states of individuals and the latter focused on ensuring the sustainability and integrity of populations and ecosystem diversity (6).

BACKGROUND

Animal welfare and conservation have found a common ground in guidelines for the ethical use of wildlife in research and management (7), but there remains a gap when we attempt to find a shared vision for success at a population level. Conservation and animal welfare share the desire to prevent harm to animals (8). To harm something or someone means to damage them or make them less effective or successful than they were. Organizations such as the Canadian Council on Animal Care (9), have developed animal welfare guidelines that are damage focused and intend to reduce harm by minimizing stress to individuals and discouraging procedures that have lasting negative population effects or affect the species' existence. There is less guidance on how to avoid harms that make a wild species "less effective or successful." In some settings, conservation is deemed successful if measures are no longer necessary to prevent extinction (10). Others suggest that avoiding extinction is far too low of a threshold for success and advocate that conservation should promote self-sustaining, diverse, healthy, and resilient species (11). Ultimately, how we assess population level welfare is context dependent (12) and the current context wildlife is facing is that unprecedented global socio-ecological changes are depriving wildlife from the resources needed to prevent harm and be successful (5, 13).

The 2016 Living Planet Index clearly links the 48 to 66 per cent decline in the more than 3,700 wild species assessed between 1970 and 2002 to anthropogenic factors including habitat degradation, invasive species, climate change, pollution, unsustainable freshwater use, and species overexploitation (14). Economic growth that drives these mega-trends is the limiting factor for wildlife welfare (5). Trade-offs between conservation and human use of ecosystem goods and services require compromise between the needs for conservation, ecosystem functioning and resilience, and human livelihoods (15). Finding a shared perspective that allows for concomitant consideration of wildlife welfare and human well-being is becoming an increasingly important endeavour to facilitate actions to protect wildlife in the face of scientific uncertainty and social conflict.

Conservationists unavoidably find themselves grappling with difficult and conflicting social and economic issues that impede actions to secure critical resources that meet the evolved needs and social expectations for wildlife (16). The salutogenesis concept derived from human well-being literature (17) may help bridge conservation and wildlife welfare to inspire actions on the major threats to wildlife. This approach asks why an individual, group, or community stays well despite stressful situations and hardships. Rather than focusing on obstacles and deficits, it deals with securing critical resources to stay well. It is consistent with the concept of harm reduction which promotes actions to build socio-ecological resilience in individuals and populations in the face of uncertainty and social conflict (13). The salutogensis concept of a "sense of coherence" (which reflects the coherence between the capacity to identify, benefit, and use resources to deal with stress and the reality of current living conditions) is consistent with (18) conceptual model which sees animal welfare compromised when adaptations possessed by the animal make an imperfect fit to the challenges it faces in the circumstances in which it lives.

In this paper, we propose a definition of population welfare as coherence between the adapted needs of a species with critical social and environmental resources. We use a case study to illustrate how this definition is applicable to species recovery planning that can inspire positive attitudes to conservation and the development of recovery plans that address the mega-trends that drive many of the harms to wildlife.

DISCUSSION

Cowichan Lake lamprey (*Entosphenus macrostomus*) is an extreme endemic freshwater parasitic fish species found only in Cowichan, Bear and Mesachie lakes in British Columbia, Canada. These three lakes are hydrologically connected; the watershed has a catchment area of 930 km^2, less than half of which is attributed to Cowichan Lake, one of the largest bodies of freshwater on Vancouver Island (6,204 ha area) (19). The outflow of Cowichan Lake is regulated through a weir which has supplied water since 1957 via the Cowichan River to meet the socio-economic and ecological needs of the watershed.

In 2003, Cowichan Lake lamprey was listed as Threatened under Canada's *Species at Risk Act* (SARA). A recovery strategy for the species was completed in 2007 (20). The basic biology of Cowichan Lake lamprey such as longevity, feed preference, spawning, and rearing requirements is largely unknown. This is mostly due to them only being recently discovered, highly cryptic and of no commercial or recreational value. It is recognized that they are an integral part of the ecosystem, like any other species, and have significant scientific value however, these animals are often not well-regarded publicly as they are a parasitic species that feeds on socially highly valued salmonids. The reputation of the Cowichan Lake lamprey has been further tainted by stories of the effects of invasive sea lamprey (*Petromyzon marinus*) on valuable fisheries in the Great Lakes (21) and by popular media depicting lamprey as "aquatic vampires." Despite their protected status, stories of fishers killing these animals or public distain for this species are common. It is likely that this species will always remain at some risk due to its extremely limited distribution (20, 22). The many unknowns and persistent risk to this uncharismatic species present challenges in promoting actions to protect the welfare of the population.

The most imminent threats to Cowichan Lake lamprey are water use and climate change both individually and cumulatively (20) and destruction of critical habitat (22). In recent drought years, plans have been approved for the emergency draw down of Cowichan Lake below historical levels to supply freshwater for the operation of a wood mill. Emergency draw downs take place in the fall after all other water resources stored in the lake are exhausted. This practice harms lamprey as it reduces available spawning and early rearing habitat. Updated climate models for the region indicate that if no changes are made to water storage and water use is maintained at current levels, these conditions will result in reduced access to spawning grounds and larval rearing habitat, decoupling the evolved needs of this species with its current environment. This has already been documented in a drought year (23). While one might conclude that this species is resilient enough to withstand periodic droughts as they have persisted in this system since the last glaciation (24), the anticipated new "normal" of repeated droughts, coupled with increased water use and decreased riparian habitat due to foreshore development may not be consistent with its adapted capacity. Lack of freshwater in the lake also affects other downstream uses including waste water management, salmon conservation, agriculture irrigation and recreational uses.

In recovery planning for the species it has been recognized that; (i) a target abundance is not currently possible to calculate due to the many unknowns about its biology; (ii) the inherent ecological value of this species is not sufficient to motivate conservation actions among some user groups as it is not recreationally or commercially important; but (iii) the primary threats to Cowichan Lake lamprey are not unique to this species. An additional reality is that protected species such as Cowichan Lake lamprey receive much less funding and effort than other more charismatic species such as BC's southern resident killer whales (*Orcinus orca*).

In the absence of specific biological targets for recovery planning, those working toward this species' recovery by necessity, focused on the environmental and social resources to meet the adapted needs of the species. The population welfare approach was, therefore, reflected in the species recovery plan which has the objectives (20, 22) of: (i) maintaining a self-sustaining population that is resilient to short-term habitat perturbations (ii) maintaining, and where possible enhancing, the ecological integrity of lamprey habitat; (iii) increasing scientific understanding through additional investigation of taxonomic status, natural history, critical habitat and threats to the species' persistence and; (iv) fostering awareness of the species and its conservation status, and encouraging active local involvement in stewardship and habitat protection. The recovery plan further recognizes that activities aimed at protecting and enhancing other species of fish and wildlife are likely to also benefit Vancouver lamprey, and vice versa (20).

Concurrent to recovery attempts for this species is the development of a Cowichan Water Use Plan that aims to accommodate the many ecological, social, and economic needs being threatened by impacts on freshwater habitats. The planning process is a partnership between the local Regional District government, Aboriginal communities, industry, and a multi-stakeholder Watershed Board. It aimed to determine better use of water resources which are sustainable and can meet future demands under climate change conditions. The needs and threats to Cowichan Lamprey have now been taken into consideration in the drafting of the Water Use Plan; most notably, the requirement of water during the summer for spawning and early rearing of eggs and larvae.

Bringing this species into the Water Use Plan has increased community awareness of the requirements of this species as well as highlighted the conservation, recreational, and resource use value of directing recovery actions to critical resources shared by lamprey, people and other species such as benthic invertebrates, amphibians, fish and other aquatics animals co-habiting the lamprey's niche. It is now recognized that activities aimed at protecting other wildlife species will likely benefit Cowichan Lake lamprey (20). Further progress to address data gaps to identify determinants of population welfare including conducting new research to identify critical habitat and completing management activities that help reduce impacts on, and better understand the threats to, Cowichan Lake Lamprey (22). Most recently, the first record of nest building and spawning of Cowichan Lake lamprey was reported (25). This work provides preliminary insights into the habitat and environmental requirements for this critical stage of the lamprey life cycle and has helped inform future research and the Water Use Plan.

Earlier recommended actions for this species included determining traditional fisheries science indices such as species abundance and recovery targets. However, there are significant challenges to estimating the abundance of Cowichan Lake lamprey. For example, it is unknown how spatial variation and capture methods combined with a complicated and undefined life history affect estimates of abundance. In addition, little has been done to determine how to assign thresholds for required numbers and demographics specific to the biological attributes of the species to support self-sustainability. In the face of these unknowns, Cowichan Lake is experiencing more frequent episodes of drought, near-shore users continue to modify the riparian habitat, environmental changes are impacting the abundance of the lamprey's prey, and human population growth places more demands on the ecosystem. The population welfare approach described in this case study promotes actions that would reduce the likelihood that well-documented harms, like climate change and riparian habitat disturbance, would make this species less effective and successful. The collaborative actions associated with this species ecosystem now not only address the population welfare needs of the Cowichan Lake lamprey but also are supporting efforts to identify and address the social resources associated with regional mega-trends. They are also supporting research and monitoring as management activities to minimize harm and achieve the recovery goals.

The recovery strategy acknowledges that protecting this species is a collective responsibility involving multiple levels of government, First Nations and community members. With more frequent applications for draw down permits and growing water use concerns, local community groups have been more active in citizen science and outreach for this species. While the consideration of the lamprey's needs in the water use plan is a critical success, its implementation awaits endorsement by local citizens and governments.

CONCLUDING REMARKS

The assets focussed approach to population welfare was consistent with the needs for recovery planning of the Cowichan Lake lamprey. It was better suited to developing consensus for action than a focus on damage to individual animals. It enabled a harm reduction perspective that recognizes that many of the threats to this species cannot be eliminated but actions could be taken to enable the population to succeed by protecting critical environmental resources to meet evolved adaptations while considering the needs of other species, including people. Harm reduction is generally used to describe a set of public health and health promotion strategies to prevent or reduce the adverse consequences to all members of the community rather than only target the hazard. It has been proposed as an approach to promote collaborative policy and action to protect wildlife health by discovering means for horizontal, cooperative actions in advance of serious, irreversible impacts (13). The population welfare perspective presented in this paper provided a bridge between animal welfare, conservation and emerging definitions of wildlife health (26) and provided a foundation for conservation across perspectives and needs. It is consistent with the concepts of one welfare, ecohealth and environmental well-being, all of which serve to foster relationships between people and their ecological system, leading to successful management, distribution, and sustainability of resources for current and future generations as well as for multiple species (27, 28)

In humans there is a close connection between a person's sense of coherence and their health and well-being (29). Key to the salutogeneis concept is that strategies that promote resilience and access to usable critical resources also will contribute to problem reduction and prevention (17). Whereas it is common for estimates of abundance to be a central pre-occupation of fisheries sciences, it may not be suited to conservation science where delays in developing and applying methods to estimate the abundance of understudied or cryptic species will allow ongoing declines of the quality and availability of resources for which they have an adapted dependency for their survival.

Wildlife population welfare as presented in this paper clearly overlaps with core concepts of conservation and population health. In each of these fields, management targets distal determinants of health, welfare, or sustainability by ensuring a species' supporting environment matches its evolved needs. Regardless of the definitions or domains of inquiry used, the perspective used in the case of Cowichan Lake lamprey enabled a; (i) shift away from focussing on estimating a target number in recovery planning; (ii) shifts in attitudes toward action for an uncharismatic species and (iii) support for actions targeting shared critical resources for animal welfare and social well-being. By linking the needs of the lamprey into larger ecosystem management plans, attitudes for species recovery improved and actions were motivated. This is consistent with findings elsewhere that recovery plans for species with greater public or agency profiles are implemented at a higher rate (30).

Successful conservation plans must be clearly linked to species biology as well as attend to the human dimensions of conservation to ensure that recovery plans are appropriately suited to each species' ecological and social situation (31, 32). We propose that population health and welfare may serve as a shared perspective that supports collaborative actions that benefits people while facilitating actions to protect wildlife in the face of scientific uncertainty and social conflict and, therefore, may more likely provoke action, especially for species where charisma and individual animal welfare are insufficient to inspire action.

AUTHOR CONTRIBUTIONS

Each author contributed equally to this paper. The case study is based on field studies undertaken by JW, the second author and previous conceptual frameworks developed by the first author, CS.

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Long-Term Safety of Intraperitoneal Radio Transmitter Implants in Brown Bears (*Ursus arctos*)

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Intraperitoneal radio transmitters have been widely used in free-ranging wild mammals, but there are no long-term studies on their biocompatibility or technical stability within the abdominal cavity of animals. Possible negative health effects may bias results from ecological studies on instrumented animals and raise concerns over animal welfare issues. The aim of this study was to evaluate the long-term technical stability and pathological effects of Telonics intraperitoneal very high frequency (VHF) radio transmitters in brown bears (*Ursus arctos*). We instrumented 305 individual bears with intraperitoneal VHF radio transmitters during a 19-year period. We surgically removed devices that had been in bears for 1–9 years and collected transmitters from animals that died 1–13 years after implantation. We took biopsies for histopathology from tissue encapsulating implants in live bears. Retrieved transmitters underwent a technical inspection. Of the 125 transmitters removed from live bears, 66 were free-floating in the peritoneal cavity [a mean (SD) of 3.8 (1.5) years after implantation], whereas 59 were encapsulated in the greater omentum [4.0 (1.8) years after implantation]. Histopathology of biopsies of the 1–15 mm thick capsules in 33 individuals showed that it consisted of organized layers of connective tissue. In one third of the bears, the inner part of the capsule was characterized by a foreign body reaction. We inspected 68 implants that had been in bears for 3.9 (2.4) years. The batteries had short-circuited four (5.9%) of these devices. This resulted in the death of two animals 10 and 13 years after implantation. In two other bears that underwent surgery, we found the short-circuited devices to be fully encapsulated within the peritoneal cavity 5 and 6 years after implantation. A significant proportion of the other 64 inspected implants showed serious technical problems, such as corrosion of metal parts or the batteries (50%), detachment of the end cap (11.8%), and erosion (7.4%) or melting (5.9%) of the wax coating. We conclude that the wax coating of the transmitters was not biocompatible, that the technical quality of the devices was poor, and that these implants should not be used in brown bears.

Keywords: biocompatibility, brown bear, foreign body reaction, implant, intraperitoneal, long-term safety, transmitter, *Ursus arctos*

INTRODUCTION

Implanted devices used in human medicine must provide science-based evidence of both the functional performance of the device and its compatibility and stability within the body of an animal before they can be approved for routine application in humans (1). There are no such requirements for implanted devices used in wildlife research. Cattet (2) reviewed the websites of six radio telemetry manufacturers in North America and found that none of them provided science-based evidence of the compatibility and stability of their products within the body cavity of an animal. Instead, the focus was on the functional performance of the device, such as battery-life and transmission range.

The use of implantable telemetry in animals started in the 1950s. Early reports focused on technical aspects of the implanted devices (3). The first reports on the use of abdominal radio telemetry in free-ranging mammals appeared in the 1970s (4, 5). In collaboration with Telonics Inc. (Mesa, AZ, USA), Melquist and Hornocker (6) developed intraperitoneal radio transmitters for use in North American river otters (*Lontra canadensis*). Since then, Telonics and other companies have been marketing intraperitoneal radio transmitters for a wide range of wildlife species.

We reviewed more than 1,500 publications on the use of implantable radio transmitters and other devices in wild mammalian species, ranging in body size from 4 g suckling white-footed mice (*Peromyscus leucopus*) (7) to adult grizzly bears (*Ursus arctos*) (8). We could not find any published studies on the long-term technical stability or biocompatibility of implanted radio transmitters and we identified only one peer-reviewed paper with a large sample size and a long time-span on health effects of such devices: Van Vuren (9) carried out 300 surgeries on 183 individual yellow-bellied marmots (*Marmota flaviventris*) in order to implant or replace intraperitoneal radio transmitters. He followed implanted animals for up to 4 years and concluded that the implants did not affect survival, growth, or reproduction. The devices were, however, clearly not biocompatible because he reported that "surgery to replace transmitters often revealed a thick, fibrous, sometimes highly vascularized membrane encasing the transmitter." Case reports and anecdotal observations indicate that implants may cause serious health problems, including mortalities, months to several years post-surgery (10–13).

Cattet (2) raised concerns over animal welfare issues and the lack of knowledge about implanted devices in wildlife. Reports on king penguins [*Aptenodytes patagonicus*; (14)], marine mammals (15), Burchell's zebras [*Equus burchelli antiquorum*; (16)], European badgers [*Meles meles*; (17)], and caribou [*Rangifer tarandus*; (18)] documented the need for long-term investigations on possible impacts of instrumentation of wildlife. Here we present data from a 19-year study on the technical stability and pathological effects of intraperitoneal radio transmitters in free-ranging European brown bears (*Ursus arctos*).

MATERIALS AND METHODS

The present work was part of an ongoing ecological study by the Scandinavian Brown Bear Research Project (SBBRP) (19). From 1997 to 2015, we carried out a total of 446 surgeries according to an established protocol (20) to implant, replace, or remove Telonics intraperitoneal very high frequency (VHF) radio transmitters involving 305 individual free-ranging brown bears [213 yearlings (162 females, 51 males), 44 subadults (2–4 years, 28 females, 16 males), 48 adults (≥5 years, 20 females 5–27 years, 18 males 5–22 years, age missing for 3 females and 3 males), the age refers to the time of first implant]. Fifteen bears that previously had their implants removed underwent a second surgery after 1–9 years to receive a new implant. We used the following models (number of units, length × diameter, weight): IMP/400/L ($n = 238$, 15.2 × 3.3 cm, 170 g), IMP/700 ($n = 139$, 15.2 × 3.3 cm, 158 g), IMP/400/L/HP ($n = 4$, 21.0 × 3.3 cm, 240 g), and IMP/400 ($n = 7$, 9.7 × 3.3 mm, 95 g).

The basic components of a Telonics IMP/400/L implant are shown in **Figure 1**. The lithium batteries, transmitter, and antenna were enclosed in a thick paper tube, wrapped in thin paper labeled with the company's name and address and the serial number of the device. These components were contained within a plastic shell cylinder with both ends closed with glued-on end caps. The plastic shell cylinder was coated with a 2.1 mm thick wax of unknown composition.

We inspected implants retrieved from live or dead bears for signs of discoloration, wear, or melting of the wax coating. The wax was then removed, the plastic shell cylinder was inspected for signs of fissures or cracks, and the attachment and sealing of the end caps were assessed. The end caps were removed and the internal parts were removed and inspected; the paper wrappings

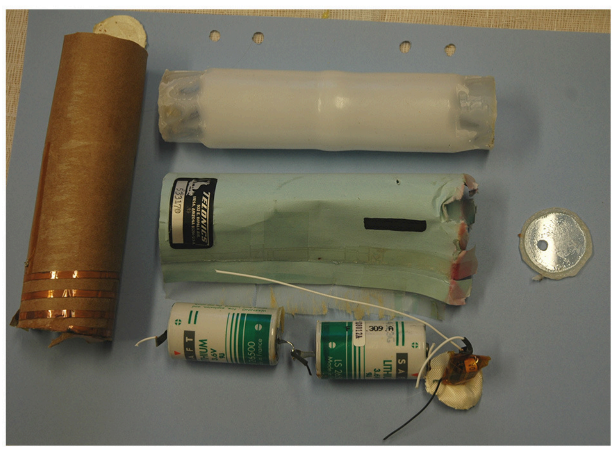

FIGURE 1 | Components of a Telonics IMP/400/L intraperitoneal VHF implant (length 15.2 cm, diameter 3.3 cm, weight 170 g). The lithium batteries, transmitter, and antenna (central bottom) were enclosed in a thick paper tube (left), wrapped in thin paper (central middle) labeled with the company's name and address and the serial number of the device. These parts were contained within a plastic shell cylinder (central top) with both ends closed with glued-on end caps (right). The plastic shell cylinder was coated with a 2.1 mm thick wax of unknown composition.

for dryness, the batteries for signs of short-circuiting and leakage, and all metal parts, including the batteries, for corrosion.

We collected biopsies from the tissue encapsulating the implants. We preserved the tissue samples in 10% phosphate-buffered, neutral formalin (Apotekproduksjon AS, Oslo, Norway) and shipped them to the Norwegian Veterinary Institute (Oslo, Norway) for histopathology. When we found pus-like content indicating possible bacterial growth inside the capsules, we used swabs (Swab-kit, Jan F. Andersen, Jevnaker, Norway) to collect samples, which were shipped with no cooling to the Norwegian Veterinary Institute for culturing by standard methods within 3 days. Thick tissue capsules (>2 mm) and capsules attached to a twisted loop of the omentum were amputated. We inspected and described biopsies before cutting 3–4 mm thick slices perpendicularly to the longitudinal axis of the capsule. The tissue slabs were dehydrated in ethanol, fixed in xylene, and embedded in paraffin before 5–6 μm thin sections were made, mounted, and stained with haemotoxylin-eosin and van Giessen according to standard procedures.

There were two major reasons to use implants in the bears. The SBBRP has a goal to follow individual bears throughout their lives and VHF implants allowed the recapture of individuals with neck collars that had been lost or had malfunctioned. The second reason was to avoid equipping yearling bears with transmitters mounted on neck collars, because young, growing bears would have to be recaptured annually for several years to change the collars. Capture and surgical protocols were approved by the Swedish Ethical Committee on Animal Research (Uppsala, Sweden; #C18/15), the Swedish Environmental Protection Agency (Stockholm, Sweden; NV-0758-14), and the Swedish Board of Agriculture (#31-11102/12).

RESULTS

At the time of denning in 2015, the 305 individual bears that had received implanted transmitters in our study had the following outcomes: for those still carrying a VHF implant [years refer to time after last implantation, given as mean (SD) (range)], 50 were alive 1.4 (±1.3) (0–5) years later, 39 were missing (no radio signals) 2.4 (±1.4) (0–6) years later, 129 had been shot (legally or illegally) 1.9 (±2.3) (0–13) years later, 20 had been killed by another bear 0.8 (±0.9) (0–3) years later, two died due to leakage from short-circuited batteries 10 and 13 years after surgery, two had died from trauma 2 months (hit by a train) and 2 years (crushed by a sliding rock) later, three had died during or shortly after capture (two from drowning and one due to dehiscence of the surgical wound), and 27 had died from unknown causes 1.3 (1.8) (0–8) years later (inconclusive necropsies, decomposed or partly eaten carcasses, implant found without any remains of the bear). Of those from which the VHF had been removed (time after removal of the implant), 17 were missing (removal, loss, or malfunctioning of radio collar) 3.1 (±2.4) (0–7) years later, 15 were shot 2.1 (±2.2) (0–8) years later, and one had been killed by another bear 1 year later.

From 2000 to 2015, we conducted 125 surgeries to remove implants that had been carried for 1–9 years. In 66 (53%) of the bears, the implants were found free-floating with no encapsulation in the peritoneal cavity and could be easily removed. In 59 (47%) of the cases, the transmitters were found trapped in the greater omentum and encapsulated by 1–15 mm thick layers of connective tissue with various degrees of vascularization. In 23 of the bears (39% of those with encapsulated transmitters), we amputated the connective tissue capsule and parts of the omentum. The bears with free-floating implants had carried the implant for 3.8 (1.5) years and those with encapsulated devices for 4.0 (1.8) years. There was no significant difference in time between these two groups (Student's t-test, $p = 0.42$). **Figure 2A** shows the proportion of encapsulated devices over time.

Two animals (Cases 1 and 2 below) with encapsulated implants had aggregates of thick, opaque and yellowish exudate between the capsule and the implant. One of them (Case 2) also had a 5-cm wide cystic mass of tissue, containing similar exudate attached to the outer surface of the capsule. Bacteriological swabs from both cases were negative. An additional bear (W1211), an adult male whose implant was replaced after 3 years, had a cystic structure, associated with the capsule, filled with a similar exudate as described above, but the material was not cultured.

We inspected 68 implanted transmitters that had been in bears for 3.9 (2.4) (0–13) years. Of these, 54 transmitters were surgically removed from live bears and 14 were retrieved from dead bears (ten shot by hunters, two killed by the transmitter, and two killed by bears). All implants showed some degree of yellowish discoloring of the wax coating. In four (5.9%) of the implants, parts of the wax had partially melted and the underlying plastic shell cylinder was visible. In five (7.4%) of the implants, the wax was visibly thinner than on new transmitters. We interpreted this as erosion of the wax due to wear. In one (1.5%) of the implants, the plastic shell cylinder had a longitudinal crack. One of the end caps was loose or open in eight (11.8%) of the implants. One (1.5%) implant had visible moisture condensed on the inside of the plastic shell cylinder. In 32 (50.0%) of the 64 intact implants, moisture had resulted in corrosion of the batteries and other metal parts. Leakage from the batteries was seen in one (1.5%) otherwise intact implant. In four (5.9%) of the implants, the batteries had short-circuited (Cases 3–6 below).

We took biopsies from the connective tissue capsule surrounding the implants from 33 bears. One individual was sampled twice. Of these, one had carried the implant for 9 years, two for 8 years, three for 7 years, three for 6 years, 11 for 5 years, four for 4 years, six for 3 years, two for 2 years, and two for 1 year (**Figure 2B**). Histological examination showed that the tissue was organized into three layers (**Figure 3**). The inner surface was sometimes covered by proliferating serosa, but in most cases, this layer was characterized by necrotic dense connective tissue organized in a regular and laminar pattern. Aggregates of yellowish, amorphous material were often located close to the surface. Areas of necrosis were found in most of the bears that had carried the implant for ≥4 years (20 of 24), whereas necrosis only was found in two of the six bears that had carried the implant for 3 years, and in none of the four that had carried it for <3 years (**Figure 2C**). The inner layer was otherwise characterized by well-organized, collagen-rich and sparsely cellular connective

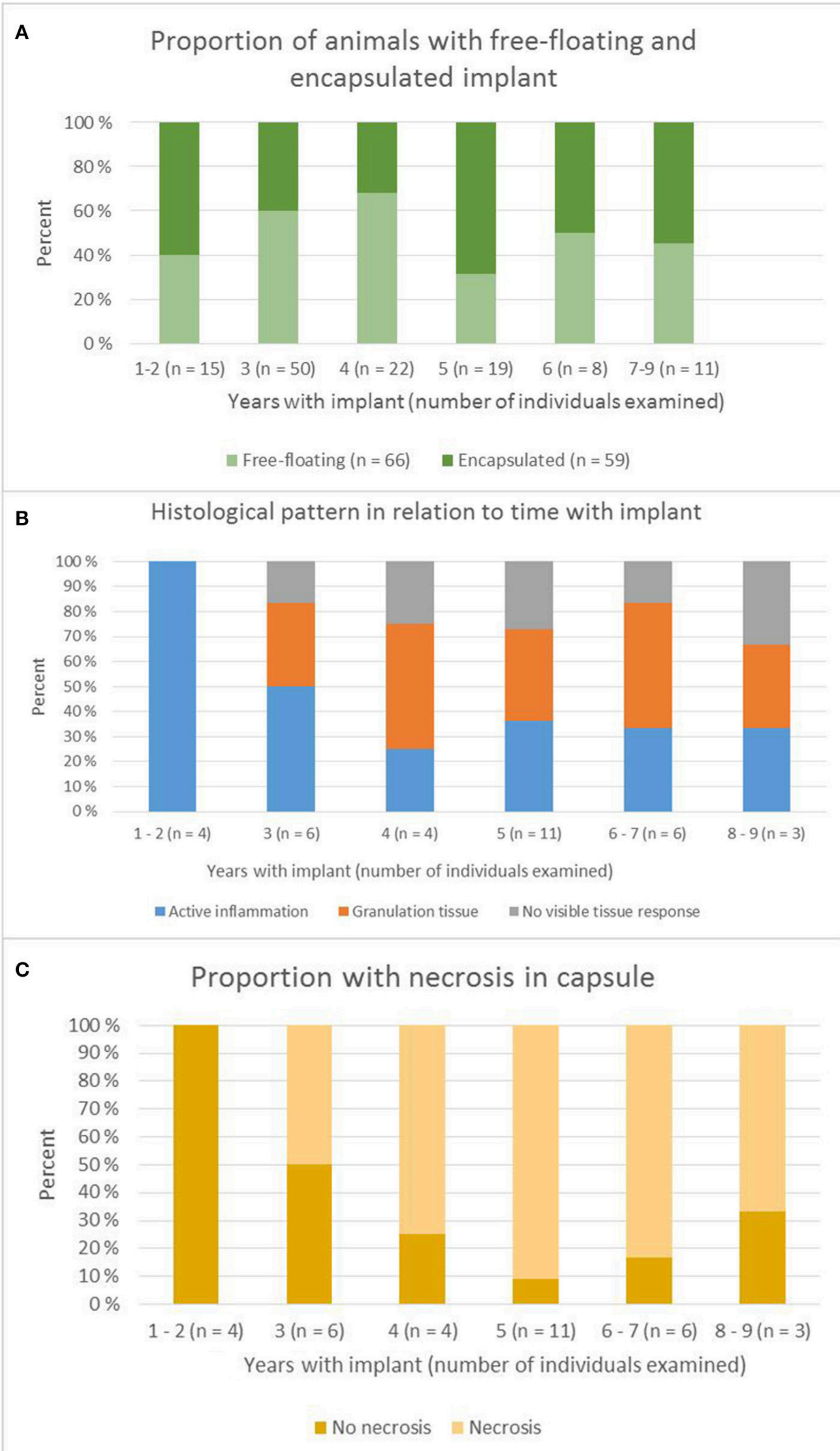

FIGURE 2 | (A) Proportion of bears with free-floating and encapsulated implant in relation to years with the device. **(B)** Histological pattern in relation to years with implant. **(C)** Proportion of capsules with necrosis in relation to years with implant.

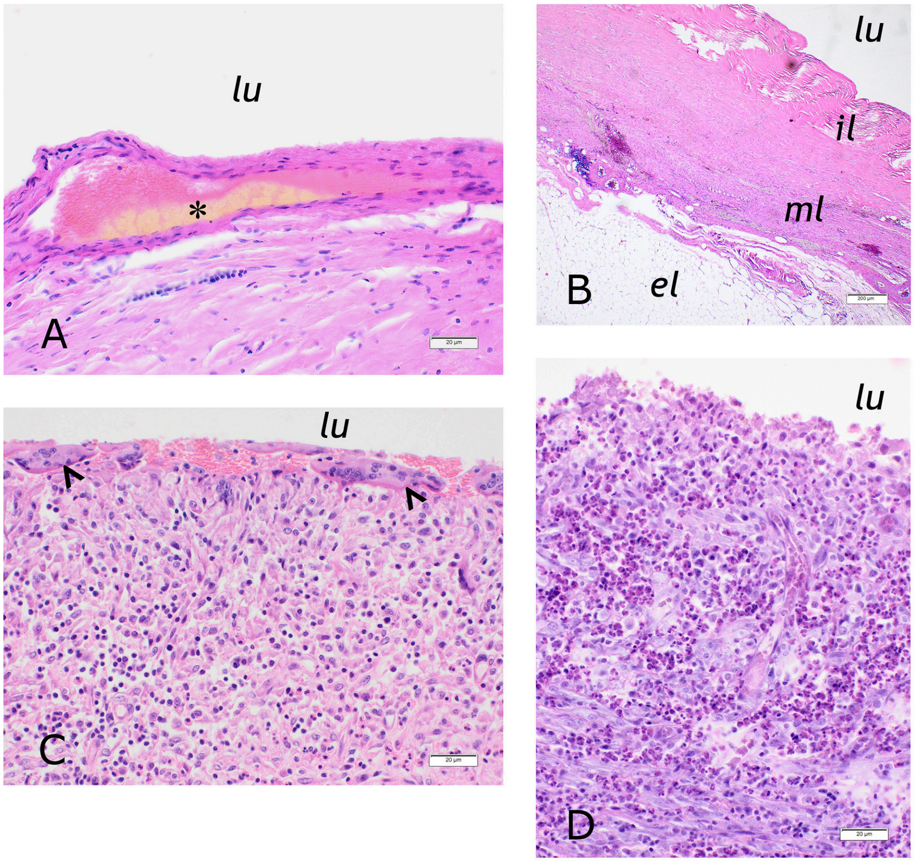

FIGURE 3 | (A) Inner surface of the implant capsule of bear BD23, a 26-years old female which had carried the implant for 2 years. Aggregates of amorphous yellowish material (asterisk) were found close to the lumen (lu) and within a layer of sparsely cellular, laminar connective tissue (HE, bar = 20 µm). **(B)** Three-layered appearance of the implant capsule of bear W9403, a 23-years old female that had carried the implant for 3 years. The inner layer (il) consisted of partially necrotic dense and organized connective tissue. The middle layer (ml) consisted of laminar, sparsely cellular connective tissue and contained vessels and occasional hemorrhages, infiltrates of lymphocytes and aggregates of foamy, slightly greenish macrophages. The outer layer (ol) was composed of fat cells (HE, bar = 0,02 mm). **(C)** Foreign body reaction in the inner layer of the implant capsule of bear BD155, a 22-years old female that had carried the implant for 1 year. Multinucleated giant cells (arrowheads) lined the inner surface. Below were infiltrates of epitheloid and normal macrophages, proliferating vessels and some eosinophilic and neutrophilic granulocytes (HE, bar = 20 µm). **(D)** Inner layer of the implant capsule of case 2/bear W0104, a 12-years old female that had carried the implant for 3 years. The tissue was infiltrated by large numbers of eosinophilic granulocytes (HE, bar = 20 µm).

tissue. Here, macrophages containing yellowish, greenish or brownish material were often found solitarily or in small aggregates. A significant inflammatory reaction was evident in a third of the biopsies, with the tissue characterized by granulomatous inflammation. The most severe cases contained numerous macrophages, epithelioid cells, multinucleated giant cells, neutrophilic granulocytes, fibroblasts, and proliferating vessels. In six of the cases, eosinophilic granulocytes constituted a significant proportion of the cellular infiltrate. The capsules from bears that had carried the implant for a long period were generally characterized by a milder inflammatory reaction than those that had carried it for a shorter period. However, we observed granulomatous inflammation in most of the cases, as only seven of the inspected capsules did not show any inflammatory cellular reaction. The middle layer of the capsule was often characterized by a well-organized, laminar connective tissue, but more active cases showed a more irregular organization with bundles and streams of highly cellular connective tissue and abundant vascularization. Prevalent findings were solitary clusters of large, foamy macrophages, often with a yellowish discoloration of the cytoplasm, and multiple, small aggregates of macrophages containing dark, brownish pigment granulae. Vascular proliferation, numerous hemorrhages and multifocal perivascular aggregates of lymphocytes were also prevalent findings. The third, outer, layer of the capsule most often consisted of adipose tissue, sometimes with mild perivascular infiltrates of lymphocytes, but often without any obvious inflammatory cellular response.

Below We Report Details on Seven Selected Individual Bears

Capture, handling and treatment of bears included in Cases 1–7 below, were carried out in accordance with an established protocol (20).

Case 1 (Figure 4)

A female bear (W8906), born in 1981 was implanted with a Telonics IMP/400/L/HP in April 1997. The implant was removed after 8 years in April 2005. The transmitter was encapsulated within the greater omentum, which was twined around its axis in a complete volvulus, so that the proximal part of the omentum formed a rope-like structure. We amputated the greater omentum involved in the twist. The capsule wall consisted of a 10–15 mm thick, grayish, and fleshy layer of connective tissue with rich vascular supply. The internal surface was irregular and yellowish, and the external serosa was hyperemic. There was a sticky, yellowish, hemorrhagic and odorless fluid between the capsule and the implant. The swab culture was negative. Histologically, the capsule wall consisted mainly of densely woven connective tissue without any obvious organization. Foci of necrotic fat were found in some areas and small hemorrhages, moderate perivascular infiltrates of inflammatory cells, mainly lymphocytes, and a small number of macrophages with dark pigments, were widely distributed. There were abundant proliferating vessels within the connective tissue. The surface of the implant had a yellowish discoloration. The inside of the plastic cylinder was covered with small, clear droplets of fluid. Both layers of the paper wrapping were moist and the batteries and other metal parts were corroded. This bear had produced four litters, with three cubs in each, in 1998, 2000, 2002, and 2004. It was shot legally in October 2005, but the hunter provided no information about the carcass.

FIGURE 4 | Implant (Telonics IMP/400/L/HP, 21.0 × 3.3 cm) and capsule from a 24-years old female bear (W8906) that had carried the device for 8 years.

Case 2 (Figure 5)

A female bear (W0104), born in 2000 was implanted with a Telonics IMP/400/L in April 2001. The implant was removed after 5 years in April 2006. The transmitter was found in the greater omentum, surrounded by a 5 mm thick capsule. A round, cystic, abscess-like structure 5 cm in diameter was attached to one side. We amputated the capsule and abscess. Both the capsule and the cystic structure contained a yellow, thick, opaque, and odorless fluid without any recognizable distinct odor. Three culture swabs from the capsule and fluid were negative. The internal surface of the capsule wall was smooth and displayed areas of orange discoloring. The texture of the capsule was firm, but the external layer of the tissue consisted of fat. Histologically, the internal part of the capsule was composed of laminar, loosely woven, and mostly necrotic tissue, which was diffusely infiltrated with macrophages and some neutrophilic granulocytes. The middle part consisted of dense connective tissue without any particular organization and the external layer consisted of fat infiltrated with macrophages and neutrophilic granulocytes. The blood vessels of the capsule were surrounded by mild to moderate infiltrates of lymphocytes. The coating of the implant was intact, but slightly discolored. No other damage was observed in other parts of the implant. This bear was implanted again in April 2009, and had the implant replaced both in April 2012 and April 2015 (Telonics IMP/700 in all occasions). No pathological changes were observed during these surgeries. The bear had litters in 2005 (two cubs), 2008 (three cubs), 2011 (two cubs), and 2014 (three cubs) and was alive at den entry 2015.

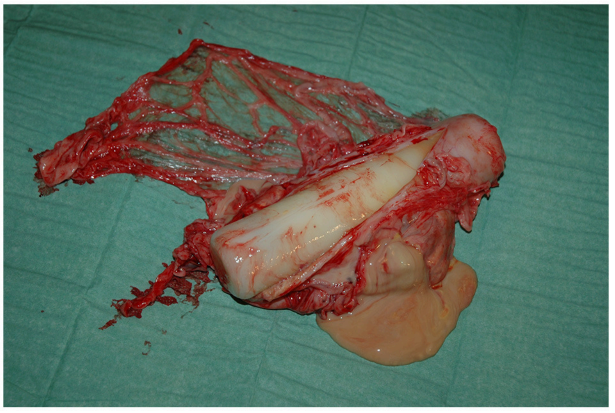

FIGURE 5 | Implant (Telonics IMP/400/L, 15.2 × 3.3 cm) and capsule with abscess-like cyst from a 6-years female bear (W0104) that had carried the device for 5 years.

Case 3 (Figure 6)

A female bear (W0010), born in 1999 was implanted with a Telonics IMP/400/L in April 2000. The transmitter was replaced after 6 years in April 2006. The implant was in the greater omentum, encapsulated by a 1 mm thick layer of tissue that did not require amputation to remove the transmitter. The tissue had irregular whitish surfaces and a texture resembling fat. Histologically, the tissue consisted of moderately vascularized, sparsely cellular adipose tissue with small, multifocal necrotic areas. The blood vessels within this tissue were surrounded by moderate amounts of connective tissue. On inspection, the wax coating of the implant had a "melted" appearance. One end cap was loose and the internal parts could not be removed without cracking the plastic shell cylinder. The paper wrappings appeared scorched and the batteries had short-circuited and were adherent to the inner surface of the plastic shell cylinder. This bear had produced litters with two cubs in 2005, 2007, and 2009. It was

FIGURE 6 | Implant (Telonics IMP/400/L, 15.2 × 3.3 cm) removed from a 7-years old female bear (W0010) that had carried the device for 6 years. The batteries had short-circuited, with subsequent over-heating of the device. The wax coating had a "melted" appearance and one end cap was detached. The batteries were adherent to the inside wall of the plastic cylinder, which had to be cracked to remove the internal parts of the device.

FIGURE 7 | Implant (Telonics IMP/400/L, 15.2 × 3.3 cm) removed from a 6-years old female bear (BD124) that had carried the device for 5 years. The batteries had short-circuited, with subsequent over-heating of the device and leakage from the batteries. One end cap was detached and the outside of the implant was partly covered by a soot-like material. All internal components appeared to be burned and were covered by the same soot.

shot legally in September 2009, but the hunter provided no information about the carcass.

Case 4 (Figure 7)

A female bear (BD124), born in 2001, was implanted with a Telonics IMP/400/L in May 2002. The transmitter was removed after 5 years in May 2007. When the peritoneal cavity was opened, the author who carried out the surgery (JA), could smell a "battery-like" odor and found that the implant was encapsulated in a 15-cm wide mass of connective tissue attached to the ventral abdominal wall cranially to the umbilicus. Parts of this tissue, including the core containing the transmitter, were removed and the abdominal cavity was closed. The tissue covering the implant was firmly attached to it and had to be removed with a scalpel. One end cap was detached. Closer inspection revealed that the implant clearly had over-heated. The outside of the plastic cylinder was partly covered by a soot-like material, and the inside smelled of battery. All internal parts of the transmitter appeared to be burned and were covered by the same soot. Both batteries had obviously been exposed to high temperatures and were partly open along the sides. The inside of the tissue that covered the implant was dark and irregular and had a "fried meat" appearance, whereas the outer surface was smooth and pale reddish. Histologically, the inner surface consisted of partly necrotic, finger-like projections of connective tissue. Next to this, the capsule wall consisted of connective tissue organized in a woven pattern. In the wall, there were large accumulations of lipid-like, brownish material in the tissue, pockets of macrophages filled with yellow/brown material, and foci of calcification and mild hemorrhages. The external layer of the capsule consisted of necrotic adipose tissue with spots of yellowish discoloration. The bear had its first litter (3 cubs) the year following implantation and was legally shot in May 2009 to avoid predation of semi-domesticated reindeer in a calving area. No pathological changes were noted at necropsy, but the report focused on the trauma from three rifle shots.

Case 5 (Figure 8)

A female bear (W0020), born in 1999, was implanted with a Telonics IMP/400/L in April 2000. This bear went missing (no radio signal) in October 2002, but was found dead in September 2010, 10 years after surgery. At necropsy, the implant was found free-floating in the abdomen. One end cap was completely detached and a metal wire (antenna) had perforated the stomach. The cause of death was peritonitis with subsequent sepsis. The wax coating was melted at both ends of the implant. The plastic cylinder had multiple, longitudinal cracks and fell into multiple pieces when the wax was removed. All internal parts were literally burned, presumably due to short-circuiting of the batteries and subsequent over-heating.

Case 6

A male bear (BD142), born in 2001 was implanted with a Telonics IMP/400/L in May 2002. This bear went missing (no radio signal) in September 2005, but was found dead in July 2015, 13 years after surgery. The cadaver was decomposed, but otherwise intact, except for a 10 × 15 cm opening into the abdominal cavity. The implant was located close to this opening. The bear's body condition was average and the gastrointestinal tract was empty. The pathologist concluded that death had occurred quickly. The implant was covered with a black material, one end cap was open, and the inside of the plastic cylinder contained abundant, black, and sticky material. The plastic cylinder was cracked and the batteries had short-circuited and were leaking. Although the necropsy report was not conclusive, it is likely that leakage from the batteries caused fatal peritonitis, with possible erosion of the abdominal wall.

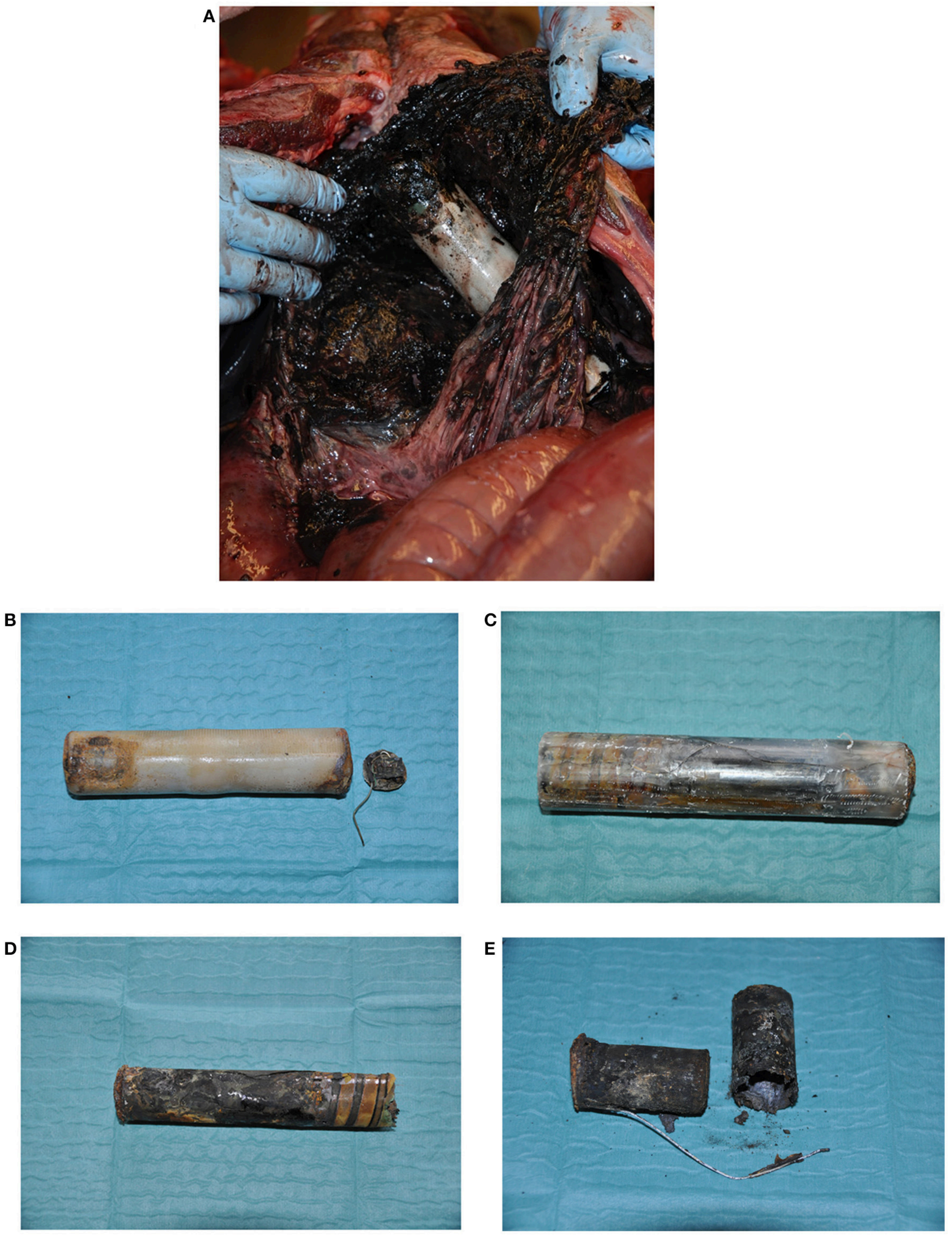

FIGURE 8 | Implant (Telonics IMP400/L, 15.2 × 3.3 cm) from a female bear (W0020) found dead 10 years after implantation. Cause of death was peritonitis, with subsequent sepsis, due to perforation of the stomach by a metal wire (antenna) and leakage from the batteries that had short-circuited. **(A)** Implant *in situ* at necropsy. **(B)** Implant with detached end cap and metal wire. **(C)** Implant after removal of the wax coating, showing several longitudinal cracks in the plastic cylinder. **(D)** Outer paper wrapping, after removal of the plastic cylinder, showing signs of over-heating and scorching. **(E)** Batteries showing signs of over-heating.

Case 7 (Figure 9)

A female bear (BD109), born in 1999 was implanted with a Telonics IMP/400/L in May 2000. The implant was removed after 5 years in May 2005. The transmitter was in the greater omentum, surrounded by a 2–3 mm thick capsule with a rich vascular supply. We amputated part of the omentum, which was in a full volvulus, with its root having the appearance of a twisted rope. The wall of the capsule had a smooth inner surface and an outer surface that was covered with adipose tissue. The middle layer consisted of fibrous tissue containing some gray to yellow tissue. Histologically, the inner layer consisted of necrotic, laminar, and loosely woven tissue over a zone of necrotic debris without any obvious organization. The middle layer consisted of laminar, densely woven connective tissue, and the external surface was covered by adipose tissue. Spots of calcification, small hemorrhages, and mild, diffuse infiltrates of neutrophilic granulocytes were present in the tissues. Some epithelioid macrophages with foamy cytoplasm were also seen, and there were multiple aggregates of yellow pigment within the capsule wall. Except for minor signs of wax wear at the ends, all parts of the implant were unremarkable. This bear was captured again in May 2008 to change the radio collar and in May 2011 to remove the radio collar. It produced two cubs in 2007 and 2010. No further information about its fate after 2011 is available.

DISCUSSION

We documented that Telonics intraperitoneal VHF radio transmitters had a high rate of serious technical failures, including an ineffective moisture barrier that caused corrosion of metal parts. We also documented that implants can over-heat and disintegrate, due to short-circuiting of the batteries, causing serious tissue trauma in one bear after 5 years and killing two other individuals after 10 and 13 years.

Telonics (21) has stated that the wax coating was stable at physiological temperature of 5–50°C. However, we observed several cases of changes in the coating consistent with partial melting. The normal deep body temperatures of brown bears are 32–34°C during hibernation and 37–38°C during mid-summer (22). The highest core body temperature we have recorded in this species, using abdominal temperature loggers, is 42.0°C. We doubt that bears can survive deep body temperatures exceeding 43–44°C and 50°C is definitely not survivable. Consequently, the wax coating is either not stable up to 50°C, as stated by the manufacturer, or the device can generate internal heat that is sufficient to melt the wax.

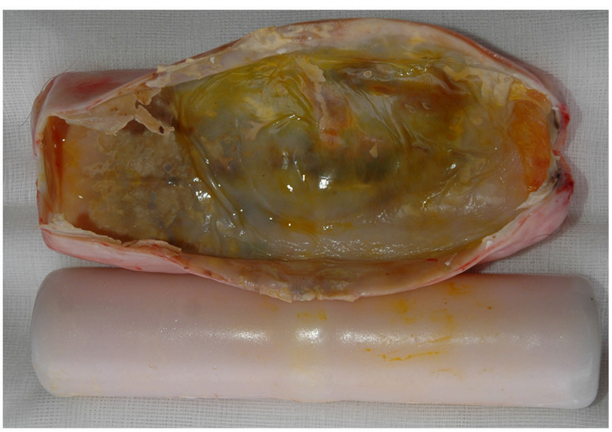

FIGURE 9 | Implant (Telonics IMP/400/L, 15.2 × 3.3 cm) and capsule from a 6-years old female bear (BD109) that had carried the device for 5 years.

Our finding of a mild to moderate granulomatous inflammation in the capsule surrounding the implant in nearly half of the instrumented bears, shows that the wax coating is not physiologically compatible. This is supported by the finding in some cases of macrophages containing granulae with yellowish pigment consistent with wax. We interpret this as a mild to moderate foreign body reaction to the coating (23). Furthermore, entrapment of the implant in the greater omentum caused a volvulus in several cases. In humans, volvulus of the greater omentum is associated with acute abdominal pain (24).

Tissue reactions to the implant appear to have started when the device became trapped in the greater omentum, i.e., encapsulation can occur in less than a year or may never happen. Four out of eight implants removed after 1 year were encapsulated. Of the 66 implants removed after 1–3 years, 30 were encapsulated and seven required amputation. On the other extreme, nine implants were found free-floating after 6–9 years.

Telonics (25) does not provide information about the chemical composition of the wax coating used on the implants. In 1983, Telonics (21) stated that "After extensive *in vivo* testing of many specialized coatings and formulations, a particular combination of physiological embedding wax and resin was determined to meet the specialized criteria for totally encapsulated telemetry units. The resultant coating is an effective moisture barrier to saline solutions, elicits little or no tissue reaction, and is stable at physiological temperatures (5–50°C)." The current product information (25) is that implants "have a dual water barrier, a sealed polycarbonate tube coated in wax; which completely encloses the transmitter electronics, power supply and the transmitting antenna. This design makes the implant less subject to mechanical damage and reduces the chance for moisture penetration over the life of the transmitter. This approach represents the best and most reliable packaging available for implants." The company also states that "implants are well-tolerated" (25). There is, however, no scientific evidence to support any of these claims and the manufacturer does not provide any advice on whether or not the implant should be removed from an instrumented animal. We found corrosion of batteries and other metal parts after only 3 years in eight implants and damage of the batteries, consistent with short-circuiting in two implants after 5 years. We also found that nearly half of the implants were encapsulated, with necrotic and inflammatory tissue reactions. This shows that the wax coating of the implant is neither an effective moisture barrier nor biocompatible.

We are unaware of any recommendations in the published literature regarding whether an implanted radio transmitter should be removed or not. The Canadian Council on Animal Care (26) stated that external transmitters ideally should be removed once an experiment or study is completed. These guidelines also cover implantable transmitters, but nothing is said about the removal of such devices. In 2018, Telonics is marketing a model (IMP/700/2) with an operational life of 10 years (25). Instrumentation is thus clearly meant to be long-term and potentially lifelong in most species.

In 1997, the SBBRP started using Telonics implants as an alternative to collars in yearling bears and later as a back-up VHF transmitter in adults equipped with GPS-collars. Based on observations during this study, our standard procedure during the past decade has been to change or remove the implants after 3–5 years, depending on the reproductive cycle of females and other considerations. Due to concerns over the poor technical quality of the implants and adverse reactions to the wax coating, the SBBRP has decided to stop using Telonics implants and all such devices carried by bears that still can be radio-tracked, will be removed.

CONCLUSIONS

In our opinion, these intraperitoneal radio transmitters should not be used in brown bears.

We have documented how a lack of attention to biological compatibility and technical stability of implanted devices can have drastic welfare implications for study animals. We recommend that standards similar to those used in human medicine be adapted for the development and use of intraperitoneal radio transmitters in wildlife.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this manuscript will be made available by the authors, without undue reservation, to any qualified researcher.

AUTHOR CONTRIBUTIONS

JA: study concept and design; JA, BY, KM, JM, SB, PS, AE, and JS: acquisition and interpretation of data; JA, KM, SB, PS, and AE: capture and handling of bears; JA, KM, and AE: surgeries and sampling; BY and KM: histopathology; JM: necropsy; JA and SB: technical inspection of transmitters; JA and BY: drafting of manuscript; JA, BY, KM, JM, SB, PS, AE, and JS: critical revision of manuscript and approval of submitted version.

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REVIEW
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Sustainable Fisheries Management and the Welfare of Bycaught and Entangled Cetaceans

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The incidental capture of cetaceans and other protected marine wildlife in fishing gear has significant welfare implications. Many thousands of cetaceans are bycaught in fishing gear in European waters and hundreds of thousands die globally. We can expect many more to survive, but suffer from such interactions. As marine policy focuses on "population level" impact assessments and "sustainability" of fishing to preserve fish populations, the impacts to the bycaught individual, and their wider social group, are often largely underestimated, despite the large numbers affected. The wide range of recorded injuries, including abrasions, cuts, bruising, and broken bones, along with the potential for panic associated with forced submersion, indicate that the welfare of bycaught cetaceans is, individually and collectively, very poor. Commercial fishing is the last human activity targeting wildlife (fish) on a grand scale where slaughter includes incidental killing of other large sapient wildlife on such a regular basis. Here, we review the compelling evidence of the short and long term welfare impacts of bycatch, and the progress made toward implementation of measures to understand and solve this significant welfare issue. We argue that policy decisions surrounding fishing do not adequately consider cetacean bycatch, including welfare impacts. Ultimately, there are welfare issues in all bycatch situations and suffering cannot plausibly be reduced without preventing bycatch. The well-documented welfare implications provide a strong argument for zero tolerance of cetacean bycatch and provide a compelling case for immediate action in fisheries where bycatch is taking place. The only way to reduce the suffering of bycaught cetaceans is to decrease, or ideally eliminate, the number of animals caught in fishing gear. Uncertainties around the scale of bycatch should not delay management, even where individual bycatch estimates are considered "sustainable." Lack of monitoring of sub-lethal impacts on populations may result in flawed impact assessments. We urge that animal welfare considerations should become an integral part of management decision-making in relation to bycatch globally. Enhanced, robust and transparent management systems are urgently required for the range of fisheries within which cetacean bycatch occurs, with the aim to better document and most importantly, work toward eliminating cetacean bycatch altogether.

Keywords: cetacean, bycatch, entanglement, welfare, fishing, Europe

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INTRODUCTION

Bycatch, including entanglement in nets and ropes, is the unintentional capture of non-target species in fishing gear. Each year, hundreds of thousands of whales, dolphins, and porpoises die from incidental capture (1) and many more will survive and suffer from interactions with fishing gear (2). Not only is bycatch a significant conservation issue for a number of species globally, it is a serious and considerable welfare issue.

An International Whaling Commission (IWC) Welfare Workshop held in 2016 (3) emphasized that entanglement in fishing gear is the most significant threat to wild cetacean welfare. Bycatch has wide reaching welfare consequences, affecting quality of life (4–6) for the many whales, dolphins, and porpoises that become injured or suffer the loss of conspecifics. As sentient and highly intelligent beings, cetaceans are considered to be in the highest category on a scale of sensibility to pain and suffering, in the same category as primates and carnivores (7).

Our understanding of the welfare implications of cetacean bycatch has increased, but no quantitative assessment and comparison of the extent of mortality, or the scale of morbidity and welfare implications for bycaught cetaceans between different fisheries exists (2). In this regard, the welfare of bycaught cetaceans is decades behind farm animal welfare and slaughter (8). The animal welfare consequences of the incidental capture of cetaceans and other protected marine wildlife would not be tolerated in terrestrial farming practices (9). Commercial scale fishing is the last human activity targeting wildlife (fish) where slaughter includes incidental take of other large sapient wildlife on such a regular basis and on this scale. Yet, there have been insufficient changes in fisheries management practices and, in general, inadequate effort to reduce the numbers of cetaceans caught in nets generally [for example, (10–12)].

Typically, the focus of research related to cetacean bycatch is that of understanding conservation and population level impacts. Further, assessment of criteria for "eco-labels" focus on the "sustainability" of fish stocks, inadequately cover protected species bycatch, and do not consider welfare at all. Such a narrow view, of both bycatch research and consideration of bycatch in eco-labels, which focus on conservation implications (of the targeted species) and ignore welfare concerns are at odds with the concerns of the general public. The general public assume, inaccurately, that fish certified as "eco-friendly" will also consider and deal with protected species bycatch. This may be part of the explanation why there has been so little action to address bycatch. Public opinion is strong against bycatch[1] and the public do not accept that cetacean and other protected species bycatch is a tolerable "by-product" of fishing. Whilst an increasing number of fisheries are labeled as "sustainable" in European waters, this assessment focuses on fish stock sustainability. "Sustainable" does not necessarily mean that fisheries can also be considered responsible with regard to bycatch, with variable and often inadequate levels of bycatch assessment, monitoring, and mitigation. The levels of bycatch of cetaceans and other protected species are not well-understood because of poor bycatch management in the majority of fisheries [see, for example, (13–15)] but known to be high in some where monitoring occurs (Birdlife International, in preparation). Hence, buying "sustainable" fish or indeed some fish products labeled "dolphin-friendly" provide no guarantees that incidental bycatch of protected species does not occur alongside the targeted catch[2]. Consumers are concerned with the welfare standards associated with the fish they buy and negative effects for incidentally bycaught species and this is indicated by the growth of such "eco-labels" (16). Perhaps the most recognized example is the Eastern Tropical Pacific tuna-dolphin issue (17), where public outrage and pressure led to better practices and dramatically reduced dolphin bycatch (although problems still remain, identified below). A strong public concern about the welfare of cetaceans and other marine species incidentally caught in fishing gear has been demonstrated. Regardless, a review of Marine Stewardship Council (MSC) fisheries, where MSC is perhaps the best recognized of all existing fisheries certification schemes, has shown that poor bycatch monitoring and reporting hinders assessment of the impact of the majority of reviewed fisheries (28) on bycatch species (Birdlife International, in preparation).

As an indication of the scale of the bycatch problem within European waters, odontocete populations likely to be impacted in some parts of the Northeast Atlantic include harbor porpoise (*Phocoena phocoena*) in static nets (18–23) and in beach seines (24); common dolphin (*Delphinus delphis*) in trawls [(25, 26), and see case study below] and bottlenose dolphin (*Tursiops truncatus*) (27). In the Mediterranean, there is evidence of population level impacts from bycatch on common and striped dolphin (*Stenella coeruleoalba*) (10, 28) and the demographically isolated population of sperm whale (*Physeter microcephalus*) (10) and in the Black Sea in static nets on an endangered sub-species of harbor porpoise, as well as bottlenose and common dolphin (29, 30).

Static fishing pot gear is a significant cause of morbidity and mortality for baleen whales, as well as nets. Entanglement in static fishing gear is the leading cause of detected mortalities of large whales in the Northwest Atlantic (31). Whilst data are limited in European waters, due to a lack of dedicated studies, there are indications that the post-whaling recovery rate of humpback whales (*Megaptera novaeangliae*) in Scottish waters may be hampered by the number of creel entanglements (32).

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[2] Forbes. (2015). 'Dolphin Safe' Labels On Canned Tuna Are A Fraud. 29th April 2015. https://www.forbes.com/sites/realspin/2015/04/29/dolphin-safe-labels-on-canned-tuna-are-a-fraud/#23395d71295e; Telegraph. (2018). Misleading 'dolphin friendly' claims could be illegal. 18th June 2018. https://www.telegraph.co.uk/foodanddrink/8250917/Misleading-dolphin-friendly-claims-could-be-illegal.html.

Smaller minke whales (*Balaenoptera acutorostrata*) appear less likely to survive any entanglement than larger species, such as humpback whale (33). The welfare impacts associated with minke whale entanglements are discussed in more detail in the case study below.

Efforts to calculate the "sustainability" of removal through bycatch can be useful to identify those marine mammal populations where bycatch (and other causes of death) are likely to result in population level impacts. For example, in the United States (34–36) and for harbor porpoise in the Baltic Sea, North Sea and Dutch waters (37–39). These studies recognize that there are limitations, biases and caveats to this approach [see for example, (40)]. The impediments to this statistical approach include the considerable uncertainty surrounding population and bycatch data in many parts of the world. Further, the mortality limits focus only on direct mortality and not indirect or sub-lethal effects and their possible population level consequences (39). Such an approach is a useful coarse statutory tool and has a role in identifying situations where bycatch is likely to be causing significant population level effects. As an example, the recent United States (US) Import Rule has been influential in identifying fisheries outside the US that import to the US. These non-domestic imports will be required to meet the bycatch standards of the US's own protected species regulations in coming years (11, 41). Bycatch legislation is, almost without exception, weaker in the rest of the world than in the US, so the US Import Rule is expected to provide an incentive to improve global bycatch measures. However, such an approach provides only part of the solution as the more subtle effects on populations over time require the development of finer-scale management tools and as such, implementation of the US Import Rule and other efforts to assess "sustainability" should be seen as a starting point for ongoing reduction in global bycatch and not as an end-point. Scheidat et al. (39) identify measures (including using the appropriate distribution for the porpoise population, rather than political boundaries, and considering cumulative pressures) to assess and implement population level measures as an interim objective, where the ultimate aim of ASCOBANS, the Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas (discussed in more detail below), is to reduce the number of such deaths to zero.

Increasing scientific literature demonstrates a need to manage human activities not only to maintain cetacean populations, but also to minimize welfare impacts on individual animals. Population level effects may take a long time to manifest or to be determined, if at all [for example, see (42)]. For those individuals that survive bycatch, but escape injured, the impact on their long-term welfare also has the potential to influence population level processes. Thus, estimation of "sustainability" based only on recorded or estimated deaths, without the consideration of sub-lethal welfare impacts across population level processes are inadequate. Whereas, animal welfare metrics can be observed in the short-term, thus enabling problems to be addressed more rapidly (43).

A broader and more ethical approach that tackles bycatch wherever it is known to occur, placing the highest priority on the fisheries with the largest bycatch, may be more effective from a welfare perspective, rather than only relating bycatch to population size and assessing whether it is "sustainable" before taking action (43). Improving measures to understand and reduce population level concerns would also reduce the number of individuals that suffer. Similarly, actions to optimize welfare can enhance conservation outcomes (44). A more balanced approach, where equal consideration is given to welfare and conservation, would comply with the emergent, and well-reasoned rational of "compassionate conservation" (45, 46).

The Treaty of Amsterdam contains a Protocol introducing legal obligations within the EU Treaty for parties to consider animal welfare in key areas of law and policy, recognizing the status of some species as "sentient beings" (47). As a result, there is a legal mandate and obligation to protect the welfare of sentient animals. In addition, it is asserted in the protocol that wild animals have intrinsic value. This highlights that while EU nations have a legal and moral imperative to address conservation issues caused by anthropogenic pressures, similarly there is also a legal and moral imperative to address animal welfare issues for sentient animals that arise as the result of anthropogenic pressures such as bycatch (48). Measures for protecting the welfare of sentient animals should be focused on optimally addressing animal needs for a particular set of circumstances by using animal-based measures based on the animal's perspective (49).

Considering the animal's perspective, here, we review the existing, compelling evidence of the extent of welfare impacts of cetacean bycatch globally, progress made toward implementation of welfare considerations in bycatch reduction, the welfare implications of bycatch mitigation strategies with a particular focus on the situation as it stands in European waters and case studies for two North East Atlantic cetaceans that face entanglement: common dolphins and minke whales.

WELFARE IMPACTS ASSOCIATED WITH BYCATCH

To examine the question of whether traditional bycatch management practices that focus on "sustainability" need to be improved to include consideration of animal welfare, here we consider the fishing gear involved, the process of capture and the types of injuries sustained in bycatch and entanglement, the longer term sub-lethal impacts for those that escape or are released and the wider social impacts upon conspecifics (2, 50–52). Some pertinent cases are summarized here.

Times to Death or Release From Gear

The suffering of an odontocete captured in fishing gear is more likely to occur over a period of minutes or possibly hours. Porpoises can become enclosed rather than entangled and can still surface to breathe (such as in pound nets, herring weirs) (53) so might be trapped for longer, and can usually be released without apparent injuries. Baleen whale entanglements in fishing gear have been recorded to occur over much longer time periods. For example, the "very slow and likely extremely debilitating demise of the North Atlantic right whale averages 6 months, but there are cases that persist for multiple years" (5). Prolonged entanglement in fishing gear negatively affects the health and welfare of individual animals and can also lead to population level effects including reduced fecundity and survival (54).

Assessment of Injuries Sustained

"There are clear differences in the types and degree of injuries received by bycaught cetaceans" (50), varying with species and with age (8). Pathological data for odontocetes indicate that the majority of bycaught cetaceans asphyxiate in the nets (8) or may drown. Before death, escape or release, injuries occur during interaction with the gear itself, through interactions with bycatch reduction devices or when the individual is hauled on board the fishing vessel (55).

Long-line fisheries can lead to entanglement of odontocetes and baleen whales and to injuries that result from depredation that include getting attached by one or more parts of the body to a baited hook (hooking) and entanglement in the fishing line. "Hooking is the result of a marine mammal being unable to dislodge itself from the hook, and the animal may remain attached to longline gear or break free, often with the hook still lodged in its mouth or other body part" (56).

Welfare assessment of stranded individuals has been studied directly resulting from fisheries in UK waters. "Post-mortem of 182 cetaceans stranded in the UK [comprising 97 harbor porpoise, 80 common dolphin, three striped dolphin, one Risso's dolphin (*Griseus grampus*) and one minke whale] from 1999 to 2005 found evidence of complex entanglements involving multiple parts of the body. External injuries included amputations (from entanglement or being cut free), broken maxillae, mandibles and/or teeth and internal injuries consisting of organ congestion, muscle tears and hemorrhaging (either from the gear or from the cetacean struggling)" (8).

Welfare assessment of free-swimming individuals demonstrated a high prevalence of injuries photographically in white-beaked dolphins (*Lagenorhynchus albirostris*) off the coast of Northumberland in the North Sea and off the coast of Iceland, from fisheries interactions and vessel strikes (57, 58).

Longer Term Health Responses

Non-lethal entanglement in fishing gear is sufficiently stressful to cause both a behavioral and physiological stress response in baleen whales (59). Fecal glucocorticoid studies have shown markedly elevated stress hormone levels in a severely entangled right whale (60), the relationships between entanglement stress and metabolic rate are complex. Long-term stress from being chronically wrapped in gear may explain why examined whales were unable to fight off the initial insult of infected gear lacerations, most likely leading to their demise (59). Visual health assessment of North Atlantic right whales using photographs demonstrated that stress responses existed that may have impacted health and fecundity even after the gear is no longer attached (61). Ultimately entanglements can lead to eventual lethal trauma through a drawn-out cumulative loss of body condition and constriction of body parts, with or without secondary infection, with expected extreme pain associated (5). Entanglements of baleen whales that eventually lead to death after a long period of suffering are, arguably, one of the worst forms of human-caused mortality in any wild animal (59).

High levels of stress are anticipated during capture and the physical and psychological stress and injuries for individuals that escape may cause prolonged suffering and/or subsequent mortality (51). Documented effects for those that escape or are released from fishing gear include behavioral alterations, physiological and energetic costs, such as associated reductions in feeding, growth, or reproduction (i.e., individual fitness) (51), potentially leading to reduced long-term survival. The full impact on an individuals' welfare and the extent to which this may affect mortality, life history events, and key biotic interactions and processes within the environment (62) are less well-known and so rarely, if ever, taken into consideration in sustainability analyses.

Wider Reaching Impacts on Conspecifics

We are beginning to understand the implications that bycatch has for conspecifics. Due to the highly social nature of many odontocetes, survival and reproductive success can depend on social cohesion and organization, and the effects of social disruption caused by bycatch mortalities may go beyond the dynamics of individual removals and impede population recovery (63, 64). Wade et al. (63) suggest that the social and behavioral traits of some odontocetes may contribute to a lack of resilience in some populations, specifically where survival and reproductive success may depend on: (a) social cohesion and organization, (b) mutual defense against predators and possible alloparental care, (c) inter-generational transfer of "knowledge," and (d) leadership by older individuals.

One of the longest running and perhaps most informative studies of sub-lethal impacts resulting from fisheries interactions is from the Eastern Tropical Pacific (ETP). Despite a dramatic decrease in the number of northeastern offshore spotted dolphins (*Stenella attenuata attenuata*) and eastern spinner dolphins (*S. longirostris*) bycaught in this fishery, from more than six million to fewer than 1000 dolphins per year, the populations are not showing signs of recovery (65, 66). The rate of calf production has also been declining since the 1980s (67). Hypotheses to explain the lack of recovery (66) have included under reporting of kills by observers, cryptic effects of the fishery undetectable by observers, such as stress induced abortion, or the separation of mothers and calves (68). Permanently separated dependent calves may then represent unobserved mortality events which are a significant welfare concern since un-weaned calves may die of starvation following orphaning. This may partially explain the lack of recovery of depleted ETP dolphin populations (69) where, in the case of mothers dying, a calf or dependent juvenile must be assumed to become a secondary victim (68). There is also some evidence that setting nets on dolphins can result in miscarriage in pregnant females (70). It is plausible that the chase and encircling of the dolphins has hindered or prevented recovery in these populations, groups of individuals that show complex social structure [(63); Butterworth et al. in preparation[3]].

[3]Vail Philippa Brakes CS, Reiss D, Butterworth A. Potential welfare impacts of chase and capture of small cetaceans during drive hunts in japan (in review).

Observations of a bottlenose dolphin calf temporarily entangled in monofilament line showed immediate alterations in the behavior of the mother and calf, as well as conspecifics (71). A similar pattern of seemingly social avoidance by conspecifics following entanglement has occurred on a number of occasions [(72) and references therein], where the costs of entanglement (e.g., infection, injury, energetic costs, inability to forage), are likely exacerbated. As well as causing distress to surviving family or social group members, the loss of key individuals may lead to the loss of important social knowledge (73). Frère et al. (74) examined genetic and social effects on female calving success (a partial measure of fitness) in bottlenose dolphins. They determined that both genetic and social factors contribute to variation in individual fitness related to female calving success. They posit that the influence of social relationships between females is consistent with either the social transmission of reproductive prowess, or with a type of homophily in which females with calves associate with other females with calves [as suggested by (75)].

PROGRESS TOWARD IMPLEMENTATION OF WELFARE CONSIDERATIONS IN EUROPEAN BYCATCH REDUCTION

The key regional scientific, legislative and policy mechanisms used to engage, collect and share data in European waters are reviewed here.

Post-mortem Analysis to Understand Welfare Impacts

Post-mortem analysis of stranded cetaceans and data from bodies collected from fishing boats provides the best opportunities for welfare assessment. Some injuries, such as external signs of acute entanglement, red or bulging eyes and multi-organ congestion, can be reliably used for bycatch diagnosis (76) and indicates the extreme conditions under which these cetaceans die. Strandings data provide an indication of the range of species that have been bycaught. For example, in UK waters, in addition to those species observed as part of the on-board bycatch observation scheme, stranded bycaught species have included minke whales, as well as long-finned pilot (*Globicephala melas*) and humpback whales. Collection of carcasses enables assessment of welfare implications and strandings can also provide an early indication of a newly emerging issue at sea, including bycatch from a novel source.

European Union Legislation

Existing European Union legislation includes no explicit provisions for the protection of cetacean welfare from incidental bycatch (8). The European Council Directive 92/43/EEC (1992) on the Conservation of Natural Habitats and wild fauna and flora, the Habitats Directive [Article 12(4)], requires "*Member States shall establish a system to monitor the incidental capture and killing of the animal species listed in Annex IV (a)*" (which includes cetaceans) and secondly, "*In the light of the information gathered, Member States shall take further research or conservation measures as required to ensure that incidental capture and killing does not have a significant negative impact on the species concerned*." Despite the clear requirement of the Directive, measures to implement it remain largely inadequate.

After more than a decade of implementation of EC Regulation 812/2004 on the incidental catches of cetaceans, compliance is inadequate and subsequently, levels of dolphin, porpoise and whale bycatch in static and mobile fishing gear are not clearly known. The existing EU Regulation 812/2004 is not entirely fit for purpose and doesn't focus on appropriate fisheries to adequately assess bycatch in EU waters. Further, 15 out of 17 Member States implementation of the Regulation has generally been poor or moderate (77).

Despite plenty of evidence in recent years to demonstrate the flaws in Regulation 812, based on this and other EU scientific reports (27, 78–83), technical conservation measures drafted by the EU Commission (84) in March 2016 [file 2016/0074 (COD)] do not significantly improve them. The proposal incorporates the main mitigation and monitoring requirements contained in Council Regulation (EC) 812/2004 and a geographic extension of the mandatory use of acoustic deterrent devices (ADDs) to all sea basins (to include full coverage in the Baltic Sea and in South Western Waters and the West of Scotland [DG (85)]. This file was considered by the European Council and Parliament, reports have been produced from each and discussions are currently in trilogue negotiations between them. Although amendments to account for and improve welfare standards in bycatch were put forward by a Member of the European Parliament Committee on Fisheries as amendments to the Fisheries Committee (86), these were rejected in a vote of the Committee of Fisheries. The amendments included "*ensure that the impacts of fishing on the welfare of animals are minimised and where possible eliminated*" (AM329), "*The use of innovative fishing gears shall only be permitted if those assessments indicate that their use will not lead to negative impacts on animal welfare, sensitive habitats and non-target species*" (AM543) and "*Fish and other marine animals are sentient beings, and the Union's fisheries policies shall therefore pay full regard to the welfare requirements of these animals*" (AM251). More generally, under the Data Collection Framework, data on incidental bycatch of all birds, mammals and reptiles and fish protected under Union legislation and international agreements, including absence in the catch, needs to be collected during scientific observer trips on fishing ships or by the fishers themselves through logbooks. Where data collected during observer trips are not considered adequate to provide sufficient data on incidental bycatch for end-user needs, other methodologies need to be implemented by Member States. The selection of these methodologies shall be coordinated at marine region level and be based on end-user needs (DG (85)].

Ascobans

ASCOBANS maintains the goal of reducing bycatch toward zero, an ambition that is motivated by welfare concerns. ASCOBANS produces species action plans that contribute to achieving this aim, including for harbor porpoise in the Western Baltic, the Belt and the Kattegat Sea (87), Baltic Sea (23) and North Sea (88) and a conservation plan for common dolphin (ASCOBANS, in preparation). Bycatch has been identified as the highest priority for action. An ASCOBANS Bycatch Working Group exists and a number of bycatch work streams and associated workshops have taken place[4].

Strandings remain on the agenda at ASCOBANS, where Resolution No.10 on Small Cetacean Stranding Response was passed at the most recent Meeting of the Parties (89). The Resolution calls on Parties to establish and fund strandings networks, including to conduct post-mortem examinations and to share data.

International Whaling Commission

The IWC has a long history of dealing with cetacean welfare issues. The IWC Welfare Workshop (3) recommended a high priority be placed on developing effective entanglement mitigation and prevention measures, and until such time as that is developed, continue support for the palliative care offered by further developing the Global Whale Entanglement Response Network and database. The Workshop further recommended that a more detailed consideration is carried out on the implications of entanglement and bycatch for small cetaceans.

In evaluating the impacts on animal welfare, assessment should consider both the severity and the duration of negative health and stress measurements (44). The more recent IWC Welfare Workshop (3) recommended monitoring of wound healing, wound progression, and time to death in cetaceans in the wild that have incurred vessel-strike or entanglement injuries, in order to provide greater understanding of the welfare implications for individuals (3).

In 2016, an IWC cetacean strandings workshop concluded that an international Strandings Network, involving experts from a number of different countries, should be established. It could help to standardize data and mitigate impacts from man-made sources[5]. IWC has now appointed a strandings coordinator.

Beyond large whale entanglements IWC also recognizes the severity of bycatch impacts on cetaceans and has now established a Bycatch Mitigation Initiative.

WELFARE IMPLICATIONS OF BYCATCH MITIGATION STRATEGIES

Marine mammal bycatch mitigation strategies encompass both the prevention and reduction of incidence and severity, and the first priority of any bycatch management strategy should be the prevention of entanglement or bycatch (54).

Recognizing the scale of bycatch, mitigation strategies have been developed in a number of fisheries. Mitigation options include management measures such as spatial or temporal management of fishing, and technical solutions including: modifying the gear, either to make it more visible (for example using acoustic devices) or reducing the likelihood of entanglement once a cetacean makes contact with the gear, or reducing the severity of entanglement (e.g., weaker line). Existing mitigation options have been reviewed in detail (53).

Banning or restricting fishing (including the use of closed areas or closed seasons) in areas used by cetaceans can be effective if properly enforced. The most generally effective mitigation of cetacean bycatch and entanglement is a reduction in effort, starting with those fisheries that have the largest bycatch (53). Reducing effort and bycatch would clearly also reduce welfare impacts. If reducing effort is not deemed possible then modifying gear or replacing gear types to reduce risk of contact or entanglement are the main strategies known to reduce risk of bycatch (53) and so would also reduce welfare impacts, as would minimizing gear loss and "wet" storage of gear at sea when not in use. The most promising solutions lie with the development of alternative gear to replace current fishing methods such as gillnets (53).

Some mitigation measures reduce the numbers of individuals killed but have additional impacts that can affect welfare. The use of active acoustic devices (such as pingers) has been demonstrated to successfully modify the behavior of some dolphins, porpoises and small whales to reduce the frequency of their interactions with gillnet fisheries (90). Pingers on drift nets successfully eliminated beaked whale bycatch in the Californian drift gill net fishery (91), where the species previously caught included Cuvier's beaked whales (*Ziphius cavirostris*), Hubb's beaked whales (*Mesoplodon carlhubbsi*), Stejneger's beaked whale (*M. stejnegeri*), Baird's beaked whale (*Berardius bairdii*), as well as unidentified Mesoplodon and ziphiid species. However, pingers may lead to displacement from important habitats, with unknown welfare implications or, theoretically if sources levels are loud enough, could potentially cause auditory damage (92).

There are also welfare concerns associated with some odontocete bycatch mitigation efforts that involve the use of trap doors, escape hatches and exclusion grids, that might be used to allow individuals to escape from a large net once a dolphin has entered. Behaviors exhibited by a number of species that interacted with a bycatch reduction device in a trawl net included the animal becoming caught in the mesh by fins, head or tail; the tail being caught or stuck in the exclusion grid; the animal remaining in the net after a stressful interaction with the grid or mesh; the animal continuing to move and remaining in the net motionless after stressful interaction with grid or mesh; and finally, of the animal being assumed dead, when potentially still alive (93).

Adaptive management principles would enable scientifically credible monitoring programmes to measure key performance indicators (46), enabling an understanding of the consequences of management decisions to make the appropriate decisions accordingly. As an example, van Beest et al. (94) found that a mix of pingers and spatial restrictions had the best effect on reducing bycatch and disturbance.

[4]http://www.ascobans.org/fr/species/threats/bycatch.
[5]https://iwc.int/strandings.

Case studies are provided here of the different issues faced by bycaught common dolphins and entangled minke whales in European waters and the associated welfare impacts.

CASE STUDY: COMMON DOLPHIN BYCATCH IN EUROPEAN WATERS

Bycatch has been identified as the greatest anthropogenic threat to common dolphins (26, 95–97) and at levels such that it may be having a population level effect in European waters (83). The most recent assessment (80) of the conservation status for the European Atlantic common dolphin population under Article 17 of the Habitats Directive was "Unfavourable-Inadequate". From a welfare perspective, a greater number of individuals bycaught from a large population is a greater concern than a smaller bycatch from an endangered population. Bycatch estimates from strandings data and observer programmes demonstrate that, whilst the figures vary from 1 year to the next, thousands of common dolphins have been bycaught in European fisheries each year over the last three decades (26, 96).

The highest levels of common dolphin bycatch were observed in the nets of mobile pelagic trawl fisheries (especially pair-trawls, where two boats fish with a net stretched out between them), with lower levels observed in static gillnet fisheries, although these may be equally significant as they may result in similar levels of total bycatch due to higher fishing effort by static net fisheries [ASCOBANS, in preparation; (83)]. Many European countries operate fishing gear in the region. A number of fisheries are not adequately monitored for bycatch, despite clear indications that bycatch is occurring, including in the offshore fleet such as pelagic freezer trawlers, high vertical opening trawlers and some bottom set gill nets (26). The full extent of bycatch in European waters remains uncertain as monitoring occurs on a very small percentage of part of the fleet and dolphins bycaught further offshore may be less likely to come ashore, be reported and subsequently post-mortemed.

Injuries Sustained

Data from on-board fishing vessels and stranded individuals provide important welfare information about impacts [for example, (8)]. More than 41% of common dolphins suffered broken beaks and others had broken maxillae or mandibles (24.2%) and/or broken teeth (8). Broken beaks are thought to result from capture in mobile fishing gear, whilst finer net marks are a more obvious sign of capture in static fishing nets. The tail, pectoral fins and head/beak were more likely to have net marks than the dorsal fin. Amputations were noted frequently in common dolphins and harbor porpoises, but it was unclear whether these were due to entanglement in nets or from being cut free (8).

In general, a large proportion of bycaught cetaceans had generalized organ congestion (liver, kidneys, spleen, and adrenal glands) caused by reduced blood flow. Internal injuries can be inflicted by the fishing equipment and also by the cetacean struggling to free itself. Soulsbury et al. (8) note that since entrapped cetaceans typically make powerful dorso-ventral and lateral movements, these probably cause the hemorrhaging and tears in the longissimus dorsi muscle, which is the primary swimming muscle. Similarly, because the pectoral fins frequently become entangled, such movements will cause muscle tears and hemorrhaging in the peri- and subscapular areas, and torsion of the body leads to internal hemorrhaging of the thoracic rete mirabile.

Potential Solutions

Sea bass pair-trawling, other pelagic vessels and set-nets result in common dolphins deaths in large numbers each winter. Due to poor sea bass stocks, a ban has been in place on the pelagic trawl fishery for sea bass in the English Channel, Celtic Sea, Irish Sea and southern North Sea during February and March, since 2015. High levels of common dolphin bycatch were still documented in these months in the winters of 2016 and 2017. Therefore, it is necessary to conduct monitoring to understand in more detail which other parts of the fishing industry, in particular the offshore fleet that is largely unmonitored such as pelagic freezer trawlers, high vertical opening trawlers and bottom set gill nets, might also have dolphin bycatch.

Better monitoring is also required on a broader range of vessel sizes within the fleet, including vessels smaller than 15 m. Monitoring should be conducted using independent on-board observers or tamper proof video cameras (remote electronic monitoring) to understand which elements of the fleet require the implementation of mitigation measures. Compulsory reporting of all bycatch incidents by fishermen should be an additional requirement, recognizing that these data are necessary and can be used sensitively to inform future management.

In addition, simple changes to fishing practices might reduce bycatch. For example, fishing only during daylight hours and fishing in waters over a certain depth have been shown to prevent common dolphin bycatch in Galicia, Northwest Spain (95). All gillnet operators in the Coorong Zone in South Australia must cease fishing and move fishing operations at least five nautical miles away if there is any dolphin bycatch. The purpose of this measure is to encourage fishers to adapt their fishing practices on the water and reduce the risk of further dolphin bycatch by immediately moving away from the location of a dolphin bycatch event (98).

Evidence suggests that common dolphin bycatch may have decreased when loud pingers were voluntarily introduced on some nets in parts of the UK sea bass pair-trawl fleet (99). Trap doors have been trailed in some trawl fisheries to reduce common dolphin deaths. The welfare concerns associated with the use of both these mitigation options were discussed above and require consideration in developing a suitable solution to common dolphin bycatch.

Development of a multi-pronged approach is required to reduce bycatch—such as requiring electronic monitoring as well as reporting bycatch incidents. Mitigation measures might include a focus on implementation of benign mitigation measures, such as moving away when dolphins are spotted and not operating at night (96). Pingers might be trialed, and tested for effectiveness, for individuals missed during a scan from the bridge of the boat or for those that approach the vessel during fishing operations. Trap doors should only be implemented with adequate trials to monitor potential welfare impacts on individuals that become trapped but are able to escape through the trap door.

Efforts will need to be collaborative across the range of nations that fish in these waters and so the ASCOBANS Common Dolphin Action Plan (ASCOBANS, in preparation) may be an important starting point if countries invest.

CASE STUDY: MINKE WHALE ENTANGLEMENT IN SCOTTISH WATERS

About 50% of post-mortemed minke whales in Scottish waters have been diagnosed as having died due to entanglement in creel lines and other ropes (100) As many as 17.7% of identified minke whales observed at sea in the Hebrides show some evidence of previous entanglement between 2009 and 2011 (101).

A wider analysis between 1990 and 2010 demonstrated that the head is the body region most commonly found with scars indicative of entanglement, suggesting that minke whales may become entangled in fishing gear whilst feeding (101). Minke whale entanglements have a higher fatality rate and are less likely to be noted ante-mortem than humpbacks and other larger baleen whales because minke whales are less powerful swimmers and so may be less likely to reach the surface to breathe whilst entangled (102). Minke whales tend to become tethered in pot lines, rather than picking up and carrying the gear. Katona et al. (103) report a single observation of a minke whale in the North Atlantic surviving submerged for 17 min as it was being freed from a fish weir. Leaper et al. (104) discuss times to death, where the trauma associated with prolonged submersion until death in this species. Pathological changes have been noted in cetacean tissues associated with death from asphyxiation (105–109) and such signs are indicative of physiological stress and a potentially protracted dying process (104).

A cetacean entangled underwater is in a potentially terminal forced dive situation. The whale may adopt one of two strategies: induce a rapid and profound dive response (though it is difficult to identify an adaptive explanation for such behavior if the whale has been entangled and potentially perceives an opportunity to break free); or start to struggle. There is evidence of the latter behavior from tissue damage to entangled marine mammals (104). If the whale struggles frantically to free itself then this effort will require an increased oxygen supply to muscles. Whereas, a whale that does not struggle may show the accentuated bradycardia seen in forced submergence (104).

Potential Solutions

Adoption of ropes with lower breaking strengths (of 1,700 lbs or less) could reduce the number of life-threatening entanglements for large whales by at least 72%, and still be strong enough to withstand the routine forces involved in many fishing operations (102). Measures that might work for humpback whales if used throughout the fishery may not be useful for much smaller and lighter minke whales. Lines that are weak enough for minke whales to escape may be possible in some shallow, sheltered areas, where the pulling load is less when gear is being hauled back on-board the fishing vessel. Nevertheless, reducing the amount of fishing rope in the water column is likely to be the most successful entanglement prevention strategy. Rope-less technologies are being developed that may help reduce entanglements in the future if widely implemented.

In summary, the welfare issues identified for both common dolphins and minke whales are likely to be severe, and indicate that the welfare of all bycaught cetaceans is often very poor. Better monitoring is required to understand the extent of entanglement for both species. Tried and tested mitigation measures to reduce the welfare impacts for both species include reducing the amount of fishing gear in the water. Technical mitigation measures available for common dolphin bycatch in mobile gear have associated welfare issues that are yet to be resolved and reliable mitigation measures for whale entanglements in fishing rope are still under development.

CONCLUSIONS AND RECOMMENDATIONS

It is the authors' contention that policy decisions surrounding fishing and bycatch do not adequately consider the variety of welfare impacts of bycatch on cetaceans. Animal welfare considerations should be an integral part of conservation decision-making from both a robust scientific and an ethical perspective. To address the ubiquitous and considerable welfare issues arising from bycatch and entanglement, more robust and transparent management systems are urgently required, with the aim to better document and work toward eliminating bycatch altogether. As a result of the demonstrable suffering resulting from bycatch and entanglement, and in line with legislative mandates across the EU, animal welfare considerations should become a central tenant to fisheries policy-decision making. Activities that put animal interests at risk should be independently regulated. Changing the government's approach to welfare is an essential precondition to achieving legitimate and effective standards of animal protection (110).

Marine mammal bycatch mitigation strategies encompass both the prevention and reduction of incidence and severity, and the first priority of any bycatch management strategy should be the prevention of entanglement or bycatch (54).

A number of different stakeholders have valuable roles in eliminating welfare impacts. Fishers themselves can be encouraged or required to document and report entanglements, accommodate independent observers on-board or use electronic monitoring to collect and bring bycaught individuals to harbor for post-mortem examination and to implement bycatch solutions. Researchers have the role of analyzing post-mortem data of bycaught individuals, as well as monitoring population health of live individuals (for example, using photo-identification to understand scarring) and developing sophisticated measures for welfare assessment. Managers have the role to legislate for improvements in fisheries and bycatch data collection and prevention. Conservation and welfare groups can raise awareness amongst the public about their consumer choices and amongst politicians and decision makers to improve legislative measures to reduce bycatch and concurrently to improve welfare. Engineers can develop fishing techniques that do not have associated bycatch. Effective bycatch mitigation will require coordinated action by the range of stakeholders and actors to develop a combination of changes in fishing practices, modification of fishing effort, technological gear fixes and international agreements that, together, can monitor and mitigate bycatch (111).

Explicit policy decisions and rigorous implementation are urgently needed to bridge the gap between our poor understanding and the reality of what is happening at sea (12). Political motivation and transparent consideration of the sub-lethal costs of bycatch and entanglement in decision making are essential.

Bycatch is not intentional, but neither can it be regarded as entirely accidental and many fishermen are involved in strategies to reduce the incidental capture of cetaceans. The approaches required will often be fishery specific, and all solutions are dependent on positive relationships and involvement with fishermen. Participation of fishermen in the management process is necessary (112), bycatch reduction approaches can be implemented successfully from the bottom-up in the hands of fishermen (113). Incentive-based management measures are likely to be most effective to engage fishermen.

There is a great need for effective mitigation measures to address bycatch of marine mammals, including in gill-net fisheries (114) and there also remains an urgent need for better entanglement avoidance and disentanglement initiatives for baleen whales.

Where mitigation methods implemented result in welfare impacts, such impacts require monitoring to understand and evaluate the consequences. The sub-lethal effects of injuries caused as a result of bycatch and stress on fitness and the length of time to asphyxiation are not as well-understood as they might be. The social implications of individuals dying are a further area that would benefit from better knowledge. However, a higher priority would be to better fund research into effective methods to stop bycatch from occurring. In addition, information about its scale requires wider publicity and better public awareness.

To reduce suffering as a result of bycatch requires, a transparent, multi-taxa approach, a framework and timeframe to reduce bycatch, incentives for fishermen: encouraging implementation of best practice: i.e., reporting all incidences, as well as application of electronic monitoring and adaptive at-sea management.

Market-based mechanisms should include retailers and suppliers working with fisheries to improve transparency of practices and governance. As a component of this, certification schemes should include the mortality and welfare considerations of bycatch in their assessments of fisheries and clear labeling of the resulting fish products. A major effort to educate seafood consumers as to the chronic and widespread welfare concerns that marine mammal bycatch and entanglements represent would help achieve their mitigation through consumer pressure.

The MSC is undertaking a review of its Fisheries Standard in 2018 and 2019. A review of MSC's requirements for assessing the impact of fisheries on endangered, threatened and protected (ETP) species requirements will form a major part of the Fisheries Standard review, where the MSC recognizes the importance of providing robust protection for these species, and the need to address the cumulative impacts of a fishery upon them (115). Conservation and welfare groups efforts are increasingly focused on supermarkets, who have a powerful role in sourcing seafood and so can influence MSC and other "ecolabels" to continually improve their standards to account for bycatch more transparently and in a more consistent way, in their assessment and accreditation processes.

We argue that current policy decisions surrounding fishing do not adequately consider cetacean bycatch, including the welfare implications of bycatch. There are welfare issues in all bycatch situations and suffering cannot be reduced without preventing bycatch. The well-documented welfare implications of marine mammal bycatch provide a strong argument for zero-tolerance on cetacean bycatch and make a compelling case for immediate action to reduce bycatch toward zero. Uncertainties around the true magnitude of bycatch should not delay management decisions, icluding where bycatch is considered "sustainable."

To deal with these welfare issues, a clear, timelimited, and effective strategy is needed to identify the steps that are required by all fisheries to reduce bycatch toward zero (12) and this should include welfare specific legislation for marine species, as already exists for terrestrial mammals. There is strong scientific, ethical, consumer, and political mandate for animal welfare implications resulting from bycatch to become an integral part of fisheries policy and conservation decision-making.

AUTHOR CONTRIBUTIONS

SD reviewed the literature and wrote the first draft manuscript. PB provided detailed input to draft manuscript. Both authors provided feedback to reviewers comments and proofread the manuscript.

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"Feelings and Fitness" Not "Feelings or Fitness"–The *Raison d'être* of Conservation Welfare, Which Aligns Conservation and Animal Welfare Objectives

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Increasingly, human activities, including those aimed at conserving species and ecosystems (conservation activities) influence not only the survival and fitness but also the welfare of wild animals. Animal welfare relates to how an animal is experiencing its life and encompasses both its physical and mental states. While conservation biology and animal welfare science are both multi-disciplinary fields that use scientific methods to address concerns about animals, their focus and objectives sometimes appear to conflict. However, activities impacting detrimentally on the welfare of individual animals also hamper achievement of some conservation goals, and societal acceptance is imperative to the continuation of conservation activities. Thus, the best outcomes for both disciplines will be achieved through collaboration and knowledge-sharing. Despite this recognition, cross-disciplinary information-sharing and collaborative research and practice in conservation are still rare, with the exception of the zoo context. This paper summarizes key points developed by a group of conservation and animal welfare scientists discussing scientific assessment of wild animal welfare and barriers to progress. The dominant theme emerging was the need for a common language to facilitate cross-disciplinary progress in understanding and safeguarding the welfare of animals of wild species. Current conceptions of welfare implicit in conservation science, based mainly on "fitness" (physical states), need to be aligned with contemporary animal welfare science concepts which emphasize the dynamic integration of "fitness" and "feelings" (mental experiences) to holistically understand animals' welfare states. The way in which animal welfare is characterized influences the way it is evaluated and the emphasis put on different features of welfare, as well as, the importance placed on the outcomes of such evaluations and how that information is used, for example in policy development and decision-making. Salient examples from the New Zealand and Australian context are presented to illustrate. To genuinely progress our understanding and evaluation of wild animal welfare and optimize the aims of both scientific disciplines, conservation and animal welfare scientists should work together to evolve and apply a common understanding of welfare. To facilitate this, we propose the formal development of a new discipline, Conservation Welfare, integrating the expertise of scientists from both fields.

Keywords: conservation welfare, animal welfare assessment, wildlife conservation, environmental ethics, wild animal welfare

INTRODUCTION

Conservation biology and animal welfare science are both multi-disciplinary fields that use scientific methods to address concerns about animals (1, 2). Both also require decision-making in complex ethical milieu and in the face of significant uncertainty (3, 4). While animal welfare science has traditionally focussed on the welfare of domestic animals living under human care, there is increasing recognition of the potential for human activities to also impact on the welfare of wild animals (5, 6). In particular, various human activities aimed at conserving populations, species, ecosystems and, ultimately, biodiversity can influence the welfare of individuals and groups of wild animals (4, 7, 8).

Briefly, there is growing evidence of animal welfare impacts associated with *in situ* conservation activities, such as habitat management, field research, and management of rare and overabundant native animals, as well as, of invasive species [e.g., (9–27)]. Likewise, *ex situ* conservation activities including captive breeding, holding animals indefinitely in zoos as "insurance populations," wildlife rescue and rehabilitation, reintroductions and research on captive animals can influence animal welfare [e.g., (2, 13, 28–37)].

Such conservation activities are strongly supported by many in society, reflecting the value placed on concepts, such as "naturalness" and "biodiversity," the continuing existence of current species and retention of "evolutionary potential" (38–41). However, activities impacting detrimentally on the welfare of individual animals may ultimately threaten their survival and fitness and thus the viability of valued populations and species [e.g., (2, 9, 12, 15, 21, 34, 42, 43)], thereby negating some of the intended conservation benefits (3). In addition, growing public awareness of, and concern about, the welfare of individual wild animals necessitates improved transparency and justification of conservation activities (1, 3, 41, 43–46). Thus, the growing urgency for conservation brings with it an equally urgent need for conservation and animal welfare scientists to engage in genuine discourse in support of collaborative research to underpin welfare-focused conservation practices.

Animal welfare is a difficult concept to define but the term is now widely used to reflect how an animal is experiencing its life (47, 48). Dominant theoretical models for understanding animal welfare have focussed on the animal's physical state or biological function (Biological function orientation), the mental experiences, both positive and negative, the animal may have as a result of its physical state/biological function (Affective state orientation) or the naturalness of its environment and/or its ability to express natural behaviors (Naturalness or Natural living orientation) (49, 50). It is now widely agreed within the field of animal welfare science that no single orientation on its own is sufficient and that components of all three theories must be integrated to holistically understand and scientifically assess animals' welfare states (48, 50, 51). Further discussion and illustrations of the limitations of focussing on only one aspect of animal welfare, in the context of conservation, are presented below in The Need for Common Language and Understanding Relating to Wild Animal Welfare.

Conflicts between those working to achieve the goals of conservation biology and those aiming to safeguard the welfare of individual wild animals are apparently on the rise (20, 45, 52). As noted, this may be because of the growing urgency and thus volume and range of conservation research and practices, as well as growing public awareness of conservation activities (3, 12, 43) and, more generally, of animal welfare [e.g., (53–56)]. This is exemplified by the moratorium imposed by the Tasmanian state government in 2000 on hot-branding as a method for identifying individual elephant seals (*Mirounga leonina*) for research purposes on Australia's Macquarie Island after media attention and public outcry about perceived animal welfare impacts (3, 57). In the scientific arena, growing concerns about the effects of conservation activities on wild animal welfare may also be attributed to our increasingly detailed, robust and evidenced-based understanding of what animal welfare is and how it can be evaluated (48, 58–62) (see below).

Such conflicts have often been attributed to incompatible ideologies [e.g., (1, 38, 52, 63–65)]. For example, McMahon et al. (20) suggested that prioritizing concerns for the welfare of individual animals, as "animal welfare advocates" seek to do, stymies the generation of scientific knowledge critical to stemming the extinction of species and the consequent loss of ecosystem services and evolutionary potential. However, the position often cited for "animal welfare advocates" is actually one of animal rights, an ethical stance that no amount of benefit from conservation activities can justify any level of individual animal suffering [e.g., (20, 39, 66, 67)].

In contrast, the role of animal welfare scientists in the conservation context is to use scientific principles and methods to evaluate impacts on the welfare of animals, both positive and negative and at individual and population levels, to inform ethical conservation decision-making and practice (42, 68–70). Accordingly, they advocate approaches to achieving conservation goals that minimize negative welfare impacts [e.g., (64, 70–72)] and, where appropriate and possible, realize or maximize any welfare benefits (44, 46, 61). In some cases, animal welfare scientists may use the outcomes of scientifically robust evaluations to recommend that an activity not proceed if the predicted or actual welfare costs are considered to outweigh the likely conservation benefits (42, 44, 70, 73, 74). For example, application of an identification marking method that would cause significant tissue injury, pain or behavioral alteration and that would not facilitate animal identification at a level (individual or group) or distance or for a duration required to achieve the objectives of the research programme would be discouraged (44).

This kind of informed decision-making is equally recommended by conservation scientists [e.g., (2, 20, 21, 43, 75, 76)]. Thus, the starting positions and goals of conservation biology and animal welfare science do not appear to be inherently incompatible. Given that activities impacting detrimentally on the welfare of individual animals often also hamper achievement of some conservation goals (2, 43, 77) and that societal acceptance is imperative to the continuation of conservation activities (3, 20, 44), it is clear that the best outcomes for both disciplines will be achieved through collaboration and knowledge-sharing. Despite this recognition, cross-disciplinary information-sharing and collaborative research and practice in conservation are still relatively rare [e.g., (2, 20, 34, 78)], with the exception of the zoo animal context (see below), so that substantial scope for synergy between the activities of conservation and animal welfare scientists remains.

The aim of this paper is to summarize key points developed by a group of conservation and animal welfare scientists discussing scientific assessment of wild animal welfare. On the basis of those discussions, we propose the formal development of a new discipline, integrating the expertise of scientists from both fields, to progress our understanding and evaluation of wild animal welfare and optimize the aims of both disciplines: this is "Conservation Welfare," an appellation coined in the World Association of Zoos and Aquariums' Animal Welfare Strategy document in 2015 (46).

PARTICIPANTS AND WORKSHOP

Workshop participants were invited from those attending the third International Compassionate Conservation Conference in Sydney, Australia in November, 2017. The over-arching purpose of the 1-day workshop was to explore the various roles of science in "Conservation Welfare." Fourteen participants from Australia, New Zealand and the United Kingdom attended, and the workshop was facilitated by the two lead authors. The participants were animal welfare scientists, conservation scientists, scientific representatives of non-governmental animal welfare organizations, wildlife veterinarians and wildlife rehabilitators.

The workshop comprised a series of group discussions exploring the meaning of animal welfare and how it might be assessed, as well as, the ways in which conservation activities might impact upon wild animal welfare. In addition, the challenges associated with understanding wild animal welfare and integrating that kind of understanding into conservation policy and practice were explored. Following the workshop, the lead authors distilled from those discussions key principles for optimizing the aims of both scientific disciplines. The dominant theme emerging from the workshop was the need for a common language to facilitate cross-disciplinary progress in understanding and safeguarding the welfare of animals of wild species.

THE NEED FOR COMMON LANGUAGE AND UNDERSTANDING RELATING TO WILD ANIMAL WELFARE

There are two key reasons why conservation and animal welfare scientists should work together to evolve and apply a common understanding of welfare as it pertains to animals of wild species. First, the way in which animal welfare is conceived influences the way it is evaluated and the emphasis put on different features of welfare. This is important because rigorous, defensible and transparent assessment of "animal suffering" is key to making informed and ethical decisions in conservation practice (2, 16, 20, 69, 70). Secondly, the conception of animal welfare influences the importance placed on the outcomes of such evaluations and how that information is used going forward, for example, in policy development and decision-making.

CONCEPTION OF ANIMAL WELFARE INFLUENCES ITS EVALUATION AND EMPHASIS–"FITNESS"

The theoretical characterization of animal welfare directly influences both the approach to its assessment and the dimensions or features emphasized in such evaluations. Specifically, what welfare is considered to be dictates the indicators measured, the level of measurement (e.g., individual vs. population level), the aspects of welfare prioritized and how the data are interpreted (61). This can be illustrated by examining the apparently different characterizations of welfare in conservation and animal welfare sciences and the practical implications of these differences.

Logically, current conceptions of welfare in conservation biology often appear to align to the immediate goals of the discipline, that is, to keep genetically valuable individuals alive and reproducing and to maintain genetic diversity within and between populations [e.g., (21, 26)]. In accordance with this, welfare is often evaluated at the population level and using variables chiefly related to the physical state or biological function of the animals. At the most general level, welfare may be extrapolated from measures of survival and reproductive success, i.e., "*fitness*" [e.g., (79–86)].

Other conservation evaluations focus on variables that reflect the animals' physiological or health status in finer detail, i.e., specific attributes of their "*fitness*," and may be undertaken at the population or individual level, depending on the purpose and on practical considerations (44). Examples include body condition, weight, coat, plumage or skin condition, injury or pathology, altered gait or the occurrence of abnormal behaviors [e.g., (26, 84, 87–90)]. Likewise, blood, saliva and fecal components indicating nutritional status or energy reserves, immune or reproductive function or "stress" may be evaluated [e.g., (13, 91–94)]. In rehabilitation, translocation and reintroduction contexts, when animals are under closer human control for longer periods, clinical examinations may be performed to evaluate the health status and potential survivability of rescued, captured or captive wild animals [e.g., (35, 95–100)]. Similarly, in the research context, the impacts of manipulations, such as identification marking or capture are commonly evaluated using measures of physical status, such as injury severity or healing, changes in body weight, condition or temperature, energy expenditure, behavior or survival estimated by likelihood of re-sighting/recapture [reviewed by (11, 22, 101–106)].

More detailed evaluations of wild animal behavior are generally undertaken to understand features of the social and ecological interactions of animals, as well as the impacts of human interventions or changes to the ecosystem on fitness and ecosystem function, rather than to understand their welfare state *per se* [e.g., (2, 9, 34, 107–112)]. Notable exceptions are the detailed studies of behavior often undertaken in the zoo context for the explicit purpose of assessing welfare state [e.g., (113–116)] and systematic evaluations of wild behavior to improve the efficacy of strategies to control invasive species [e.g., reviewed by (117–119)].

Conception of Animal Welfare Influences Its Evaluation and Emphasis–"Feelings"

In the field of animal welfare science, welfare is generally conceptualized as a property of an individual animal. More specifically, welfare is a property of individuals of species considered to have the capacity for both pleasant and unpleasant mental experiences, i.e., experiences that matter to the animal itself; this capacity is otherwise known as sentience (58, 120–122). Such experiences are generated by processing of information about the animal's internal physical state and/or its external circumstances and are variously called affects, affective states, emotions or "feelings" (48, 51). Thus, while welfare can be assessed at the population level (as routinely occurs in assessment of farm animal welfare), the underlying assumption is that population-level indicators reflect the mental experiences of the various individuals within the group (62, 123, 124), rather than a population collectively possessing welfare *per se*.

In accordance with this conceptualization, there is now wide acknowledgment in this scientific field of the importance of animals' mental experiences as the feature of ultimate relevance for understanding their welfare (48, 58, 121, 122, 125). Related to this is recognition of the importance of assessing the potential for both negative (unpleasant) and positive (pleasant) experiences to holistically understand welfare state at any point in time (58, 59, 61, 62, 126). Thus, animal welfare evaluations aim to interpret the indicators of physical/functional state, i.e., biological function or "fitness," in terms of the mental experiences that those indicators are likely to reflect, i.e., "feelings."

In support of this approach, there is growing understanding of the neurophysiological bases of mental experiences, such as thirst, hunger, pain, breathlessness, nausea, fear and others, as well as evidence of the links between measurable indicators of physical/functional states and the occurrence of such mental experiences in some non-human animals [e.g., (126–132)]. Importantly, affective states can also influence physical/functional states; thus the two are inextricably and dynamically inter-related and should be interpreted as such (48, 50, 133). For example, it is well-established that dairy cattle, pigs and poultry which are more fearful of their human handlers exhibit lower productivity and/or reproductive success than their less fearful cohorts (134). This advancing biological understanding and evidence facilitates cautious interpretation of the kinds of data already collected in some conservation research as reflecting the mental experiences of the animals and thus their welfare state, e.g., hydration status or changes in body condition (94) as indicators of thirst and hunger, respectively (132).

Conception of Animal Welfare Influences Its Evaluation and Emphasis–"Feelings" and "Fitness"

Framed in this way, the limitations of using survival and reproductive success as proxies for welfare are clear. Simply surviving until the point of evaluation does not guarantee acceptable or desirable welfare, as animals can survive despite experiencing chronic unpleasant states (13, 135–138). This recognition may influence decisions between lethal and non-lethal population control strategies or attempts at rehabilitation and release vs. euthanasia for rescued wildlife [e.g., (15, 17, 18, 23, 24, 28, 35, 139, 140)]. Likewise, measures of survival and reproductive fitness are not useful for evaluating welfare impacts when animals are intentionally killed for conservation purposes [lethal control of invasive species or culling overabundant or nuisance native animals: e.g., (18, 25, 32, 73, 141–143)], or when they die due to unintended effects of conservation activities [e.g., (9, 15, 72)].

Alternatively, although low reproductive success might reflect physiological states that align with poor welfare, such as malnutrition or severe stress [e.g., (13, 15, 17, 144)], failure to reproduce, *per se*, is not necessarily indicative of a specific negative experience that would compromise welfare (4) and vice versa (137). This point might be important when considering the welfare both of valued animals that are not reproducing [e.g., cheetahs in captivity; (145, 146)] and when reproductive control is used to manage wild populations [e.g., (23, 147)].

Likewise, a sole focus on biological function can lead to interpretation of "normal" health or function as sufficient evidence of good or acceptable welfare or lead to emphases on "inputs" (i.e., good husbandry or care) that may not translate into acceptable "outputs" (i.e., good welfare) (34, 46, 133, 148). To illustrate these risks, many domestic farmed animals have good biological function and are highly productive, in terms of survival, growth and reproduction, but have poor welfare due to limited opportunities for normal behavioral expression and the attendant unpleasant mental experiences (135, 136, 149). Healthy wild animals may have unpleasant experiences too. Examples include significant anxiety or fear during capture, captivity or after transfer to a new location or social group (2, 12, 34, 125), or less well-understood experiences, such as loneliness, boredom or frustration in captive environments (61, 150, 151). Focussing only on indicators of physical status or biological function can also result in failure to look for or recognize indicators of the wide variety of unpleasant experiences that can compromise welfare (48, 152). Related to this, there is also a danger that the theoretical underpinnings of welfare evaluations may be conceived, *post-hoc*, to fit the limited data that can currently be collected in practice, rather than the preferred strategy of the established conceptual framework of welfare guiding the approaches to data collection and the identification of gaps to advance knowledge for future assessments (153).

In the context of killing, a focus on biological function may lead to over-estimates of welfare impacts. One commonly held view amongst animal welfare scientists is that death *per se* does not equate to poor welfare [cf. (154)]; an animal's experiences of its welfare state exist only while it is alive and able to consciously perceive features of its internal state and/or the world around it (42, 48, 51). Thus, negative welfare impacts take the form of unpleasant experiences, such as pain, breathlessness, nausea or fear before the irreversible loss of consciousness [i.e., the point at which experiences are no longer possible (152)]. Measures of physical state (i.e., behavior or physiology) made after this point no longer reflect conscious mental experiences and, although they are often aesthetically unpleasant to observe, they do not reflect welfare state (25, 32).

Previously Proposed Concepts to Unite Conservation and Animal Welfare Sciences

Several authors have previously indicated the need for a common language to unite conservation and animal welfare sciences and have attempted to identify common metrics to do so and to more clearly delineate the point at which biological fitness and welfare converge. "Stress" was proposed as that unifying concept, and measurements of stress have been widely used to evaluate the fitness and welfare impacts of human-generated conditions and procedures on animals of wild species [e.g., (42, 75, 78, 91, 92, 94, 155, 156)]. Stress has usually been characterized according to physiological responses, primarily activation of the hypothalamic-pituitary-adrenal (HPA) axis elicited by external threats or disruptions to internal conditions, i.e., homeostasis (157, 158).

As such, measurements of stress are often used to infer how well the animal is "coping" with its environment (159). But the affective significance of such stress, coping or lack of coping and thus the relationship to welfare state, is not clear (160). For instance, "stress responses" can also occur in situations actively sought out by animals and which would intuitively appear to be related to positive experiences e.g., hunting, mating (91). In addition, the responses and responsiveness of the HPA axis can change depending on the pattern and duration of the stressors [e.g., (92, 113, 161)], stress may have negative (e.g., reduced reproduction) or positive (e.g., escaping a predator) consequences for fitness (75), and behavioral strategies may be used instead to "cope" with conditions that are nonetheless unpleasant to the animal, e.g., hiding, expressing abnormal repetitive behaviors (114, 162).

In response to these limitations of using "stress," several authors proposed "distress" as the point at which physiological stress becomes intense and/or prolonged enough to be detrimental to both welfare and fitness (75, 113). Distress is variously defined as "a chronic condition reflecting the biological cost of repeated or cumulative stressors" (157) or "when stress induces allostatic [homeostatic] overload or becomes pathogenic" (163). So defined, distress reflects some point toward the extreme end of the continuum of physiological stress; the point at which stress becomes distress is empirically identified as when diversion of resources away from core functions, such as reproduction, feeding or immune function can be quantified (13, 157, 164). The concurrent measurement of stress (i.e., HPA activation) and biological cost (e.g., suppressed reproductive function) makes this concept valuable for assessing the conservation implications of stressors that may also impact on welfare (13, 137).

In contrast, in the field of animal welfare science, distress is generally characterized as "one or more negative psychological states indicative of poor wellbeing or that decrease wellbeing" (165) or as a "wide range of unpleasant emotional experiences" (166). Thus, distress in this field unequivocally represents the extreme end of a continuum describing affective, mental or psychological states while stress (and distress in the conservation context) appears primarily to represent a physiological response, with ambiguous relationships to affective state. Accordingly, these concepts do not occupy the same continuum. An important corollary of this is that the absence of evidence of extreme stress responses and/or fitness costs is not evidence of the absence of unpleasant experiences and poor welfare state.

This affect-related concept of distress is more consistent with the current conception of welfare favored by the majority of animal welfare scientists (48). However, given that distress is characterized as a range of different unpleasant experiences and that different mental experiences reflect different problems for the animal to solve via their behavioral and physiological responses (61), there is unlikely to be one single empirical metric of both reduced fitness and poor welfare nor even a single set of measurable indicators that can be used to practically evaluate distress (167). It is more meaningful to evaluate welfare according to the evidence about the intensity and duration of specific unpleasant experiences, such as breathlessness, pain, thirst and hunger (62). Doing so also facilitates the development and implementation of strategic approaches to avoiding or mitigating those specific experiences (152).

Thus, the problem with concepts, such as stress, distress and others like "suffering" is the lack of clarity about their meaning and their relationships to the mental experiences of animals and the associated lack of a scientific framework for assessing these scientifically nebulous concepts (51, 168). Interestingly, although such pragmatic models have been advocated for more than 15 years, there has been limited uptake in practice, and collaborative research and activity between animal welfare and conservation scientists is still rare (2). Perhaps this is because, more fundamentally, a common understanding of what animal welfare is conceived to be must be achieved first.

CHARACTERIZATION OF WELFARE ALSO INFLUENCES THE SIGNIFICANCE ASSIGNED TO, AND THUS THE APPLICATION OF, OUTCOMES OF WELFARE ASSESSMENTS

As well as influencing the approach to, and emphasis within, scientific assessments, the conceptual foundations of welfare influence the ways the outcomes of those assessments are interpreted, prioritized and applied. Specifically, how welfare is understood may influence the following: decisions about whether welfare is assessed at all; how strongly minimization of negative welfare impacts is emphasized; how information from welfare assessments is integrated into conservation decision-making; and how that knowledge informs the development of policies, guidelines and legislation. Salient examples from the New Zealand (NZ) and Australian context are presented below.

Overall, it is argued that understanding welfare as what is experienced by, and thus what matters to, the animal itself increases our responsibility in three areas: to systematically evaluate welfare impacts; to genuinely include that knowledge in conservation decision-making practice; and to give it more appropriate prominence in those decisions than is currently apparent (52).

Whether or Not to Devote Resources to Welfare Assessment and How Strongly Minimization of Negative Welfare Impacts Is Emphasized

Many kinds of conservation activities proceed without explicit or formal scientific evaluation of potential welfare impacts. In NZ, these include routine management of threatened native animals (such as captive breeding and release, intensive monitoring, and regular movement between populations), control of invasive animal populations, wildlife rescue and rehabilitation, and permanently holding native and exotic wild animals in captivity. Decisions about whether to undertake formal welfare assessment may be made implicitly or explicitly by various stakeholders with various objectives; such decisions may sometimes involve conflicts of interest, i.e., not wanting to know about the welfare impacts of activities considered to be desirable for other reasons, including for the achievement of conservation objectives. While it may be argued that many such activities are "routine" or based on "best practice," the lack of ongoing welfare assessment limits opportunities to update practices as scientific understanding and technical capacity grow (169), thereby limiting opportunities to minimize negative welfare impacts.

Characterization of welfare may also influence the emphasis put on minimizing negative impacts in the context of conservation research. In NZ, research on wild animals must be approved by animal ethics committees (AECs) authorized under the Animal Welfare Act (1999) (170); approval depends on demonstrating an understanding of the potential negative impacts on the subject animals' welfare as well as the likely benefits of the research. However, there may be unrealized opportunities for minimizing welfare impacts associated with research procedures, and it behooves AECs and the applicants seeking approval to regularly challenge the status quo in terms of what might be considered to be "unavoidable" negative welfare impacts. As a parallel, while surgical procedures performed on laboratory animals almost inevitably cause some degree of pain, NZ AECs put the onus on applicants to demonstrate how such pain can be minimized and that pain relief strategies are the best currently available [e.g., (153, 171, 172)]. Likewise, academic journals in the field of animal welfare science are increasingly demanding evidence, above and beyond appropriate regulatory approval, of strategies to avoid, mitigate or minimize negative welfare impacts on research animals [e.g., Animal Welfare journal; (43)].

To better realize these sorts of opportunities, research directed at minimizing existing welfare impacts associated with conservation activities should be encouraged and specifically funded (153). As one example, systematic evaluations of the effects of identification marking techniques on the welfare of subject animals are still rare relative to the number of studies applying such techniques to wild populations [e.g., reviewed by (11, 22, 101, 103)], and more are needed (169). Whenever the type, severity, duration, distribution or variability of negative welfare impacts are not well-understood, preliminary studies that formally assess the impacts of the proposed procedures should be required by AECs before granting approval for major studies applying those procedures in wild populations (44, 153, 169).

WHETHER AND/OR HOW TO INTEGRATE INFORMATION FROM ASSESSMENTS INTO DECISION-MAKING

In line with the points made above, decisions about whether and how a wider range of conservation activities proceed should be informed by impacts on the animals involved (20). As noted, such decisions are complex and involve multiple stakeholders with differing priorities [e.g., (1, 45)]. However, such decisions cannot be taken knowledgeably and ethically if welfare impacts are not rigorously and transparently evaluated (72, 74). Assessments that emphasize the importance of mental experiences to an animal's welfare and that cautiously interpret measured physical/functional variables accordingly may result in greater weight being given to the welfare outcomes in conservation decision-making. Alternatively, there is a risk that evaluations focussing only on "objective" clinical indicators of biological function will inspire less concern for animal subjects of conservation activities, leading to prioritization of other objectives in conservation decision-making.

To illustrate, despite rigorous scientific research demonstrating the negative experiential impacts of poisons used to lethally control various invasive mammal species in NZ and Australia [e.g., (18, 25, 32, 173, 174)], both small-scale domestic applications (e.g., household rodent control) and mass poisoning programmes continue to use the least humane agents because they are effective and safe for humans (118, 175). In the last 30 years, relatively little progress has been made toward developing effective and safe alternatives that are demonstrably more humane for the millions of sentient animals so affected (175, 176). Perhaps explaining those welfare impacts in terms of the severely unpleasant and protracted experiences that the animals may have before loss of consciousness (25, 32, 174) would influence the weight assigned to welfare when deciding to continue to use those agents.

Framing welfare impacts in terms of the unpleasant experiences animals might have may therefore also be useful for informing public sentiments and political decisions regarding lethal vs. non-lethal control of both native and introduced species. With regard to non-lethal methods, wild animals clearly demonstrate species-specific indicators of experiences, such as extreme fear, anxiety, rage and/or frustration during the processes of capture and transport for purposes, such as relocation, re-homing or permanent penning [e.g., (2, 15, 34, 92)]. Other unpleasant experiences, such as pain or exhaustion may arise due to physical injury or capture myopathy [e.g., (177, 178)].

Importantly, scientific studies now provide evidence of ongoing negative welfare impacts in animals relocated rather than humanely killed [e.g., (15, 17, 24, 139, 140)]. Other studies compare potential impacts associated with all components of lethal vs. non-lethal methods to allow holistic decision-making (18, 24). Impacts occurring after the period of capture, temporary holding and release may take the form of extreme hunger due to unfamiliarity with foraging opportunities (34), or fear and pain due to the animal's reduced ability to escape predators in the new location or because of aggression from resident conspecifics (2, 15, 140). For animals captured from the wild and brought into captivity, for example, for permanent penning or taming, there is undoubtedly a period of severe fear and anxiety as they habituate to confinement and human proximity (78, 179); some individuals never successfully acclimate, meaning such experiences likely persist to some degree [e.g., (33, 180–183)]. Disruption of social groups and restricted movement may lead to other, less well-understood unpleasant experiences, such as loneliness, frustration, boredom, depression or grief [e.g., (62, 150, 151)].

Similarly, decisions about whether to rehabilitate or promptly euthanize "rescued" wildlife should not be evaluated only in terms of the conservation status of the species and the genetic merit of the individual, but also by considering the potential for significant and/or chronic unpleasant experiences, such as pain, sickness and fear, both during and after the rehabilitation process [e.g., (30, 95, 97, 184–186)]. In both cases, the potential for longer-term negative welfare impacts is often not formally evaluated in conservation decisions, and, in any case, the significance of such impacts for the animal itself may be overwhelmed by public sentiment about the value of sustaining life at any cost over a humane death [e.g., (96, 187)].

WHETHER AND/OR HOW TO CONSIDER INFORMATION IN DEVELOPMENT OF POLICY AND LEGISLATION

As well as influencing current conservation decision-making, research and practice, the conceptual basis of welfare may also influence development of policies, guidelines and laws that, in turn, guide future practice. In particular, emphasizing that some animals experience unpleasant (and pleasant) states which affect their welfare highlights the significance of legislative discrepancies and the limitations of using survival or biological function to infer welfare in conservation and other policies and guidelines.

In NZ's Animal Welfare Act 1999 (170) and Codes of Welfare enacted under that Act, persons in charge of wild animals held for the purposes of exhibition, containment or rehabilitation are obligated to meet the animals' physical, health and behavioral needs and to act to avoid or alleviate any unnecessary or unreasonable pain or distress [e.g., (188)]. Other wild animals are variously recognized and treated under the law (see below). Although there is general reference in the law to one specific unpleasant experience, i.e., pain, and an amalgamation of others under the appellation "distress" (54), the importance of unpleasant experiences for animal welfare is not explicitly articulated, which may encourage emphasis on physical state, the limits of which have been discussed above. The importance of interpreting observable or measurable indicators as reflective of animals' mental experiences in the legal context has recently been exemplified in a number of successful legal prosecutions for animal welfare offenses in Canada and the UK (168, 189, 190).

For free-living wild animals or animals living in a wild state (i.e., feral domestic animals), there exist incongruities among NZ laws or even among sections of the same Act that appear to facilitate de-prioritization of animals' mental experiences in certain contexts (41). These "exemptions" to general requirements to safeguard animal welfare become more difficult to defend for economic, conservation or practical reasons if the experiences of the animals themselves are central to our collective conception of welfare. To illustrate, under Section 30A of the NZ Animal Welfare Act, "a person commits an offense who wilfully ill-treats a wild animal." Ill-treatment is defined as "causing the animal to suffer pain or distress that, in its kind or degree, is unreasonable or unnecessary." However, it is legally acceptable to purposefully use control methods scientifically demonstrated to be relatively less humane than existing alternatives for some sentient wild animals, either because of their classification as "pests" or because it is "generally accepted" to treat them in that particular way (170). Some of these exemptions relate to fulfillment of the purposes of other acts, such as the Conservation Act 1987 (191) and the Biosecurity Act 1993 (192) (Animal Welfare Amendment Act (No.2) 2015 (193) subsection 30A4) or the Animal Welfare Act, Section 181, relating to the Agricultural Compounds and Veterinary Medicines Act 1997 (194), when the activity involves the use of any substance for direct management or eradication of vertebrate pests. Nonetheless, the question arises: "is the suffering caused to these wild animals 'necessary'?" (41, 52, 195).

There are also examples of animals of the same species being treated differently under the law when they are classified differently for human purposes. For example, feral cats (*Felis domesticus*) are designated as pests and are thus exempt from certain welfare protections under various NZ laws, as described above. In contrast, owned cats of the same species (*Felis domesticus*) and cats used for the purposes of research, which presumably have the same biological capacity for unpleasant experiences that compromise their welfare, are much more strongly protected under the NZ Animal Welfare Act. These categorizations and legal exemptions serve to reinforce existing species and contextual biases (41, 74) and are likely to stymie progressive development of more humane methods for managing wild populations, both of which are detrimental to wild animal welfare overall.

EXAMPLES OF "CONSERVATION WELFARE" IN THE ZOO COMMUNITY

As noted above, collaborative research and practice among conservation and animal welfare scientists occur only sporadically. Explicit and deliberate evaluations of welfare occur in some specific areas of biological conservation, particularly in context of research involving wild animals, when approval from a regulatory body is required, and for animals kept in zoos.

Zoos arguably play roles in *ex situ* conservation by providing genetic repositories for threatened and endemic species and by educating the public about animals and conservation [e.g., (196–198)] [but cf e.g., (199)]. In these roles, the zoo community is demonstrating a commitment to "Conservation Welfare" in various ways, most notably by adopting a contemporary characterization of animal welfare and scientific principles and methods of assessment to guide zoo design and practices [e.g., (115, 200–204)]. Two key examples are the World Association of Zoos and Aquariums Animal Welfare Strategy (46) and the Zoo and Aquarium Association (Australasia) members' accreditation programme [(205, 206); n.d.]. Both documents are based on a characterization of animal welfare and assessment framework reflecting the centrality of animals' mental experiences. To become accredited ZAA members, Australasian zoos and aquaria must demonstrate the ways in which they provide care and husbandry practices and habitats designed to minimize unpleasant experiences and maximize opportunities for animals to have positive experiences [(205, 206); n.d.].

For various reasons, this approach may be easier and also more pressing for the zoo community to action than for biologists working in other areas of conservation practice. Maintaining public support is of primary importance for the continued existence of zoos, and zoo practices, including those reflecting a commitment to animal welfare, are under increasing public scrutiny (204). Zoo scientists are able to evaluate welfare at the level of the individual animal over time and are able to collect much more detailed data than field biologists usually can (10, 75). Increasingly, this kind of information and a focus on animals' mental experiences is guiding habitat design [e.g., (133, 207)] and the evolution of zoo policies and guidelines (116), ZAA's Animal Welfare Position Statement (205) and is being given greater weight in conservation decision-making in the zoo community [e.g., Periera (208) "Tiger returned to SF zoo after transfer to Sacramento made her homesick"; Anon (209) "Zoo pays tribute to much-loved lions"; Johnston (210) "Auckland zoo puts down 'unhappy and agitated' gibbon"]. Individual zoo organizations, and increasingly the zoo community as a whole, are showing leadership in this regard, and there is great potential for zoo biologists and welfare scientists to collaborate more closely with their field research colleagues to optimize policies and practices to better achieve both welfare and conservation goals more broadly [e.g., (211, 212)].

CONCLUDING REMARKS: A FUTURE OF CONSERVATION WELFARE

To address some of the challenges identified above, the establishment of a new discipline of "Conservation Welfare" is recommended. Its major role would be to reveal key synergies between the sciences of conservation and animal welfare with the aim of providing an integrated foundation upon which the two could interact constructively to further the objectives of both. Finding common ground has apparently been hindered thus far by notions that these are competing disciplines or schools of thought, or even ideologies. In part, this has been due to different ways members of the two disciplines have understood animal welfare, with conservation scientists generally emphasizing "fitness" and welfare scientists "feelings," as illustrated here. This dichotomy has led to apparently incompatible views on the nature and significance of animal welfare impacts and the related implications for wildlife policy and management. Some of these difficulties have been considered here, and these observations raise the question of how this impasse can be resolved.

It is concluded that to make progress scientists in both disciplines will need to arrive at compatible understandings of animal welfare; in other words, it will behoove both groups to use a common language when considering welfare matters in the conservation context. Thus, instead of reinforcing the existing "fitness" *or* "feelings" dichotomy, cross-disciplinary progress may be achieved by recognizing the scientifically current and widely accepted animal welfare conceptual framework that integrates these two elements as dynamically interacting components within animals, i.e., that animals embody a "fitness" *and* "feelings" unity. Understanding this unity underpins the conceptual foundations of animal welfare and rigorous and robust science-based methods used to assess animal welfare impacts in circumstances that compromise and/or enhance welfare.

It is still necessary to consider various matters in more detail than was possible here. They include: what the precise implications will be for informed decision-making in the conservation arena; what will constitute humane conservation practices and/or management; how public perceptions and values will evolve to interact with welfare and conservation decision-making and practice; and how high standards of individual and/or group animal welfare can be monitored and achieved practically in conservation biology whilst most effectively meeting both conservation and animal welfare objectives.

AUTHOR CONTRIBUTIONS

NB and DM designed and facilitated the workshop during which the ideas expressed in this paper were collectively generated by all authors. NB wrote the first draft of the paper and all other authors provided critical review of the drafts.

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Animal Welfare in Conservation Breeding: Applications and Challenges

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Animal welfare and conservation breeding have overlapping and compatible goals that are occasionally divergent. Efforts to improve enclosures, provide enriching experiences, and address behavioral and physical needs further the causes of animal welfare in all zoo settings. However, by mitigating stress, increasing behavioral competence, and enhancing reproduction, health, and survival, conservation breeding programs must also focus on preparing animals for release into the wild. Therefore, conservation breeding facilities must strike a balance of promoting high welfare, while minimizing the effects of captivity to increase population sustainability. As part of the Hawaii Endangered Bird Conservation Program, San Diego Zoo Global operates two captive breeding facilities that house a number of endangered Hawaiian bird species. At our facilities we aim to increase captive animal welfare through husbandry, nutrition, behavior-based enrichment, and integrated veterinary practices. These efforts help foster a captive environment that promotes the development of species-typical behaviors. By using the "Opportunities to Thrive" guiding principles, we outline an outcome-based welfare strategy, and detail some of the related management inputs, such as transitioning to parental rearing, and conducting veterinary exams remotely. Throughout we highlight our evidence-based approach for evaluating our practices, by monitoring welfare and the effectiveness of our inputs. Additionally we focus on some of the unique challenges associated with improving welfare in conservation breeding facilitates and outline concrete future steps for improving and evaluating welfare outcomes that also meet conservation goals.

Keywords: behavioral monitoring, captive breeding, conservation breeding, opportunities to thrive, welfare assessment, avian welfare

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INTRODUCTION

A good state of welfare is generally representative of animals that are well nourished, safe, lack pain, fear, and distress, and have the ability to develop and express species-typical relationships, behaviors, and cognitive abilities (1–3). Measuring and accomplishing these aims requires tailored approaches, since the needs of every species (and individual) can be different. Moreover, an animal's welfare state can change temporally, with development, or with fluctuating external stressors (2). Therefore, welfare goals need to be assessed with regularity, even when management actions have not changed.

At San Diego Zoo Global (SDZG), we address the necessity and complexity of meeting the needs of species and individual animals through our Opportunities to Thrive program (**Table 1**). Developed to replace the seminal Five Freedoms established by the UK's Farm Animal Welfare Council (4), this program provides guidance for managing all animals in our collection, and our conservation breeding programs. Conservation breeding involves the captive propagation of endangered species to help maintain genetic diversity, produce viable individuals for release and ultimately mitigate species' extinction (5). Positive indicators of animal welfare are essential components of effective conservation breeding programs because they are correlated with reductions of physiological indicators of stress (6), the incidence of health issues (7), and increases in reproductive success (8). However, unlike many zoo settings, conservation breeding facilities need to execute a welfare strategy explicitly aimed at increasing the likelihood of successful reintroductions to the wild.

One SDZG program that has embraced the Opportunities to Thrive in pursuit of conservation breeding goals is the Hawaii Endangered Bird Conservation Program (HEBCP). The HEBCP seeks to prevent extinction and support the recovery of wild populations, primarily using captive propagation, and reintroduction techniques, alongside state, federal, and local partners. We have cared for a total of 16 endemic Hawaiian species across our two breeding facilities, including most recently, Nene (*Branta sandvicensis*; Hawaiian goose), Puaiohi (*Myadestes palmeri*), Palila (*Loxioides bailleui*), ʻAlalā (*Corvus haweaiiensis*), and ʻAkikiki (*Oreomystis bairdi*). Some species recovered sufficiently for us to end their conservation breeding programs (e.g., Nene and Puaiohi), and others have been recently added as their conservation status has declined in the wild (e.g., ʻAkikiki). Since 1993, we released over 800 Hawaiian birds into the wild.

The Opportunities to Thrive guides our integrated animal management strategy by lending structure to our welfare efforts. We use each opportunity to highlight a set of desired outputs (e.g., increased foraging or fewer stress-related behaviors), which we target with a series of inputs (i.e., welfare-focused management actions). We then evaluate whether our actions solicit the intended outputs, which allows us to better plan future inputs. There is overlap between tactics for addressing the opportunities, so these should be viewed as a broad coordinated approach. We summarize our methods in **Table 1**, and describe our rationale and the challenges we face throughout the paper. While some details to our approaches may be unique to the species under our care, the application of these principles are not limited to avian facilities.

OPPORTUNITY FOR A STRATEGICALLY-PRESENTED, WELL-BALANCED DIET

Avian species show considerable variation in their natural diets and welfare of birds in captivity depends heavily on meeting their nutritional needs through normal foraging and feeding behavior. Diets should provide all necessary nutrients, and be of adequate quantity, quality, and variety. Food also needs to be presented in a manner and a frequency appropriate to the species, in a way that can facilitate an evaluation of dietary choices. The individual animal's condition, size, physiological, reproductive, and health status must also be considered during diet formulation (9). Imbalanced diets can be linked to poor health (e.g., (10, 11) with associated veterinary costs, poor egg production, and low chick viability (12).

Even if an optimal diet is offered, it cannot be assumed that animals consume the desired proportion and quantities of its components. We use common hands-on evaluation techniques, such as weighing feed intake when hand-rearing chicks by placing them on a scale during feeding sessions, and calculating the nutrient composition of items consumed (10, 13). Meanwhile, for our birds that require space and privacy to rear their own young, we assess these measures observationally. We monitor parental interactions at the nest via CC-TV, noting how many times each parent feeds their chick during a set period of the day, and we record the quantities and type of food that parents have removed from their food pan when it is collected at the end of the day.

On the infrequent occasion that we handle a bird, we conduct assessments of their body condition, scoring their muscle mass, and fat reserves in addition to taking weight. Body condition scoring (BCS) is a numerical, subjective measurement of muscle definition, and superficial fatty tissue, which helps assess a bird's general health relative to their food supply. Low BCS scores are associated with lowered reproductive success, poor recovery from illness, and with disease or age (14). High BCS scores are associated with reproductive disorders, arthritis, diabetes, and other chronic conditions (15). Although BCS is an effective tool, the scoring system used for each species can be different. For instance, we adapted a pectoral muscle and fat store scoring system (16) for ʻAlalā and Palila.

Optimizing nutrition in a captive breeding setting can be a challenge without data on the quantities wild birds eat, or on the chemical, and nutritional composition of native foods. Moreover, since the provision of food offers opportunities for animals to display natural feeding behaviors, an understanding of species-typical foraging, and food processing is required to assess desired nutritional welfare outcomes. For these reasons, we evaluate not just the nutritional aspects of feeding, but also the foraging competency of our birds. For instance, wild Palila forage primarily by prying open seed pods from a native tree; a foraging skill that captive birds can lack (17). We provision the birds with a predetermined number of pods and track their foraging proficiency by later checking how many remain, and how many pods are opened successfully.

OPPORTUNITY TO SELF-MAINTAIN

Animals need the opportunity to engage in positive behaviors to proactively avoid discomfort and rest when appropriate. Examples of these behaviors include self-grooming and bathing, as well as the ability to move freely and avoid undesirable weather

TABLE 1 | Summary of welfare actions, organized by the Five Freedoms and their relation to the Opportunities to Thrive.

Freedom	Opportunity	Management actions (inputs)	Assessment techniques (outputs/outcomes)
From hunger and thirst	Strategically presented, well-balanced diet	Formulate diets to meet species' requirements through life history, including breeding, and chick rearing	Records kept for food consumption and food type preferences, measurements of body scores, and weight that assess pectoral muscle condition and fat stores
From discomfort	Self-maintain	Aviaries designed for shelter, adequate perching, room for flight, with minimal human contact	Behavioral observations of stress and positive self-maintenance behavior
From pain injury or disease	Optimal health	Telemedicine health checks, animal care staff training	Documentation of health based on physical exam, body weight, and condition, and biomaterial evaluation (blood, feces, tissue)
To express normal behavior	Expression of species-typical behavior	Offer native foods, naturalistic enrichment, nest building, pair bonding, parental care	Behavioral observations of pair bonding, nest activity. Appropriate use of enrichment.
From fear and distress	Choice and control	Dynamic perching, social housing options, multiple nest platforms, and opportunities for mate choice	Using behavioral observations to measure the choices made and amount of time engaged with options presented

These opportunities differ from the five freedoms by focusing on positive indicators of welfare, rather than the absence of negative ones.

or social conditions. Self-maintenance behaviors are a common positive welfare marker (18).

We designed our aviaries with the opportunity to self-maintain in mind. While the exact dimensions of the aviaries vary by species, each bird is provided with ample areas to shelter in native vegetation, roost, bathe, fly, feed, perch, and walk, all while minimizing human contact. To evaluate whether these inputs actually promote self-maintenance, our team conducts twice daily health and well-being checks, often from behind one-way glass. The team also meets daily to discuss observations of unusual behaviors that may be cause for concern or be markers of improvement. These daily observations and discussions are distilled into a written daily report that is circulated to all relevant off-site staff, such as veterinarians. If an issue arises, immediate monitoring is initiated, but for chronic issues, a longer term behavioral assessment protocol is enacted. For instance, after keepers voiced concerns that daily husbandry activities (e.g., feeding and cleaning) could increase stress-related behaviors, we devised an observational protocol to determine if housing or husbandry inputs could alter stress outcomes. These observations assessed self-maintenance (e.g., preening) and stereotypic or stress behavior (e.g., pace-flying) before and after routine husbandry to best measure changes to welfare outcomes during daily routines.

Conservation breeding environments necessitate limited human-animal contact in order to ensure the birds are as wild as possible in preparation for future releases. However, this limits the usage of hands-on training for welfare checks, and increases our reliance on remote monitoring, such as CC-TV or hidden observation areas, to track positive indicators of welfare.

OPPORTUNITY FOR OPTIMAL HEALTH

We strive for more than the absence of pain and disease, and instead aim to foster healthy well-being. This shift means we proactively look for positive markers of health, instead of waiting for the negative consequences of poor health to manifest.

A team of SDZG veterinarians and registered veterinary technicians provide on-site medical care at both breeding facilities and ʻAlalā release facilities 2–3 times per year. During on-site visits, birds are examined to follow up on existing medical issues or to diagnose and treat new medical concerns. This may include physical or visual examinations, diagnostic imaging, triage care, surgery, and biological sample collection and analysis. Birds in the release program are examined to ensure fitness and health prior to release. Biological samples are collected during the pre-release exam process and also from birds in the conservation breeding program for future disease investigations. Capacity building with staff during onsite visits fosters collaboration and allows opportunity to train staff in essential skills.

Due to the remote nature of this conservation effort, immediate on-site medical care by a veterinarian is not always possible. As a result, HEBCP husbandry staff has been trained by SDZG veterinary staff in basic treatment and diagnostic sample collection techniques. This onsite training provides a platform to efficiently practice telemedicine (e.g., practicing remote, electronically communicated health care) through video conferencing, photograph review, and phone consultations (19). Diagnostic blood samples, fecal samples, and carcasses are processed on-site by HEBCP staff and sent by overnight mail to SDZG for evaluation by SDZG pathologists and clinical veterinarians. This turn-around allows for rapid evaluation of samples and response to medical cases.

Providing veterinary care at remote sites provides unique challenges, but the close collaboration with HEBCP husbandry and field staff, SDZG clinical veterinarians, and veterinary pathologists, nutrition, and laboratory staff helps us provide the highest quality of care in this conservation breeding program.

OPPORTUNITY TO EXPRESS SPECIES-TYPICAL BEHAVIOR

While it has long been recognized that the performance of species-typical behavior can have positive outcomes for animal welfare, the concept has been unevenly applied across zoo settings (20). Sometimes referred to as "ethological needs" or "behavioral needs" (21), there is growing evidence that animal welfare is improved by the performance of species-typical behaviors. An environmental enrichment program that addresses these behavioral needs can reduce stress and stereotypic behavior (20, 22). In addition to the welfare benefit, maintaining natural behaviors in conservation breeding programs is important because artificial captive environments can prevent the development of survival skills, such as foraging, escaping from predators, and navigating unknown spaces (23).

In addition to supporting natural feeding and self-maintenance behavior with targeted welfare inputs, we also encourage the expression of normal social behavior; an indicator of positive animal welfare (24). We address this by housing birds in species-typical social arrangements. For example, young ʻAlalā are gregarious in the wild, but adults are territorial. Therefore, we house them in age cohorts comprised of 4–6 individuals until they reach maturity, and then transition them to single-pair breeding aviaries separated by at least 100 meters. We have preliminary data suggesting that ʻAlalā pairs may have greater reproductive success in distant compared to proximate aviaries, indicating that the welfare benefits associated with greater privacy from other pairs may positively influence reproduction.

Beyond the social setting, we designed inputs to allow the expression of species-typical breeding behavior. Nest-building, egg incubation, chick rearing, and other behaviors associated with the reproductive cycle are critical behavioral needs. These behaviors can be all-consuming, and divert birds' attention away from expression of problem behaviors such as stereotypies. Thus, we offer potential breeding pairs a variety of nesting material, allowing them to construct their own nests. Not only does this provide an enrichment opportunity, but by gauging the level of interest and investment in nest building behavior, our team can determine the breeding phase of birds. For instance, ʻAlalā engage in a "cup form" behavior in the later stage of nest building, and a peak in this behavior indicates that the female is likely to lay her first egg of a clutch (25). This behavioral outcome is critical for predicting when to use adaptive management strategies to increase the likelihood of a successful hatch.

Due to the incredible value of each egg and chick, the early stages of many conservation breeding programs focus on the survival of chicks to retain the genetic diversity of target species. However, as captive flocks grow and species-specific rearing techniques improve, there is often more capacity for the expansion of parental rearing. Accordingly, HEBCP has a long history of conducting highly skillful artificial incubation and chick rearing, and over time we shifted away from artificial

TABLE 2 | Example observation protocol: ethogram for monitoring ʻalalā breeding pair interactions.

Behavior	Definition
OCCURS IN 2 MINUTE PERIOD?	
Proximity	The birds come within one body length of each other for at least 10 s.
Co-attention	While foraging or searching for food or sticks both birds focus on the same item or area. Both beaks must be oriented toward the same item or area, close enough to allow potential aggression. Examples include both birds inspecting the same crevice or both pulling food from the same food item.
Contact sitting	Two birds sit touching sides or within one body width apart (not jumping around or feeding). Birds may twine necks around each other.
Allopreening	One bird preens, nibbles, or rubs another with head, beak, or neck; if mutual, score behavior for both birds involved, e.g., birds A and B are preening each other at the same time, score A:B and B:A.*
Beg	Bird pumps head up and down while holding wings out and pumping them up and down. Can be accompanied by a begging call.
At nest	Bird stands or sits on one of the nest types (crown or tub) for at least 5 s. Please mark the bird and type of nest.
Nest build	Bird interacts with a stick, grass, or other nest material while standing on either the nest tub or crown. Please mark the bird and type of nest (crown or tub).
OCCURS IN 30 MINUTE PERIOD?	
Threaten	Threatening behavior that does not involve physical contact toward another bird. Includes: raising scapular feathers, head down threat, head up threat, lunges, attempts at biting, pecking, or striking with wing, foot, etc., flight buzz, successful and unsuccessful attempts to steal an object or food item (without contact being made)*
Contact aggression	One bird aggresses another and makes actual physical contact. Examples include: biting, pecking, striking, or landing on another bird, moving another bird's head away with the aggressor's own head/beak, successful, and unsuccessful attempts to steal an object or food item (with contact being made).
Pace fly	Bird flies rapidly back and forth along the length of the aviary. Each pass (one length of the aviary) counts as one pace.
Cup form	Bird lays on their stomach in the nest (almost like a belly flop) and wriggles feet/wings. A pause in the wriggling motion denotes the end of one cup form. Multiple cup forms can occur in short periods of time and each should be noted.
Cooing	Typically a male behavior. The male makes a cooing noise while dipping his head up and down below his shoulders.
Copulate	Two birds attempt or succeed in copulating. Copulations are characterized by the female tail wagging and the male mounting the female.

*Thirty minute observations using this guide aim to capture aggression, pair bonding, and measure stress. The 30 min are broken into 2 min time chunks. Relatively common behaviors are noted only once per 2 min period if they occur, and rarer behaviors are noted every time they occur in the 30 min period. If birds express threats, contact aggression or pace flying, it indicates lower levels of pair compatibility, and higher levels of stress. In contrast, pairs that exhibit relatively more allopreening, allofeeding, and contact sitting are considered to be well bonded and exhibiting positive signs of welfare. *behaviors adapted from Jolles et al. (31).*

rearing and to allow more birds to incubate and provide care for their own offspring. Additionally we are moving toward allowing mate choice for new pairs (see next section). These husbandry changes no doubt address a suite of pair-bonding and parental behaviors whose performance is beneficial for the welfare of the birds because they encourage species-typical behaviors, and alleviate the potential negative welfare outcomes associated with "forced" mate pairing (26) and removal of offspring (27).

We also manage a larger experience-based enrichment program that includes the provision of additional opportunities to perform species-typical behavior, such as problem solving, so that lessons learned can guide future enrichment strategies. Monitoring the outcomes of these provisions, such as individual-level engagement with provided enrichment, allows us to continually adapt and increase challenges as birds reach release. Through our iterative process of observing, learning, and managing the birds in our care, we continually improve our approximations of their wild-type behaviors, which are otherwise poorly understood.

OPPORTUNITY FOR CHOICE AND CONTROL

Having choices allows animals to exert control over their environment, which helps regulate emotional responses to stressful situations (28). In zoo settings, having choices about space use, or social interactions can reduce behavioral and hormonal signs of stress (29, 30). We give choices to the birds in their everyday lives. Each aviary has numerous perch types that vary in height, and level of cover. We offer breeding pairs multiple aviary chambers, so they can chose their proximity to their mate. Particularly in breeding season, we evaluate each pair's amount and type of social contact with behavioral observations, and take action to separate or resocialize birds depending on pair interactions (see **Table 2** for example of observation protocols). Recently we also began giving birds a choice in where to build their nest and the amount of supportive infrastructure provided, allowing them artificial, but "easy," or natural, but "more difficult" opportunities. Implementing these nesting options served a dual purpose because we measured preferences for a given nest type, while also offering the birds an additional choice.

Having choice can also matter when it comes to picking a mate. In giant pandas, for example, allowing free mate choice before pairing can improve the reproductive success of pairs, especially if the choice is mutual between both members of the pair (32). However, metrics for mate choice can differ by species, and there is a dearth of information on the breeding behavior of many endangered species. Therefore, when establishing a new breeding population with ʻAkikiki, we immediately set up opportunities for mate choice and behavioral observation protocols to help us explore how to monitor breeding preferences by systematically measuring stress and pair bonding behaviors. As a result of this effort, ʻAkikiki bred for the first time in captivity.

CONCLUSIONS

Despite the successes of HEPCP, there is still much to learn about optimizing welfare and the breeding potential for each species. While we consider high standards of welfare to be a priority goal for all species, we identified several challenges that are applicable to the care of many endangered species. For instance, the lack of knowledge about species-typical diets and behavior can make assessments difficult. Additionally, the need to stay as "hands-off" as possible means we cannot rely on traditional operant training techniques and instead must utilize behavioral observation in multiple contexts. By continuing our efforts to research and monitor the birds, we hope to continue improving our welfare outcomes alongside our conservation goals. The more we learn about the unique species under our care, the more we can provide them with opportunities to thrive.

AUTHOR CONTRIBUTIONS

AG, RS, and NL contributed conception and design of this manuscript. AG wrote the first draft of the manuscript. NL, GV, RS, MK, AF, DB, SF, and BM wrote sections of the manuscript. All authors contributed to manuscript revision, read and approved the submitted version.

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A Global Reassessment of Solitary-Sociable Dolphins

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Dolphins are typically regarded as highly social animals. However, some individuals live apart from their own species and may come to socialize with people through a recognized series of stages which are presented and expanded on in this paper. The term "solitary-sociable dolphins" has been used to describe these animals and such individuals have been identified from several different species and reported in many parts of the world. In many instances, the interactions with people that may follow their original isolation, and which typically become more intense over time, have created situations where the welfare of the animal has been compromised by disturbance, injury, the feeding of inappropriate items and aggressive human behavior. Several solitary-sociable dolphins have also been deliberately injured and killed by humans. People who interact with these dolphins may also put themselves at risk of injury. This paper reports on recent cases drawing on published and unpublished sources. Since 2008, 32 solitary dolphins have been recorded including 27 bottlenose dolphins (25 *Tursiops truncatus* and two *Tursiops aduncus*), two striped dolphins and three common dolphins. Four solitary belugas have also been recorded. There are some ten solitary dolphins and one beluga known at the present time. Laws and guidelines currently in place to protect solitary-sociable dolphins need to be strengthened and interactions with people should be avoided or, at the least, carefully managed to protect both the dolphin and the humans involved in the interaction. Terms, such as disturbance and harassment which are included in laws need to be clearly defined. Additionally, management plans for solitary-sociable dolphins need to be developed and adapted on a case by case basis taking into account the individual dolphin's sex, age, personality, stage of sociability and home range. It is also important that government officials and local stakeholders work together to implement guidelines which set out how the public can observe or interact with the dolphin safely.

Keywords: bottlenose dolphin, solitary dolphin, sociable dolphin, lone dolphin, solitary-sociable dolphin, beluga, animal welfare

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INTRODUCTION

The phenomenon of "solitary-sociable dolphins" has been described by various authors and cases have been reported from all over the world and across many decades [e.g., (1–3)]. The vast majority of such animals are bottlenose dolphins (*Tursiops truncatus* and, to a lesser extent, *Tursiops aduncus*) possibly because, as predominantly inshore coastal species, they are more likely to come into contact with humans than other dolphins (1, 4). This behavior has also been reported in belugas

(*Delphinapterus leucas*), narwhals (*Monodon monoceros*), orcas (*Orcinus orca*), tucuxis (*Sotalia fluviatilis*) and other dolphin species, including common (*Delphinus delphis*), striped (*Stenella coeruleoalba*), dusky (*Lagenorhynchus obscurus*), Risso's (*Grampus griseus*) and pantropical spotted (*Stenella attenuata*) dolphins (5).

Wilke et al. (2) described these animals as dolphins "who have little or no contact with conspecifics and who regularly closely approach humans, often including touch, social, sexual and play behaviors." Müller and Bossley (6) suggested that it is likely that there are different "types" of solitary dolphins exhibiting different behaviors and that a single definition for these animals would be simplistic and confusing. Wilke et al. (2) proposed a number of stages that an individual animal passes through as he or she changes behavior from being simply "solitary" to being a "friendly solitary." Using these stages, we categorize recent cases and also propose two new additional stages.

Interactions between wild dolphins and humans have been increasing around the world often encouraged by local tourist agencies (7) and, as solitary-sociable dolphins often restrict their movements to a small area, they may be relatively easy for the public to access (6). Human-dolphin interactions may lead to various management and welfare problems and even the death of the animal and it is, therefore, appropriate that consideration is given to the management and protection of such dolphins (3) and also the safety of humans entering the water with them.

In this paper we review current knowledge regarding solitary-sociable delphinids and monodontids and detail cases recorded since 2008. We consider the stages that they can pass through as they become increasingly sociable and how to improve the protection afforded to them.

METHODS

We sought the most recent information about solitary-sociable dolphins by (i) sending a request for information via the MARMAM online mailing list, (ii) conducting a variety of internet searches, including using academic databases and (iii) contacting those involved in monitoring their local dolphin populations. We also advertised this work as ongoing at the 2018 meeting of the Scientific Committee of the International Whaling Commission.

The information gathered is displayed in two tables; one for animals recorded in Europe and one for animals from other parts of the world. Criteria for inclusion of an animal included that it had to belong to the family of delphinids or monodontids and that it had to have been seen since 2008. Any dolphins that died or disappeared before 2008 are not included in our tables. The animal also had to have been recorded on its own for a prolonged period (at least a few weeks). Then we considered the behaviors exhibited and assigned the dolphins to one of the stages (and, if possible, levels) of sociability described below in section Stages of Sociability. Wherever possible we contacted scientists and other observers who had reported the animals to verify information.

The solitary belugas are not assigned to any of the stages of sociability here as it is not clear whether their behavior develops in the same way as it does for dolphins (C. Kinsman 2018, pers. comm., 9 November). This is an area that merits future research as in Canada there have been an increasing number of solitary belugas reported in recent years (see **Table 3**), and this year there has also been a case of a solitary beluga in the waters off the United Kingdom (see section Cases of Solitary-Sociable Dolphins Since 2008).

WHY AND HOW DOLPHINS BECOME SOLITARY AND SOCIABLE

Bottlenose dolphin society is described by Müller and Bossley (6) as "a complex mixture of associations" and solitary individuals may be considered at one end of the range of observed sociability. Group sizes may range from one to over 100 and may be influenced by habitat structure and activity patterns (12). Bottlenose dolphins typically live in a "fission-fusion" society and group composition changes continuously and frequently (12–14). Food availability and loss of habitat may sometimes determine dolphin social structures and could lead to solitary behavior (4, 6). Different factors, or a combination of factors, may prompt a dolphin to become solitary for a prolonged period and it is important to note that such an animal will not necessarily start interacting or socializing with humans.

Differences between individuals in terms of their behavioral choices could mean that some animals are more likely to become solitary than others (6). Connor et al. (13) reported that in Sarasota Bay, Florida and Shark Bay, Western Australia some female bottlenose dolphins are more solitary whilst others are more social. Some dolphins may become solitary because of their individual life experience. Thus, the death of a male dolphin's coalition partner, the loss of a whole group or a mother (due to illness, bycatch or hunting) or the poor health of an individual because of illness or injury could all potentially lead to a dolphin becoming solitary (6). In Brazil, "Viola" the solitary tucuxi allowed humans to touch it after its mother was killed by a fisherman (15). In Mexico, "Pechocho" the bottlenose dolphin is also believed to have become solitary after his mother died.[1] Solitariness could, therefore, in some cases, be a response to trauma (6). It is also possible that young dolphins that have not learned the necessary social skills from their mother have problems integrating into dolphin society.

The majority of recorded cases of solitary dolphins come from areas close to the coast, perhaps because the open ocean is a more dangerous place for a lone animal or because they are more likely to be observed and recorded when they are in coastal areas (6). The available evidence indicates that, fairly obviously, for a solitary dolphin to become a solitary-sociable dolphin, it has to be in an area where it can come into frequent contact with people.

Many of the reported cases of solitary dolphins come from Europe (see **Tables 1**, **2**) and Müller and Bossley (6) cite the past decimation of various dolphin populations in Europe as

[1] https://riodoce.mx/sincategoria/el-pechocho-delfin-silvestre-domesticado

TABLE 1 | Solitary-sociable dolphins 109AD−2008 by region and species [adapted from Goodwin and Dodds (5)].

Region	Bottlenose dolphin (*Tursiops truncatus* and *Tursiops aduncus*)	Other species
Europe, Middle East, and North Africa	39	3 (species unknown)
South Africa	2	0
Caribbean and Americas	10	20 (13 beluga, 3 orca, 1 narwhal, 1 pantropical spotted dolphin, 1 tucuxi, 1 species unknown)
Australia and New Zealand	9	6 (4 Common dolphin, 1 Dusky dolphin, 1 Risso's dolphin)
Asia	2	0
Total	62	29

a factor which could contribute to the increased likelihood of a dolphin becoming solitary. They suggest that, in the past, dolphin social groups overlapped and so an individual that was leaving one group, could easily find another group to join. In areas where numbers have been reduced, social groups may be more separated and so an individual may find itself alone for a longer period before it encounters another group and it could, potentially, become solitary during this period. Simmonds and Stansfield (21) proposed that, in the United Kingdom, an increasing number of solitary bottlenose dolphins could be due to the distance between the relatively few remaining groups, and that individuals which disperse or are displaced from their natal group may end up on their own because they simply do not find another group to join.

Lockyer and Müller (4) stated that the time it takes for a dolphin to become sociable (meaning here that it readily interacts with people in the water) depends, in part, on the frequency of interactions and the patience and determination of the humans who interact with the animal as well as the age of the dolphin, whether or not it has experienced aggression from humans in the past, and its personality.

Stages of Sociability

Whatever the reason for the dolphin's initial solitariness, its subsequent development into a "sociable" dolphin that interacts with humans happens through a process which has been described by Wilke et al. (2), who identified four stages:

Stage 1: a solitary dolphin establishes itself in a limited home range. The area has sufficient prey and an area where the dolphin likes to rest, such as next to a buoy or moored boat. The dolphin may follow boats or approach fishing gear but it does not approach humans.

Stage 2: The dolphin may start to follow boats more regularly and to engage in bow-riding as well as investigating ropes, chains, buoys etc. The dolphin is interested in people who enter the water to swim with it, but it maintains a distance.

Stage 3: The dolphin becomes accustomed to one or more people who have deliberately tried to habituate it. Humans swim and dive with the dolphin, touch it and even hold its dorsal fin so that they can be pulled through the water. The dolphin may initiate some of these interactions and thereby help the habituation process.

Stage 4: Thanks to media reports, the dolphin becomes a tourist attraction. People come from further afield to see and swim with the dolphin. The dolphin may start to exhibit dominant, aggressive and sexual behaviors.

Wilke et al. (2) suggest that some solitary dolphin cases only progress to Stage 2 or Stage 3. While some dolphins allow human contact quite quickly, for others it takes more time before they will accept interactions and touching in the water and such habituation requires considerable effort from the humans initiating it (22).

It is also possible that a dolphin may turn up in a new location or a new part of its home range in a condition in which he or she is already "friendly" toward humans due to experiences in its previous location (2). Indeed, Doak (23) noted that whereas some solitary-sociable dolphins have very limited home ranges (e.g., "Fungie" in the Dingle area of Ireland), others range more widely or move their home bases on occasion. In the more recent cases of solitary dolphins, "Clet" and "Fiete" traveled great distances and did not demonstrate site fidelity for extended periods. "Clet" was first seen in Brittany (France) before being recorded in Cornwall, Wales, the Isle of Man and Scotland.[2] "Fiete," meanwhile, traveled over 2,000 km from Kiel (Germany) to Saint-Malo in Brittany in a period of 2 months.[3]

Wilke (2007), cited in Goodwin (14), suggested developing Stages 3 and 4 further to include the following levels:

Level 1: the dolphin only interacts with boats during its sociable period,

Level 2: the dolphin interacts with humans but does not allow direct physical contact,

Level 3: the dolphin allows direct contact but usually only with certain people,

Level 4: the dolphin allows direct contact with anyone. It does not demonstrate socio-sexual or dominance behaviors,

Level 5: the dolphin allows direct contact with anyone and regularly exhibits socio-sexual and dominance behaviors.

Goodwin and Dodds (5) proposed two further stages. They suggested that a Stage 5 dolphin would continue to interact with humans and boats but would also spend more time engaged in other types of interactions including with other cetacean species, seals and/or birds. We consider that interactions with other species could happen during a number of the stages e.g., "Kylie" the solitary-sociable common dolphin in the Firth of Clyde, Scotland is in Stage 3 or 4 but is sometimes sighted with a harbor porpoise (*Phocoena phocoena*) (17). We do not see this as a discretely separate stage. Goodwin and Dodds (5) also proposed a Stage 6 where the dolphin begins to interact with its own species again.

[2]https://www.mwdw.net/clet-the-dolphin-seen-in-manx-waters/
[3]http://www.al-lark.org/2017/03/fiete-a-great-traveler-dophin.html

TABLE 2 | Solitary and solitary-sociable dolphins in Europe since 2008.

Stage (Level) reached	Name of dolphin	Location	Species*	Gender	First seen	Last seen/date of death	References
1	Unnamed	Monfalcone, Italy	Dd	Presumed F	Jun. 2010	Aug. 2011	(16)
1	Stormy	Wales, UK	Dd	?	Dec. 2014	Apr. 2015	[4]
3 or 4 (2 or 3)	Kylie/Colin/Donna	Firth of Clyde, Scotland, UK	Dd	F	Approximately 2001	Present	(17); M. Cosentino, 2018, pers. comm., 2 June.;[5]
–	Benny	Thames Estuary, UK	Dl	?	July, 2018	Present	[6,7]
1 or 2	SC1	Vinodol Channel, Croatia	Sc	F	Aug. 2004	Last seen Jul. 2009	(18)
1	?	Mali Lošinj harbor, Croatia	Sc	?	Aug. 2008	Last seen 11 Sept. 2008	(19)
1 or 2	Rudolf	Ostend and Nieuwpoort, Belgium	Tt	?	2007	Last seen 2008 (or possibly 2010)	(20); [8]
2	? (possibly Rudolf)	Knokke-Heist, Belgium	Tt	?	Jul. 2010	Last seen Oct. 2010	(20)
4 (4)	Bobi	Karin Sea, Croatia	Tt	M	Apr. 2014	Last seen 2016 (or possibly 2017)	[9,10,11,12]
2	? (possibly Bobi)	Slano, Croatia	Tt	?	Jun. 2017	Seen a few times. Possibly still present	D. Crljen, 2018, pers. comm. 18 June; [12]
4 (5)	Dusty/Sandy/Mara	North Clare/Inis Oírr, Ireland	Tt	F	2000	Present	R. Meade, 2018, pers. comm. 7 May; [13,14,15,16,34,64]
1	Nimmo/Salty	Galway, Ireland	Tt	?	Since at least 2008	Present	[17]
2	Doogie/Dougie	Tory Island, Ireland	Tt	F	2006	Last seen? 2008?	(5); [18,19, 64]
4 (3)	Fungie	Dingle, Ireland	Tt	M	1983	Present	[20]
2 (5)	Clet/Nick/Nobby/ George II/Hobnob	France, UK, Ireland	Tt	M	2008	Last seen summer 2015	[2,21,22,54]
1	Fiete/Freddy	Brittany, France and Kiel, Germany	Tt	M	2016	Aug. 2017	M. Perri, 2018, pers. comm., 18 May; [3,23]
2	Gaspar/Jean Copo'h/Jean Floc'h	Brittany, France and Galicia, Spain	Tt	M	2003	Last seen 2010	[24,25,26]
1	Lilou/Wifi	Brittany, France	Tt	M	2007	?	[27,28]

(Continued)

[4] http://www.seawatchfoundation.org.uk/unusual-solitary-dolphin-moves-to-aberystwyth/
[5] https://www.facebook.com/clydeporpoise/posts/1716608158447857
[6] http://www.bdmlr.org.uk/index.php?mact=News,cntnt01,detail,0&cntnt01articleid=1012&cntnt01origid=15&cntnt01returnid$=$54
[7] https://www.kentonline.co.uk/gravesend/news/benny-could-be-here-to-stay-192434/
[8] http://www.spiegel.de/international/zeitgeist/rudolf-the-bottlenose-dolphin-frolics-on-belgian-coast-a-711454.html
[9] https://www.croatiaweek.com/swimmers-warned-not-to-swim-with-bobi-the-bottlenose-dolphin/
[10] https://www.blue-world.org/bobi-solitary-adriatic-dolphin/
[11] https://www.youtube.com/watch?v=L0YBilFsqTM
[12] https://www.24sata.hr/fun/kupace-u-slanom-iznenadio-dupin-koji-se-brckao-s-njima-528246
[13] http://www.iwdg.ie/news/?id=2572
[14] https://www.independent.ie/irish-news/watch-dusty-the-wild-atlantic-way-dolphin-gives-fungi-a-run-for-his-money-with-show-for-island-daytrippers-35888275.html
[15] https://www.irishtimes.com/news/ireland/irish-news/second-dolphin-takes-up-residence-off-aran-island-1.1939115
[16] http://www.irishdolphins.com/webpilot/list/details.asp?l=10&contentid=57
[17] http://connachttribune.ie/galways-latest-maritime-attraction-performs-crowds-898/
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[19] https://video.nationalgeographic.com/wild/unlikely-animal-friends/00000144-16d7-dcf1-a954-57df5eb90000
[20] https://www.independent.ie/irish-news/news/dont-panic-beloved-fungie-the-dolphin-suffers-deep-gash-from-boat-propeller-34769753.html
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[24] http://www.laopinioncoruna.es/coruna/2009/07/16/delfin-gaspar-asusta-buzos-puerto-fontan/304305.html
[25] http://www.abc.es/20101213/local-galicia/delfin-gaspar-201012130911.html
[26] https://www.youtube.com/watch?v=O2hgKXDt3eg
[27] https://voilesetvoiliers.ouest-france.fr/croisiere/grande/voilier-loick/un-dauphin-pas-commun-24ef3743-1cf2-7148-8fa7-24ff3fb9f7cd
[28] https://www.reseaucetaces.fr/groupe-de-travail-sur-les-dauphins-solitaires-et-familiers/dauphins-solitaires-and-familiers-en-france/
[29] http://www.bdmlr.org.uk/index.php?mact=News,cntnt01,detail,0&cntnt01articleid=991&cntnt01pagelimit$=$15&cntnt01returnid=54
[30] https://www.facebook.com/Randy-Dony-le-dauphin-1672284889658475/

TABLE 2 | Continued

Stage (Level) reached	Name of dolphin	Location	Species*	Gender	First seen	Last seen/date of death	References
4	Randy/Dony/Georges	UK, Ireland, France, Holland, Belgium.	Tt	M	April, 2001	Present (Currently in Brittany, France)	29,30
3 (3 or 4)	Elcano	Northern Spain, Western France	Tt	M	Feb. 2013	Last seen Sept. 2013	31,32
3 or 4 (5)	Zafar/Toto	Brittany, France	Tt	?	Jun. 2017	Present	61,33
0	?	Portsmouth and Isle of Wight, UK	Tt	?	Jun. 2017	?	29
3 or 4 (2)	Splashy	Cornwall, UK	Tt	M	Jul. 2017	Last seen Mar. 2018	D. Jarvis 2018, pers. comm., 29 May; A. Lowe 2018, pers. comm., 16 March

**Dd, short-beaked common dolphin (Delphinus delphis); Dl, Beluga (Delphinapterus leucas); Sc, striped dolphin (Stenella coeruleoalba); Tt, bottlenose dolphin (Tursiops truncatus); Ta, Indo-Pacific bottlenose dolphin (Tursiops aduncus).*

RESULTS

Cases of Solitary-Sociable Dolphins Since 2008

There are many cases throughout history of solitary-sociable dolphins. **Table 1** provides a summary of animals up until 2008 and is based on an earlier inventory (5). This table may not be complete but it gives some idea of the numbers concerned. Of the 91 animals listed, 62 were recorded as bottlenose dolphins [61 *T. truncatus* and one *T. aduncus,* noting that until 1998 all bottlenose dolphins were treated as the same species, *T. truncatus* (24)].

Two lists of the solitary and solitary-sociable delphinids and monodontids reported since 2008 are presented; one for Europe (where the majority of known solitary dolphins occur) and one for the rest of the world (see **Tables 2**, **3**). Some of these animals are also included in the numbers in **Table 1** as they were in residence in 2008 and continued to be so for a period afterwards (including, in some cases, up to the time of writing).

Since 2008, 36 solitary delphinoidea have been recorded including 27 bottlenose dolphins (25 *T. truncatus* and two *T. aduncus*), two striped dolphins (*Stenella coeruleoalba*), three common dolphins (*Delphinus delphis*) and four belugas (*Delphinapterus leucas*). Twenty-three of these animals were recorded in Europe and thirteen from other locations around the world. Of these, eleven are still solitary at the time of writing ("Dusty," "Nimmo" and "Fungie" in Ireland, "Kylie" in Scotland, "Benny" in England, "Randy" and "Zafar" in France, "Pechocho" and "Lucero" in Mexico, "Jojo" in the Turks and Caicos Islands and the unnamed animal in Coffs Harbor, Australia).

Identifying individual solitary dolphins can be difficult if the animal does not have known distinctive markings and, also, if it is wide-ranging. In Ireland, for example, there appear, at first glance, to be quite a high number of solitary dolphins whereas actually, in some cases, the same dolphin has been given different names in different locations. For example, the dolphin known as "Dusty" in Doolin, County Clare, has now relocated to Inis Oírr where she is called "Sandy" (R. Meade, 2018, pers. comm., 7 May). She has also been referred to as "Mara" by some sources ([34], R. Meade, 2018, pers. comm., 6 June). ["Mara" should not be confused with "Marra," a solitary dolphin that was seen in Cumbria, UK and that died in 2006 (3)].

We have attempted to categorize the dolphins (but not the belugas) according to the stages outlined in **Figure 1** (see section Stages of Sociability for details). Categorizations are based on the information available to us in articles, personal communications and videos. We recognize that these may not include all interactions that have taken place between humans and a given dolphin and, therefore, may not fully represent the actual stage reached by each animal.

Although all of the dolphins listed in **Tables 2**, **3** exhibited solitary behavior, some of them did not, or have not yet, become "sociable" and are considered to be Stage 0 or Stage 1 in the sociability process. For example, the striped dolphin reported by Nimak-Wood et al. (19) was not observed in contact with humans although the authors considered that it did demonstrate behaviors which showed signs of related behavior, such as spending time close to a mooring buoy. One of the reasons put forward by the authors for the lack of human interaction is that the dolphin was present in a harbor where swimming was prohibited and therefore the opportunity for dolphin-human interaction was limited.

[31] http://maisouestelcano.blogspot.com
[32] https://www.youtube.com/watch?v=onl3GFlDzj8
[33] https://vimeo.com/223415504
[34] http://www.dailymail.co.uk/news/article-2024070/Meet-real-life-Flipper-The-extraordinary-relationship-woman-wild-dolphin-friend.html

The short-beaked common dolphin described by Genov et al. (16), also did not exhibit the sociable behaviors and interactions with humans that characterize most solitary-sociable dolphins, but is included here because of its continued presence in one location over a period of time and because of its solitary nature. This dolphin could be considered to be Stage 1.

TABLE 3 | Solitary and solitary-sociable dolphins in the Rest of the world since 2008.

Stage (Level) reached	Name of dolphin	Location	Species*	Gender	First seen	Last seen/date of death	References
–	Q	Cape Chignecto, Nova Scotia, Canada	Dl	M	2008	Last sighted 19 August 2010 with serious injuries	(8); C. Kinsman 2018, pers. comm., 9 November; [37]
–	Leucas/Luke/The Liverpool whale	Halifax, Nova Scotia, Canada	Dl	M	May 2015	Last sighted 9 August 2015 (apparently healthy)	C. Kinsman 2018, pers. comm., 9 November; [38,39]
–	Nepisiguit Beluga	Bathurst, New Brunswick, Canada	Dl	M	June 2017	Last sighted in July 2018 accompanied by another beluga	[77]
5	Solitary Social Dolphin/Yera/Sally/ Dolly/Beyoncé	New South Wales, Australia	Ta	F	Sept 2012	No longer solitary	(9); [40,41]
0	?	Coffs Harbor, New South Wales, Australia	Ta	?	?	Present	G. Storrie 2018, pers. comm., 1 May
4 (5)	Stinky/Humpy/Randy	Gran Cayman	Tt	M	Approximately 2009	2012	[42,43,44]
4 (4)	Pechocho	Gulf of California, Mexico	Tt	M	Approximately 1992	Present	(10); [1,45]
4 (4)	Lucero	Veracruz, Mexico	Tt	F	Approximately 2003	Present	[46]
4 (4)**	Beggar/Mooch	Florida, USA	Tt	M	1990	Died 2012	(11); [40]
4 (4)**	Dolphin 56	East Coast, USA	Tt	M	1979	Last seen Jul 2011	[47,48]
5	Kaimi	San Francisco, USA	Tt	?	Jul 2016	No longer solitary	W. Keener 2018, pers. comm., 23 February; [49]
4 (5)	Jojo	Turks and Caicos Islands, West Indies	Tt	M	1980	Present	(2, 5); [50]
4 (?)	Moko	North Island, New Zealand	Tt	M	March 2007	Died Jun 2010	I. Visser, 2018, pers. comm. 22 June; [51,52,53]

Dl, Beluga (Delphinapterus leucas); Tt, Bottlenose dolphin (Tursiops truncatus); Ta, Indo-pacific bottlenose dolphin (Tursiops aduncus).
***Interactions were limited to provisioning and touching.*

[35] http://www.bdmlr.org.uk/index.php?mact=News,cntnt01,detail,0&cntnt01articleid=1012&cntnt01pagelimit=15&cntnt01returnid=54
[36] https://www.pla.co.uk/BDMLR-and-PLA-joint-press-statement
[37] https://www.ctvnews.ca/q-a-lost-beluga-whale-thrills-maritimers-1.315665
[38] https://www.cbc.ca/news/canada/nova-scotia/beluga-whale-sighting-in-liverpool-harbour-worries-marine-biologist-1.3119905
[39] http://www.whalestewardship.org/www.whalestewardship.org/Leucas_2.html
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[41] https://www.theguardian.com/environment/2014/jan/07/lonely-dolphin-making-human-friends-but-experts-ask-swimmers-to-stay-away
[42] https://www.caymancompass.com/2012/10/01/marine-experts-to-examine-lone-dolphin/
[43] http://www.foxnews.com/science/2012/10/11/us-scientists-puzzled-by-lone-dolphin-in-cayman-islands-deemed-dangerous.html
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[45] https://www.facebook.com/periodicoeldebate/posts/10156096436855903
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[48] http://www.nj.com/news/index.ssf/2012/08/dolphin_56_where_are_you.html
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[50] http://turksandcaicostourism.com/turks-caicos-attractions/jojo-the-dolphin/
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[52] http://www.projectjonah.org.nz/Teacher+Resources/Solitary+Dolphins/Moko+the+dolphin.html
[53] https://www.nzherald.co.nz/nz/news/article.cfm?c_id=1&objectid=10657370

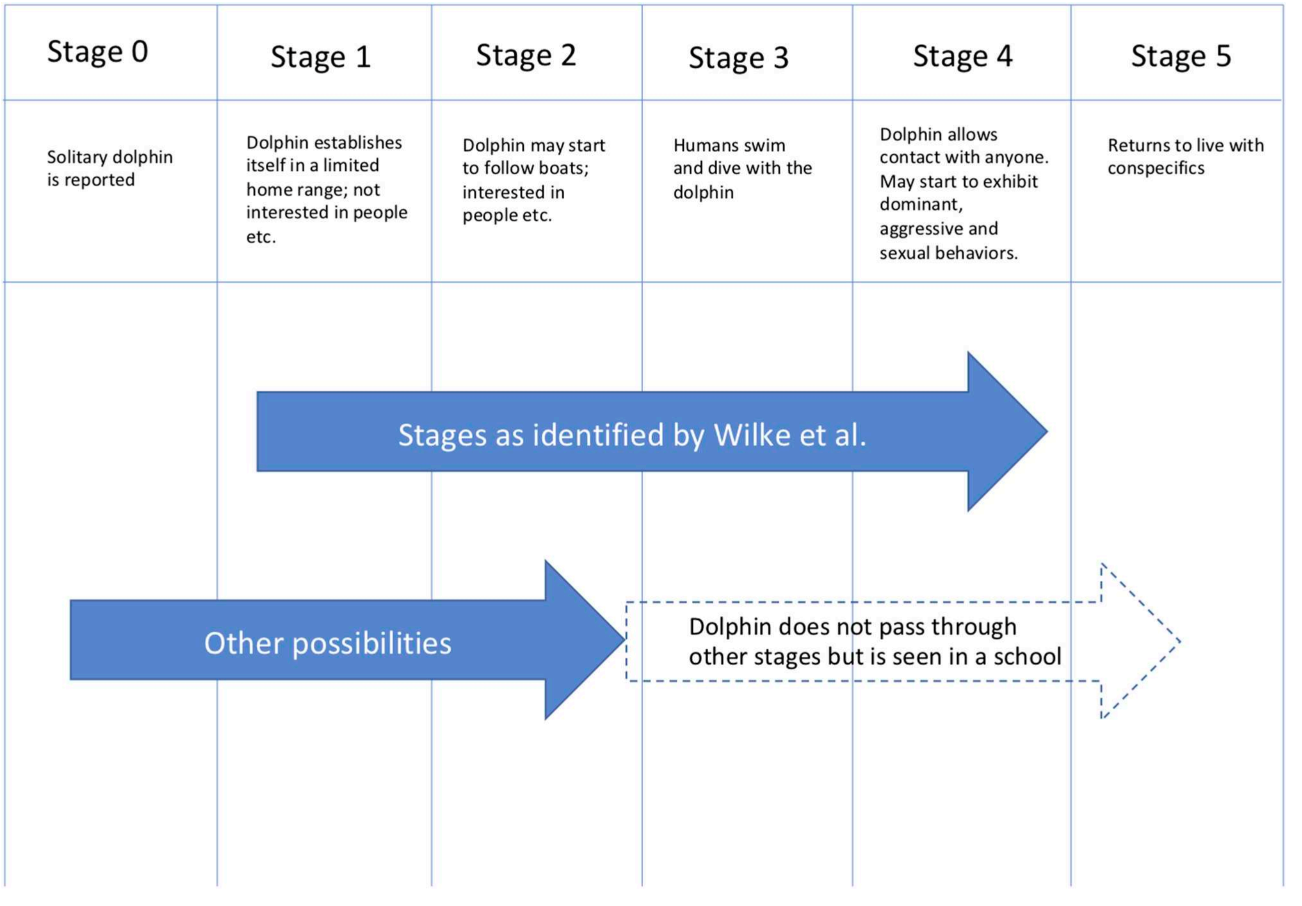

FIGURE 1 | Solitary dolphin "sociability" stages [including some details adapted from Wilke et al. (2)].

"Benny" the beluga is an interesting case because not only is it solitary, but it is also a long way from its native habitat. "Benny" was first sighted in the Thames Estuary in southeast England in July 2018 and was still present at the time of writing[35]. Efforts are being made by the Port of London to keep the public away from the beluga, to restrict boat traffic in the area and to encourage people to observe the animal from a distance.[36] So far, "Benny" has not exhibited any sociable behaviors.

Some dolphins are difficult to categorize because they do not seem to fit clearly into the stages and levels described. "Clet," for example, as a great traveler, did not really reach Stage 3 because he did not allow certain humans to swim with him and so, perhaps, he should be considered Stage 2. However, he did demonstrate aggressive behavior toward people and other species (e.g., harbor porpoise) and directed sexual behavior toward the underside of a boat.[54] Such behaviors would fit into Wilke's (2007) Level 5 which was proposed for animals in Stages 3 and 4, yet "Clet" did not appear to have reached either of these stages.

[54]http://www.seawatchfoundation.org.uk/clet-the-travelling-bottlenose-dolphin/

"Moko" in New Zealand, was clearly a Stage 4 dolphin but, it is not possible to allocate him to a particular level. He would only allow certain people to interact with him (Level 3) and yet he would sometimes demonstrate socio-sexual and dominance behaviors (Level 5) (I. Visser, 2018, pers. comm., 22 June). This demonstrates that, even though we can attempt to categorize and understand solitary dolphins, they are individuals and some animals may exhibit behaviors which do not appear to follow the pattern shown by the majority.

Of the 36 cases of solitary dolphins and belugas recorded since 2008, the sex of 25 of them has been recorded. Of these 25 animals, 18 (72%) of them have been identified as male and 7 (28%) were female. It is possible that mistakes were made in determining sex and so these figures do not necessarily show that males are more likely to become solitary than females.

The Reassessment of the Stages of a Solitary-Sociable Dolphin

Based on a reassessment of available information from the last 10 years (as described above and in **Tables 2**, **3**), we propose two additional stages; Stage 0 and Stage 5. A stage 0 dolphin is simply one seen to be persistently on its own; it is not seen within a limited home range and may be seen in multiple locations.

FIGURE 2 | "Dave" the solitary-sociable dolphin, interacting with a group of people in Kent, UK (Photo: Terry Whittaker).

FIGURE 3 | Large numbers of people traveled to see "Dave" and to interact with her (Photo: Terry Whittaker).

It is distinguished from Wilke et al.'s Stage 1 animal that has established a home range.

Stage 5 relates to those seemingly rare cases where the dolphin returns to live with other conspecifics and ceases to be solitary. Such cases are hard to document because sometimes an individual disappears and it is not known whether it joined a pod, relocated or died. This Stage corresponds with the Stage 6 proposed by Goodwin and Dodds (5).

This proposed new categorization of stages (which incorporates those of Wilke et al. (2) is shown in **Figure 1**. The Figure also highlights that some individual dolphins do not necessarily pass through all stages. For example, a dolphin that is seen on its own for a period of time may subsequently join a school of other dolphins.

DISCUSSION—THE LIFE OF THE SOLITARY-SOCIABLE DOLPHIN

In discussing the life of the solitary dolphin, we draw on examples not only from the last 10 years, but also some cases prior to 2008 where helpful.

The Benefits of Interacting With Humans

Solitary dolphins may seek out interactions with humans including touch, social, sexual and play behaviors (2). This contact, to some extent at least, seemingly replaces the social interaction and physical contact that would otherwise be provided by conspecifics (2) and can become very important to the individual animal. Bloom et al. (25) reported that a solitary dolphin in Northumberland, England regularly partook in interactions with swimmers and boats. The dolphin actively engaged in recreational activity with humans during 121 of 194 opportunities (62%) during the study period. Another dolphin living in British waters, "Dave" (see **Figures 2**, **3**), was seen to spend almost a third of her time accompanied by humans or boats (26) whilst "Filippo," the dolphin who lived in Manfredonia harbor in Italy, exhibited different behaviors within different areas of his home range. Within the port he was observed interacting with boats and humans only 16% of the time, whereas outside of the port he dedicated 65.9% of his time to this behavior (27).

Doak (23) suggested that the touch and social interaction provided by humans is important for the welfare of these solitary animals. In the case of "Pita," a female bottlenose dolphin who was resident in Belize, she became calm and relaxed when swimmers swam slowly with her and gave her gentle rubs (28). Mizrahi et al. (29) reported that "Holly," the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) resident off the Sinai Peninsula in Egypt, allowed people to touch her and then, later, sought out this physical contact. Although the dolphins may benefit, to a certain extent, from their interactions with humans, Lockyer and Müller (4) stated that the dolphins do not appear to depend on these interactions and that they are often temporary. For example, "Fanny" who regularly swam with a young girl, left her companion when she needed to find a new area to feed in and "Dolphy," from Banyuls-sur-Mer in France, would only interact with people until her "dog companion" entered the water whereupon she would immediately ignore the humans (4).

Welfare Concerns for Solitary-Sociable Dolphins

Concern for the welfare of free-ranging dolphins that interact on a regular basis with humans has been expressed by a number of authors (3, 22, 30). Human behavior can have a negative impact on the dolphin when the dolphin's needs are not taken into consideration and the dolphin is disturbed when it is resting or feeding (2). "Dave," for example, did not feed when there were people in the water with her and her diving activity also altered, suggesting that she was foraging less (26). Such disturbances may be unintentional on the part of the humans but can have a negative impact on the welfare of the dolphin.

Unfortunately, people sometimes direct inappropriate behaviors toward the animals. Swimmers interacting with "Pita" were observed grabbing her fins, trying to ride her and touching sensitive areas, such as her genitals, face and blowhole (28). "Dave" was also subjected to these types of human behavior and parents were even seen putting their children on her back (26). Tourists interacting with wild botos in Brazil have also been observed trying to ride or restrain the dolphins, hitting them and feeding them inappropriate items (31).

Although food provisioning has rarely formed part of the development process for solitary-sociable dolphins, and some dolphins are reported to have refused the handouts offered to them (22), there are cases where solitary dolphins have been fed by humans. The solitary bottlenose dolphin known as "Beggar" was so named because he was regularly provisioned by humans and would beg for food by "orienting vertically in the water with his head out and mouth open…and accepting food," (11). It is possible that "SC1" in Croatia and "Marra" in the UK were also provisioned by local fishing boats (18, 21). In Mexico, "Lucero" has been fed by local fishermen and tourists who come to swim with her (E. Morteo, 2018, pers. comm., 5 June). Such provisioning can become a welfare issue when dolphins are fed inappropriate or contaminated food items (11, 32) or, potentially, when they approach boats for food and are badly treated in return.

Provisioned dolphins also risk ingesting fish-hooks and other tackle. When "Beggar" was found dead in Florida, USA, it was concluded that he had been in poor health for some time and that this was partly attributable to his interaction with humans. He had wounds from boat strikes, fishing hooks and fishing line in his stomach as well as squid beaks which indicated that he had received more food from humans than from foraging on his own.[55] Provisioning can also alter the dolphins' natural foraging habits (30). Studies reported by Foroughirad and Mann (33) have shown that provisioned female bottlenose dolphins living in the population in Shark Bay, Australia provided less care to their calves and that the calves had higher mortality rates than those born to non-provisioned females. After management measures were introduced to reduce the time that females spent being provisioned, calf survival rates increased (33).

Their close proximity to humans and presence in shallow waters puts solitary dolphins in danger of accidental stranding and injuries. "Marra," for example, live stranded in May 2006 and it was suspected that this incident occurred because she was actively seeking human interaction and was spending time in shallow water (21). She was successfully refloated by British Divers Marine Life Rescue (BDMLR) and continued to interact with people until her death later that year.[56]

Wilke et al. (2) reported that anthropogenic causes have resulted in the deaths of a number of solitary dolphins; with proximate causes including oil spillages, underwater explosions, boat strikes and even death after being taken into captivity. Samuels et al. (22) reported solitary dolphins getting entangled in fishing gear and being wounded by fish hooks (including, in one case, in the eye).

Bejder et al. (34) noted that when wild animals become habituated to contact with humans it can lead to negative outcomes for individual animals, for example if they lose their fear of motorized vehicles. In fact, many solitary-sociable dolphins have been injured by boats. "Freddie," a solitary bottlenose dolphin in the north-east of England, was badly injured when he was struck by the propeller of a police launch (35), "Pita" had various scars which appeared to be caused by propellers (28) and the beluga known as "Q" was photographed with severe wounds on his back which may also have been the result of propeller strikes.[57] The solitary striped dolphin reported in Croatia in 2008 had scars between its dorsal fin and tail which were possibly caused by a propeller (19) and "Dave" received a serious injury to her tail (probably caused by a propeller strike) which can be seen in **Figure 4** (26). She disappeared shortly after receiving this injury and it is possible that she died from her wounds. "Marra" had various wounds in the months before her death possibly caused by a propeller and rope entanglement and she died from septicemia resulting from a bacterial infection which usually enters hosts through open wounds (21).

FIGURE 4 | After "Dave" received a severe wound to her tail, attempts were made to give her fish laced with antibiotics (Photo: Terry Whittaker).

Elwen and Leeney (36) noted that some cetaceans may learn to avoid boats after a negative experience (such as a biopsy or capture) but most studies have shown that injuries do not lead to behavioral changes. Therefore, even if an animal has been struck by a boat, it will not necessarily learn to avoid boats in the future and is still at risk from further accidents. For example, the Heaviside's dolphin (*Cephalorhynchus heavisidii*) which Elwen and Leeney studied post-injury, continued to approach the research boat and to bow-ride (36).

Unfortunately, there are many reports of wild dolphins, including solitary-sociable dolphins, being deliberately harassed and injured (22, 32). This may be after they come into perceived or real conflict with people when their behavior disrupts human activity (such as fishing), damages property (for example, fishing gear) or when they exhibit aggressive behaviors (22). "Jojo" (who is still resident in Turks and Caicos) reportedly had 37 injuries between 1992 and 1999 all of which were related to interactions with people (22).

Deliberate attempts to shoot, spear or injure dolphins with a variety of weapons have been recorded (22, 32). For example,

[55]https://start1.org/news/beggar-the-dolphin-did-contact-with-humans-lead-to-his-death/

[56]https://www.seawatchfoundation.org.uk/bottlenose-dolphin-trapped-in-maryport-harbour-rescued-and-set-free/

[57]http://www.whalestewardship.org/www.whalestewardship.org/Q.html

"Beaky," who was seen in various places in the United Kingdom in the 1970s, had a scar from a healed bullet wound (4). Samuels et al. (22) reported that "Opo," "Nudgy," "Dobbie," and "Costa Rican" (from New Zealand, USA, Israel, and Costa Rica, respectively) were all deliberately killed by humans. "Filippo" was also killed deliberately. He was found dead on 6th August 2004 having been stunned by an illegal fishing bomb and wounded with a harpoon (G. Pietroluongo, 2018, pers. comm., 2 April), The subsequent necropsy on his body found that it was riddled with shotgun pellets; evidence of earlier cruel interactions (G. Pietroluongo 2018, pers. comm., 2 April). Five other dolphins ("Percy," "Tião," "Horace," "Simo," and "Nina" from the UK, Brazil, New Zealand, Tunisia and Spain) may also have been killed as they disappeared mysteriously after negative interactions with local people (22).

Interactions With Other Animals

Some solitary dolphins do interact, at least occasionally, with conspecifics. For example, "Holly" was occasionally seen with other dolphins and she even mated and gave birth to three calves during her "solitariness" (29). For the 4 years prior to her death in December 2004, "Holly" was accompanied by her only surviving female calf (29). "Pita" was also sometimes seen with members of her own species (28) and the presence of rake marks on "Percy" were taken to be evidence of interactions with other dolphins (37). "Beggar" was usually seen on his own but he was sometimes spotted with other dolphins some of whom copied his begging behavior (11). "Dolphin 56" could be seen with other dolphins on occasion but he demonstrated an interest in interacting with humans, that his conspecifics did not.[58]

"Françoise" was a bottlenose dolphin that belonged to a group which was resident in a lagoon on the Atlantic coast of France (4). She exhibited solitary-sociable behavior some of the time (approaching swimmers, divers and boats, bow-riding and rubbing against ropes) but she also spent time with her group when she actively avoided boats and swimmers. In Brittany, researchers saw "Fiete" with other bottlenose dolphins on two occasions. On the first of these occasions he prompted an unusually intense amount of socializing amongst the dolphins but also spent some of the time on his own at the back of the research vessel (M. Perri, 2018, pers. comm., 14 November). His interactions with other dolphins were alternated with periods of typical solitary dolphin behavior, such as spending hours following the same boat and swimming around a mooring buoy.

Sometimes solitary dolphins interact with individuals from other species. The striped dolphin studied in the Vinodol Channel in Croatia ("SC1") was seen with another individual (species unknown) in 2006 and with a short-beaked common dolphin in 2008 (18). Similarly, the common dolphin known as "Kylie" has been seen interacting with a harbor porpoise and engaging in "affiliative" behaviors, such as travel, play and neutral association [(17); M. Cosentino, 2018, pers. comm., 12 March].

There are also cases of solitary dolphins interacting with domestic animals. "Dougie," in Ireland, for example, regularly interacted with a pet dog who would swim with him every day,[59] "Dolphy," "Beaky," and "Simo" in Wales were known to have swum and played with dogs (4) and **Figure 5** shows a dog approaching "Moko" in New Zealand.

FIGURE 5 | "Moko" with a surfboard he had "stolen" and a dog swimming after him (Photo: Ingrid Visser).

FIGURE 6 | "Moko" being pursued by a swimmer in Whakatane, New Zealand (Photo: Ingrid Visser).

Risks to Human Safety

It is a commonly held belief that dolphins are of a friendly disposition and that they want to help and protect people who enter the water with them. Although there is evidence that this may sometimes be the case,[60] there are also various accounts of solitary dolphins injuring humans in the water with them. Such aggressive behaviors from the dolphins are often the result of inappropriate human interactions (26, 38). Wilke et al. (2) suggested that inappropriate or overly energetic interactions on the part of humans may cause sexual arousal in the dolphin, which has the potential to turn into sexual aggression. In New Zealand "Moko," for example, would exhibit socio-sexual and dominance behaviors if people who he was not interested in

[58]https://www.youtube.com/watch?v=Icq0CHQV3js

[59]https://www.youtube.com/watch?v=l2vU8U0j_4E

[60]https://www.dolphins-world.com/dolphins-rescuing-humans/

FIGURE 7 | "Moko" playing with a surfboard by pushing it underwater to make it shoot up into the air (Photo: Ingrid Visser).

interacting with tried to make physical contact with him (I. Visser, 2018, pers. comm., 21 June). He would breach over people, push and bump them, knock them off surfboards and prevent swimmers returning to shore. **Figures 6** and **7** show "Moko" interacting with people in the water

It has been suggested that male solitary-sociable dolphins are more likely to show aggressive behavior toward humans including sexually aggressive behavior (2, 9, 23). Samuels et al. (22) reviewed the behaviors of 29 solitary-sociable dolphins and stated that at least 13 of them had directed sexual behavior at humans, buoys and/or boats. It can be dangerous for humans to be on the receiving end of robust dolphin behavior (2). "Zafar," who is currently resident in Brittany, has directed such attention to humans, pushing divers to the bottom and preventing kayaks from maneuvering.[61]

In the most extreme reported case of a violent interaction, "Tião," a Brazilian bottlenose dolphin, injured 29 people and caused the death of a 30-year-old man after butting him; the man died from internal injuries (38). The context of this may be important. People had subjected "Tião" to a number of inappropriate behaviors such as grabbing his fins, hitting him, jumping on him and even trying to insert ice-lolly sticks into his blowhole (38) which would have been potentially life-threatening as it could have impaired the dolphin's ability to breathe and dive. There is another case, from Gran Canaria, Spain in 2001, where robust interactions with a free-swimming dolphin appear to have resulted in the death of a swimmer (39).

Various videos uploaded to YouTube show "Dusty" the dolphin exhibiting aggressive behavior toward humans who try to approach her in the water [62, 63] and Berrow (40) reported that she damaged one woman's ribs by ramming her, whilst another swimmer suffered internal hemorrhaging. Samuels et al. (22) reported that some solitary-sociable dolphins have "abducted" people who later needed to be rescued by boat. "Percy" was reported to have pushed a swimmer out to sea in south-west England and "Dave," "Marra," and "Georges" (all dolphins seen in UK waters) were often "rough" with their human "playmates" and stopped people from leaving the sea on occasion (3, 4, 21). "Pita" was also aggressive toward people when they tried to leave the water and would push and bump into swimmers and occasionally rub her genitals against them (28). "Beaky" would butt people aggressively, usually when there were a lot of people in the water with him (4). "Dave" and "Marra" were both seen breaching on top of a number of people, which could have caused serious injury (21, 26). In the UK, there was also concern for the safety of the people who swam with "Georges" including risks not directly related to the dolphin, such as people swimming out of their depth or risking hypothermia (21).

Humans who interact with dolphins may also be at risk of being bitten. "Beggar," the dolphin who was regularly fed by humans, was reported to have bitten people on various occasions and this sometimes resulted in a need for medical treatment (11). "Percy" also reportedly bit people when he was "over-excited" due to a large number of people being in the water with him at the same time or when he felt that his playtime with a known human was threatened (4, 37). In Brazil, provisioned wild botos have also bitten humans (31).

The risks to human health and safety as well as the welfare concerns apparent for the dolphins themselves, highlight the need for specific management and protection for these animals.

Protection for Solitary-Sociable Dolphins

Wilke et al. (2) reported that there did not appear to be specific legislation in place protecting solitary-sociable dolphins anywhere where these animals were present, although many countries have regulations for watching or swimming with cetaceans in general.

The widespread human desire to approach or interact with dolphins inappropriately, in ways which can be dangerous to both dolphins and people, means that the management of human behavior is necessary (3, 7). Unfortunately, this sometimes comes too late and in Brazil, in 1994, it was only after "Tião" had fatally injured someone that a management plan was put into place (38). The plan involved educating the public, working with the media and trying to prevent dangerous interactions between the public and the dolphin (38). No further accidents or incidents were recorded before the dolphin apparently left the area, proving that the management plan protected the humans interacting with the dolphin although it is unclear whether it protected the dolphin, as it is possible that "Tião" was deliberately killed by people taking "revenge" for his role in the death of a human (22).

Some efforts to manage interactions between humans and dolphins have improved the survival chances for certain solitary-sociable dolphins (22). In Ireland, the Irish Whale and Dolphin Group (IWDG) has held various public meetings to address management issues regarding solitary dolphins (40). Doak (23) reported that some communities inform the public, via notice-boards and leaflets, about best practice when it comes to how to treat the local solitary dolphin. In some cases, special "guardians" have been assigned to ensure that the dolphin is safe and not harassed or injured by the public (23). In France, the

[61] http://zafarledauphin.blogspot.com
[62] https://www.youtube.com/watch?v=-X09Y1aEtM0
[63] https://www.youtube.com/watch?v=B3RIpd0FiE4)

FIGURE 8 | "Moko" the solitary-sociable dolphin interacting with the public under the supervision of his guardian (wearing the yellow cap) (Photo: Ingrid Visser).

dolphins "Dolphy" and "Fanny" both had guardians who worked alongside local supporter groups and under the supervision of the University of Marseille (23). Some of "Moko"'s interactions with people were monitored by a guardian (see **Figure 8**).

It is important that the guardians are working to protect the dolphins and to inform the public. Some solitary dolphins have developed relationships with specific humans who interact with them regularly, for example "Mara" ("Dusty"/"Sandy") in Ireland and "Jojo" in the Turks and Caicos.[64], [65] According to Wilke et al. (2), humans who form relationships with solitary dolphins can become possessive regarding "their" dolphin and this may lead to problems for the dolphin if the person is not inclined to share information about what the dolphin does and does not like regarding interactions with humans.

When "Dave" was resident in southeast England she attracted a lot of attention (see **Figure 3**) and local volunteers worked with non-governmental organizations to patrol the beaches, monitor the dolphin, talk to members of the public and put up posters about the potential dangers for both swimmers and dolphin during interactions (26). Such was the public's enthusiasm to get into the water with the dolphin that the local police were also called in on several occasions to help protect her and two arrests were made. The Kent Tourist Board, local council and other agencies were involved in meetings about dolphin and human safety (26).

In New Zealand, local companies that took people to swim with dolphins, actively helped protect a solitary-sociable dolphin called "Maui" by limiting the number of people allowed in the water with her, or by not taking tourists to swim with her at all (41). As the Department of Conservation also strictly enforced regulations, "Maui" had limited contact with people. In the Turks and Caicos, "JoJo" has been officially protected since the 1990s.[66] The "JoJo Dolphin Project" promotes legal protection for marine mammals (including "JoJo"), and aims to educate the public on how to interact with wild dolphins.[67]

In Belize, human interactions with "Pita" (which could include her being approached by up to four boats at a time or having as many as 30 people in the water with her) were, generally, not supervised although some guidelines about dolphin-human interactions were available (28). In Brazil, activities involving interactions with wild dolphins, such as feeding and swimming with botos is not regulated, codes of conduct are often not followed and those running businesses promoting these interactions do not receive any specialized training (31). In general, there is a lack of legislation relating to tourism involving animals in Brazil and that regarding dolphins is limited to preventing disturbance by boats (31). Alves et al. (31) recommended the development of specific legislation to regulate feeding, touching and swimming with botos. The Ministério Públic Federal (Public Prosecutor's Office) has recently released a recommendation that tourist operators in the Amazonas should stop promoting physical interactions between tourists and wild animals.[68]

In some countries, conservation legislation may offer some protection to solitary-sociable dolphins. In the United Kingdom, dolphins are protected by the Conservation of Offshore Marine Habitats and Species Regulations 2017, the Conservation of Habitats and Species Regulations 2017 and the Wildlife and Countryside Act 1981 (as amended).[69] Both of the 2017 Regulations state that "a person who deliberately disturbs wild animals…is guilty of an offense," (42, 43). Disturbance includes that which "is likely to impair their ability…to survive, to breed or reproduce, or to rear or nurture their young," (42, 43). Part 9 of the Wildlife and Countryside Act 1981 states that "if any person intentionally or recklessly disturbs any wild animal included in Schedule 5 as (a) a dolphin or whale (cetacea), … he shall be guilty of an offense" (44). As interactions with solitary-sociable dolphins have been shown to lead to injuries which could impair their survival prospects as well as to incidents which have led directly to the deaths of various dolphins, it is not unreasonable to refer to interactions with these animals as "disturbances" and, therefore, offenses according to these laws.

In both the USA and New Zealand, it is illegal to "harass" dolphins (45, 46). In New Zealand, "disturbing" a dolphin is also considered an offense under The New Zealand Marine Mammal Protection Act 1978 (46). The New Zealand Marine Mammals Protection Regulations (47) state that "persons may swim with dolphins…but not with juvenile dolphins." Details about how vessels should behave around dolphins is given in detail. The Australian National Guidelines for Whale and Dolphin Watching 2017 also provide detailed information regarding which types of boats can partake in dolphin watching and how they can and cannot approach the animals with details about caution

[64] https://www.youtube.com/watch?v=jM6WTXSmG78
[65] http://deanandjojo.org/dean-and-jojo_wild-dolphin/
[66] https://www.reseaucetaces.fr/groupe-de-travail-sur-les-dauphins-solitaires-et-familiers/dauphins-ambassadeurs-daujourdhui/
[67] http://www.ieyenews.com/wordpress/the-jojo-dolphin-project/
[68] http://www.mpf.mp.br/am/sala-de-imprensa/docs/recomendacao-ecoturismo-e-interacao-animais-silvestres
[69] https://www.gov.uk/government/publications/protected-marine-species/cetaceans-dolphins-porpoises-and-whales

zones and no-approach zones (48). Regarding "habituated solitary dolphins" the Guidelines state that feeding, touching or swimming with these animals is "not beneficial to the dolphin and puts the animal at greater risk of injury or death due to boat strike or entanglement. In addition these interactions are often in breach of state regulations," (48).

Many countries discourage the public from swimming with dolphins. In Ireland the National Parks and Wildlife Service (NPWS) produced guidelines in 2000 reminding people that dolphins are wild animals and discouraging interactions, such as swimming with them or attempting to manhandle or interfere with them (40). The Department of Transport, Tourism and Sport (49) published guidelines for interactions with whales and dolphins in Irish coastal waters including details of how vessels should be handled around cetaceans and stating that people should not attempt to swim with them. Swimming with dolphins is not recommended in Australia unless the relevant authority has given permission and it is recommended that "if approached by a whale or dolphin a swimmer must move slowly to avoid startling the animal and must not attempt to touch it or swim toward it," (48). "Attempts at swimming with whales or dolphins should stop if the animals show signs of disturbance or agitation," (48).

Sometimes it may be necessary for the authorities to specifically prohibit certain interactions. In France, the mayor of Penmarc'h, Brittany, put an order in place to prevent people from swimming with "Zafar" in 2017.[70] The Cayman Islands Government advises the public not to swim with wild dolphins, noting that lone dolphins in particular can be unpredictable and dangerous.[71] In the USA, NOAA Fisheries (2018) state that the viewing of marine mammals must be carried out in a way that does not harass the animals and closely approaching or interacting (or attempting to interact) with whales, dolphins and porpoises is discouraged including swimming with them, petting them, touching them or trying to get a reaction from them.[72]

In some places there are schemes in place to encourage responsible encounters with cetaceans. The Dolphin SMART program in the USA aims to promote responsible dolphin watching practices (50). It encourages people to;

"Stay at least 50 yards from dolphins,

Move away cautiously if dolphins show signs of disturbance,

Always put your engine in neutral when dolphins are near,

Refrain from feeding, touching, or swimming with wild dolphins,

Teach others to be Dolphin SMART."

The UK's WiSe Scheme trains vessel operators on how to best approach and interact with marine wildlife whilst minimizing disturbance.[73] As well as their cetacean code of conduct, they have developed a further "Sociable, solitary dolphin code of conduct" which highlights the fact that maintaining a distance from these animals can be impossible if the animal approaches the vessel (WiSe Scheme, 2018)[73]. The Code of Conduct says that it is important to ensure that solitary-sociable dolphins do not follow vessels into harbors/marinas but that, if they do, the harbor authorities must be informed and that they should contact BDMLR or Marine Connection to find out whether further action needs to be taken.

The WiSe Scheme (2018) highlights the risk of injury from propellers and the fact that solitary-sociable dolphins are often very attracted to them and therefore it is recommended that engines are put into neutral if a dolphin approaches. Boat owners are also warned of the danger posed to passengers if a dolphin rubs against the boat, rudder or propeller, subsequently unsteadying the vessel. If the dolphin does not move away, even after turning off the engine, it is recommended to return to harbor with a steady speed. Feeding and resting areas should be avoided and if the animal is seen engaging in these behaviors it should not be approached. For boat owners operating in an area with a resident solitary-sociable dolphin, it may be appropriate to fit a propeller guard. It is important not to swim with, touch or feed these dolphins as such behavior can lead to the animal being injured or disturbed and even to its death.

Simmonds (3) called for better protection for solitary-sociable dolphins and for increased efforts to prevent them from becoming accustomed to contact with humans in the first place. Hawkins (9) proposed a number of ways, including relocation, in which the habituation of a solitary dolphin could be avoided. Solitary dolphins which do not become accustomed to interacting with humans may have an increased chance of starting to interact with conspecifics again. "Kaimi," for example, was solitary for 1 year in San Francisco Bay, USA before being joined by an adult female (possibly her mother) (W. Keener, 2018, pers. comm., 4 June). Recently, they have been joined by two further dolphins (W. Keener, 2018, pers. comm., 4 June). In terms of the Stages (see **Figure 1**), "Kaimi" went from Stage 0 to Stage 5 without passing through the other stages.

Santos (38) also recommended that regulations and guidelines are needed to prevent dolphins and humans from being injured. Such guidelines may need to be specific to certain circumstances. In tropical countries, for example, people are in the water almost all year round and all day long. When "Tião" was in Brazil, he often had as many as 300 people in the water with him (M. Santos, 2018, pers. comm., 19 March).

A management plan can help protect solitary-sociable dolphins and, according to Hawkins (9), should include "(1) stakeholder engagement, (2) monitoring and research, (3) management responses, compliance and enforcement, (4) communication strategy, (5) public education and (6) environmental considerations."

Wilke et al. (2) recommended that those who manage solitary-sociable dolphins should consider whether it is possible for the dolphin to return to normal dolphin society and to assist in this outcome if possible. A solitary-sociable dolphin from Australia, which had progressed to stage 4 of sociability, was relocated in 2013 and later joined a group of wild dolphins (9);[74]. This dolphin was young (between 3.5 and 4.5 years old)

[70] https://www.letelegramme.fr/finistere/quimper/penmarc-h-interdit-de-nager-pres-des-dauphins-04-11-2017-11728087.php

[71] http://doe.ky/marine/whales-and-dolphins/

[72] https://www.fisheries.noaa.gov/topic/marine-life-viewing-guidelines

[73] https://www.wisescheme.org

[74] https://www.dolphinresearchaustralia.org/dolphin-rescue-sussex-inlet/

when first sighted and its solitary-social period was relatively short-lived. After about 4 months of being solitary and isolated in St George's Basin, the dolphin would allow physical contact from swimmers. After detailed assessment it was decided to relocate the dolphin to the open ocean.[75] Although she continued to interact with people for a time, these interactions gradually decreased and she appeared to reintegrate into dolphin society (9); [76].

Another translocation took place in 2017, of a solitary male beluga who was moved from New Brunswick to the St Lawrence Estuary in Canada.[77] He was not yet exhibiting sociable behavior and it was considered appropriate to move him to an area where he could find other belugas and contribute to the breeding population there. A year later, in July 2018, he was sighted in the company of another male beluga off Cape Breton in Nova Scotia. This sighting was not in an area inhabited by his natal or any other beluga population and it is not clear at the time of writing whether he has returned to live with conspecifics or not (C. Kinsman, 2018, pers. comm., 9 November).

As well as managing human behavior around solitary dolphins, in some cases, it may be possible to "train" the dolphin so that certain behaviors are discouraged (9). According to Wilke et al. (2) there was some short-term success at teaching "Jojo" not to sexually display toward humans and teaching dolphins to re-socialize with conspecifics might be a possibility in some cases.

RECOMMENDATIONS FOR MANAGEMENT OF SOLITARY-SOCIABLE DOLPHINS

It is clear that solitary dolphins are particularly vulnerable and that their interactions with humans need to be carefully managed to prevent them from being negatively impacted (51). Such careful management can also ensure that humans are not injured or put at risk either. How a specific dolphin should be managed will depend on its sex, age and personality (2). The size and character of the dolphin's home range will also influence what kind of management is needed and what is feasible (2).

Although it may appear that discouraging interactions between humans and dolphins is in the dolphin's best interest, it has been suggested that a dolphin in the later stages of sociable-solitariness may receive some benefit from its interaction with humans in terms of improved welfare (2). We recommend that the stage of sociability needs to be considered when a management plan is being devised. For example, dolphins in stages 0, 1 and 2 may be best protected by strictly discouraging and limiting interaction with them. For dolphins in later stages it may be argued that the situation is different but if, for whatever reasons, human interactions are permitted they clearly require very strict supervision to try to ensure that the dolphins are not disturbed or injured and, likewise, that human health and safety is guaranteed. The sea should always be viewed as a dangerous environment and people entering the water to interact with large wild predators need to be fully cognizant of the risks.

[75]http://www.environment.nsw.gov.au/media/OEHMedia13050201.htm
[76]http://whalespotter.com.au/?p=1815).
[77]https://gremm.org/en/le-beluga-de-la-riviere-nepisiguit-est-revu-bien-vivant/

Appropriate protection will need to be implemented by government officials who can limit access to the dolphin and who can ensure that a management plan is developed for the specific situation and adapted as necessary depending on how things change over time (2). Local stakeholders, such as fishermen will need to be involved and people from the local community can also be recruited to help educate the public. Guidelines about how to interact with the dolphin are essential including the basic tenet that observation is preferable to interaction. This will also ensure that people are not at risk of injury or other negative consequences from interacting with the dolphin.

Wilke et al. (2) recommended various points that could be included in a management plan:

- An off-limits area where humans are not allowed to enter thus allowing the dolphin to feed or rest without being disturbed;
- A limit to how many people interact with the dolphin at any one time;
- Restricting the number and/or type of boats which can approach the dolphin, particularly considering the risk of propeller injury;
- Promoting good behavior and respect between boat owners so that no conflict arises between those trying to approach the dolphin;
- No touching of the dolphin's sensitive spots (blowhole, eyes, genital area), and,
- No feeding of the dolphin.

The importance of using diplomacy and good communication skills at all points is essential (2). If conflict arises between those people who want to interact with the dolphin, or if people who use the area where the dolphin lives believe that their needs are not being taken into consideration, resentment can grow which can have negative consequences for the dolphin and the humans involved in the conflict.

We also propose that to adequately protect solitary-sociable dolphins through the implementation of a management plan, it is necessary to clearly define what constitutes disturbance and harassment, so that it is clear which human behaviors are acceptable and which are not.

CONCLUSION

The fates of many solitary-sociable dolphins show that these animals are, to a great extent, at the mercy of people's desire to interact with them. Their welfare can be negatively impacted if they are disturbed whilst they attempt to rest or forage, are insensitively touched and prodded by those who wish to commune with them, are fed inappropriate items or are accidentally struck by boats. There are also cases of dolphins being deliberately injured or killed by those who take a dislike to them or who seek some kind of "revenge."

Depending on where these animals live they may receive some form of protection under the law or due to the diligence of local people but there exist no general guidelines as to how they should be managed during the different stages of sociability. We recommend above (section Recommendations for Management of Solitary-Sociable Dolphins) how solitary and solitary-sociable dolphins can be better protected.

In summary, Stage 0 dolphins should be monitored but left alone unless they get into trouble whilst Stages 1–4 dolphins need to be monitored and a management plan developed for their safety and that of the people who come into contact or choose to interact with them. The following mnemonic may help to get the message across about how to protect solitary dolphins:

Dolphin CARE:

Choose not to disturb or otherwise interact with the dolphin

Alert the authorities if necessary

Respect the dolphin

Enjoy watching from a distance.

AUTHOR CONTRIBUTIONS

LN researched the current cases of solitary-sociable dolphins and wrote most of the manuscript. MS proposed the topic and supervised, edited, and contributed various sections.

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Corrigendum: A Global Reassessment of Solitary-Sociable Dolphins

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In the original article, there were mistakes in **Table 2** and **Table 3** as published. The references for the dolphin "Doogie/Dougie" in **Table 2** and those for the dolphins "Q, Leucas/Luke/The Liverpool whale, Solitary Social Dolphin/Yera/Sally/Dolly/Beyoncé, Stinky/Humpy/Randy, Pechocho, Lucero, Beggar/Mooch, Dolphin 56, Kaimi, Jojo and Moko" in **Table 3**, were incorrectly published.

The corrected **Table 2** and **Table 3** appear below.

Additionally, there were also mistakes in the Footnotes. Incorrect links were published in Footnotes 12, 19, 56, and 67. The correct links for those footnotes appear below.

The authors state that this does not change the scientific conclusions of the article in any way. The original article has been updated.

[12]https://www.24sata.hr/fun/kupace-u-slanom-iznenadio-dupin-koji-se-brckao-s-njima-528246
[19]https://video.nationalgeographic.com/wild/unlikely-animal-friends/00000144-16d7-dcf1-a954-57df5eb90000
[56]https://www.seawatchfoundation.org.uk/bottlenose-dolphin-trapped-in-maryport-harbour-rescued-and-set-free/
[67]http://www.ieyenews.com/wordpress/the-jojo-dolphin-project/

TABLE 2 | Solitary and solitary-sociable dolphins in Europe since 2008.

Stage (Level) reached	Name of dolphin	Location	Species*	Gender	First seen	Last seen / date of death	References
1	Unnamed	Monfalcone, Italy	Dd	Presumed F	Jun. 2010	Aug. 2011	(16)
1	Stormy	Wales, UK	Dd	?	Dec. 2014	Apr. 2015	[4]
3 or 4 (2 or 3)	Kylie / Colin / Donna	Firth of Clyde, Scotland, UK	Dd	F	Approximately 2001	Present	(17); M. Cosentino, 2018, pers. comm., 2 June.; [5]
–	Benny	Thames Estuary, UK	Dl	?	July 2018	Present	[6,7]
1 or 2	SC1	Vinodol Channel, Croatia	Sc	F	Aug. 2004	Last seen Jul. 2009	(18)
1	?	Mali Lošinj harbor, Croatia	Sc	?	Aug. 2008	Last seen 11 Sept. 2008	(19)
1 or 2	Rudolf	Ostend & Nieuwpoort, Belgium	Tt	?	2007	Last seen 2008 (or possibly 2010)	(20); [8]
2	? (possibly Rudolf)	Knokke-Heist, Belgium	Tt	?	Jul. 2010	Last seen Oct. 2010	(20)
4 (4)	Bobi	Karin Sea, Croatia	Tt	M	Apr. 2014	Last seen 2016 (or possibly 2017)	[9,10,11,12]
2	? (possibly Bobi)	Slano, Croatia	Tt	?	Jun. 2017	Seen a few times. Possibly still present	D. Crljen, 2018, pers. comm. 18 June;[12]
4 (5)	Dusty / Sandy / Mara	North Clare / Inis Oírr, Ireland	Tt	F	2000	Present	R. Meade, 2018, pers. comm. 7 May; [13,14,15,16,34,64]
1	Nimmo / Salty	Galway, Ireland	Tt	?	Since at least 2008	Present	[17]
2	Doogie / Dougie	Tory Island, Ireland	Tt	F	2006	Last seen? 2008?	(5); [18,19,64]
4 (3)	Fungie	Dingle, Ireland	Tt	M	1983	Present	[20]
2 (5)	Clet / Nick / Nobby / George II / Hobnob	France, UK, Ireland	Tt	M	2008	Last seen summer 2015	[2,21,22,54]
1	Fiete / Freddy	Brittany, France and Kiel, Germany	Tt	M	2016	Aug. 2017	M. Perri, 2018, pers. comm., 18 May; [3,23]
2	Gaspar / Jean Copo'h / Jean Floc'h	Brittany, France and Galicia, Spain	Tt	M	2003	Last seen 2010	[24,25,26]
1	Lilou / Wifi	Brittany, France	Tt	M	2007	?	[27,28]
4	Randy / Dony / Georges	UK, Ireland, France, Holland, Belgium.	Tt	M	April 2001	Present (Currently in Brittany, France)	[29,30]
3 (3 or 4)	Elcano	Northern Spain, Western France	Tt	M	Feb. 2013	Last seen Sept. 2013	[31,32]
3 or 4 (5)	Zafar / Toto	Brittany, France	Tt	?	Jun. 2017	Present	[61,33]
0	?	Portsmouth & Isle of Wight, UK	Tt	?	Jun. 2017	?	[29]
3 or 4 (2)	Splashy	Cornwall, UK	Tt	M	Jul. 2017	Last seen Mar. 2018	D. Jarvis 2018, pers. comm., 29 May; A. Lowe 2018, pers. comm., 16 March

**Dd, Short-beaked common dolphin (Delphinus delphis); Dl, Beluga (Delphinapterus leucas); Sc, Striped dolphin (Stenella coeruleoalba); Tt, Bottlenose dolphin (Tursiops truncatus); Ta, Indo-Pacific bottlenose dolphin (Tursiops aduncus).*

TABLE 3 | Solitary and solitary-sociable dolphins in the rest of the world since 2008.

Stage (Level) reached	Name of dolphin	Location	Species*	Gender	First seen	Last seen / date of death	References
–	Q	Cape Chignecto, Nova Scotia, Canada	Dl	M	2008	Last sighted 19 August 2010 with serious injuries	(8); C. Kinsman 2018, pers. comm., 9 November; [37]
–	Leucas / Luke / The Liverpool whale	Halifax, Nova Scotia, Canada	Dl	M	May 2015	Last sighted 9 August 2015 (apparently healthy)	C. Kinsman 2018, pers. comm., 9 November; [38,39]
–	Nepisiguit Beluga	Bathurst, New Brunswick, Canada	Dl	M	June 2017	Last sighted in July 2018 accompanied by another beluga	[77]
5	Solitary Social Dolphin / Yera / Sally / Dolly / Beyoncé	New South Wales, Australia	Ta	F	Sept. 2012	No longer solitary	(9); [40,41]
0	?	Coffs Harbour, New South Wales, Australia	Ta	?	?	Present	G. Storrie 2018, pers. comm., 1 May
4 (5)	Stinky/Humpy/Randy	Gran Cayman	Tt	M	Approximately 2009	2012	[42,43,44]
4 (4)	Pechocho	Gulf of California, Mexico	Tt	M	Approximately 1992	Present	(10); [1,45]
4 (4)	Lucero	Veracruz, Mexico	Tt	F	Approximately 2003	Present	[46]
4 (4)**	Beggar / Mooch	Florida, USA	Tt	M	1990	Died 2012	(11); [42]
4 (4)**	Dolphin 56	East Coast, USA	Tt	M	1979	Last seen Jul. 2011	[47,48]
5	Kaimi	San Francisco, USA	Tt	?	Jul. 2016	No longer solitary	W. Keener 2018, pers. comm., 23 February; [49]
4 (5)	Jojo	Turks & Caicos Islands, West Indies	Tt	M	1980	Present	(2, 5); [50]
4 (?)	Moko	North Island, New Zealand	Tt	M	March 2007	Died Jun. 2010	I. Visser, 2018, pers. comm. 22 June; [51,52,53]

**Dl, Beluga (Delphinapterus leucas); Tt, Bottlenose dolphin (Tursiops truncatus); Ta, Indo-pacific bottlenose dolphin (Tursiops aduncus).*
***Interactions were limited to provisioning and touching.*

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MINI REVIEW
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The Dividing Line Between Wildlife Research and Management—Implications for Animal Welfare

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Wild animals are used for research and management purposes in Sweden and throughout the world. Animals are often subjected to similar procedures and risks of compromised welfare from capture, anesthesia, handling, sampling, marking, and sometimes selective removal. The interpretation of the protection of animals used for scientific purposes in Sweden is based on the EU Directive 2010/63/EU. The purpose of animal use, irrespective if the animal is suffering or not, decides the classification as a research animal, according to Swedish legislation. In Sweden, like in several other European countries, the legislation differs between research and management. Whereas, animal research is generally well-defined and covered in the legislation, wildlife management is not. The protection of wild animals differs depending on the procedure they are subjected to, and how they are classified. In contrast to wildlife management activities, research projects have to implement the 3Rs and must undergo ethical reviews and official animal welfare controls. It is often difficult to define the dividing line between the two categories, e.g., when marking for identification purposes. This gray area creates uncertainty and problems beyond animal welfare, e.g., in Sweden, information that has been collected during management without ethical approval should not be published. The legislation therefore needs to be harmonized. To ensure consistent ethical and welfare assessments for wild animals at the hands of humans, and for the benefit of science and management, we suggest that both research and management procedures are assessed by one single Animal Ethics Committee with expertise in the 3Rs, animal welfare, wildlife population health and One Health. We emphasize the need for increased and improved official animal welfare control, facilitated by compatible legislation and a similar ethical authorization process for all wild animal procedures.

Keywords: wildlife, research, management, animal welfare, 3R, legislation, ethical assessment

INTRODUCTION

Since the world's first animal protection legislation was established in England in 1822, several countries have implemented protection of animals as a part of the national legal framework. In spite of having a far-reaching legal Swedish framework for the protection of animals, there are shortcomings regarding the protection of wild animals, a situation not unique for Sweden (1, 2). The Swedish Animal Welfare Act (1988:534) includes all animals kept in captivity, but does not include free-ranging wildlife. However, if wild animals (vertebrates and cephalopods) are used for research, they are classified as research animals and are covered by the Animal Welfare Act and Swedish regulations for research animals (SJVFS 2017:40, case no L150 [L150]). The Directive 2010/63/EU (EU Directive) on the protection of animals used for scientific purposes (3) has been implemented in the Swedish legislation. Importantly, Sweden maintained a definition of research animals which also includes animals in scientific procedures where they are not necessarily exposed to any suffering. Gaining knowledge is fundamental in the Swedish legislation. It is the purpose, i.e., to obtain knowledge, that decides if an animal is a research animal. According to the EU Directive, it is not permitted to use wildlife in animal experiments, but competent authorities may grant exemptions if the purpose cannot be achieved by using animals bred for the purpose of research (Article 9.1, 9.2). Capture and handling must be carried out by competent persons and using methods which "do not cause the animals avoidable pain, suffering, distress or lasting harm" (Article 9.3). Staff who perform research procedures and handle the animals must be adequately trained (3). Research activities have to meet several requirements, including an authorization issued by the competent authority (in Sweden; Swedish Board of Agriculture) that allows the researcher to perform studies on animals, and an ethical approval for each research project from an animal ethics committee (AEC). One exception from ethical approval in the Swedish legislation (L150) includes scientific observations of wild animals which do not cause stress or suffering. Conversely, when wild animals are subjected to management activities (here defined as activities promoting the balance between the needs of wildlife with the needs of people through population, environmental and disease monitoring and control) no such authorizations are required, even though wildlife management often includes similar animal practices as research. Hunting in general is an integral part of managing wildlife in Sweden but is not defined as wildlife management within the scope of this article. The Swedish hunting legislation (Hunting Act [SFS 1987:259]) includes some welfare aspects on wildlife, except for animals used in research. The legislation states that wildlife shall not be exposed to unnecessary suffering during hunting, but does not express animal welfare or ethical requirements explicitly for management activities. In fact, neither the Swedish Hunting legislation nor the EU Directive *per se* mention or define the term "wildlife management." This means that the welfare of wild animals used for research purposes is covered by the legislation, but not the welfare of wild animals subjected to management activities.

Irrespective of the intention—research or management—the welfare of wild animals subjected to capture, anesthesia, handling, sampling, marking and sometimes selective removal (i.e., culling) may be compromised (2, 4). Negative impact on individual animal welfare can affect research quality as well as management results at group and population levels (5, 6). It is often difficult for responsible authorities to define the dividing line between wildlife research and management, and to identify the correct legislation for different situations. Moreover, contrary to research activities, it is difficult to control wildlife management activities from an animal welfare perspective. As a result, some wild animals are more protected than others, depending on which category they belong to. The aim of this review is to discuss the differences, similarities and overlap between wildlife research and management and its effects on animal welfare, with Sweden as an example.

THE GRAY AREA BETWEEN USING WILD ANIMALS FOR RESEARCH OR FOR MANAGEMENT PURPOSES

The purpose of research is to answer a scientific question. When an activity is performed purely from a management perspective, for example preserving an animal species or monitoring population health, it is not necessarily classified as an animal experiment. The EU Directive does not apply to "practices undertaken for the primary purpose of identification of an animal" nor to "practices not likely to cause pain, suffering, distress or lasting harm equivalent to, or higher than, that caused by the introduction of a needle in accordance with good veterinary practice" (Article 1.5) (3). Whether or not a procedure falls under the EU Directive is based on the purpose of the procedure and if the procedure causes negative welfare effects above the threshold (3, 7). Red foxes (*Vulpes vulpes*) are selectively removed for the protection of arctic foxes (*Vulpes lagopus*) in the alpine terrain of Sweden. If data collected during this management process is used to gain scientific knowledge, the procedure should be considered animal research. If so, it should be subjected to an ethical review and project approval by the competent authority. Data from management activities, e.g., assessing population size, migration behavior, home ranges and health, are often published by governmental authorities. In Sweden, publishing data from a procedure, irrespective of its intention, should be considered research. Additional information may be collected as part of a management procedure, including clinical and physiological variables to ensure health and welfare on anesthetized animals (8, 9). If these data are analyzed and published, it is considered as research in several European countries (7). It is disadvantageous for science to be unable to use collected data because of lack of ethical assessment and project approval. The opposite situation can also occur when authorities in Sweden want to use data from ongoing research (e.g., GPS positions) for management purpose, like tracking down wolves (*Canis lupus*) for culling (10). This will not be permitted if culling is not clearly stated as a purpose in the ethical approval (11). Discussions about the gray area are also held in Norway regarding marking of wild reindeer (*Rangifer tarandus tarandus*) for identification purposes (7). The challenge of an unclear dividing line between research and management in relation to the EU legislation was recognized during an international consensus meeting on the use of wild animals in field research (NORECOPA, 2017) (7). The EU Directive emphasizes the 3Rs—Replacement, Reduction, and Refinement (3, 12). A procedure such as marking an animal for identification and tracking involves capture, anesthesia and the placement of a tracking device on the animal, e.g., a collar or tag, or a transmitter in the abdomen (13–15). Even if the primary cause is identification, it is very likely that such a procedure may cause effects that are at least as negative to animal welfare as the insertion of a needle, i.e., stress, fear, and pain. In fact, such a procedure may not be defined as the least invasive method for identification (4), and would be scrutinized from a 3R-perspective if classified as a regulated procedure requiring an ethical assessment and permission from the competent authority. Ringing of birds is an important tool for population monitoring. The ringing procedure does not need ethical approval in Sweden if the procedure only includes capture, taking measures and applying a leg ring (16). There are some risks associated with bird ringing (17) and it can be argued that the stress of mist net capture and handling probably has a greater negative impact than the pain of a needle for many birds. In comparison, ethical permission is needed for all survey test fishing, i.e., using electric fishing and nets. The Swedish legislation is not consistent, i.e., catching fish for population assessments needs approval by the competent authority and AEC but capturing birds does not. Hence, there are gray areas regarding which actions are defined as animal research or wildlife management.

The Importance of Ethical Assessment, Animal Welfare and the 3Rs in Wildlife Research and Management

Research projects that fall under the scope of the EU Directive must pass an ethical evaluation for approval (3). The project evaluation must include a harm-benefit analysis with regard to animal suffering and the predicted gain for society. In Sweden, there are six regional AECs. Each committee consists of 14 members. The chairman and vice-chairman are lawyers and the rest are equal numbers of researchers (or experimental animal technicians) and laymen. The Animal Ethics Committees primarily assess the use of traditional laboratory animals in biomedical research (18, 19). It is a recurring problem that the legislation is less adapted to research on wild animals. One example is the approved euthanasia methods which the AECs have to grant exemptions from when researchers catch fish in nets. The fish die slowly in the nets, which is not an accepted euthanasia method for research animals but is a standard method for population assessments of fish. Another example is using the measure of pain and stress equal to the insertion of a needle as the cut-off point for invasive procedures. In wildlife studies, pain and suffering are often not comparable to biomedical studies in terms of the procedures used. More importantly, wild animals may fare at least as badly from capture and handling since they have neither training nor any relationship with humans. According to the EU Directive, research projects must be planned according to the principle of the 3Rs (3, 12) which means that if there are no available alternatives to using animals, the number of animals should be the least possible to achieve statistically significant scientific results and that procedures should be performed in the most humane way possible. The 3Rs were originally designed for laboratory animals kept in research facilities (12), but are also applicable to free-ranging wildlife (20, 21). Species, research purposes and design, environment, and possibilities for close long-term monitoring of animals differ from those in traditional laboratory settings (5, 22). Nevertheless, replacement with computer simulations and environmental-DNA, reduction through optimized experimental design and sharing of data, and refinement with better methods of capture, anesthesia, handling, marking and design of equipment such as transmitters are examples of 3R strategies in wildlife research (20, 23, 24). Scrutiny of capture methods and how to define humane end-points for research on wild animals must be considered by the AECs. A humane end-point can, for example, be the maximum time allowed for helicopter chase of an animal or the number of attempts to descend upon the animal before immobilization. The project plan should include a description on how animals should be treated if they are injured when captured, and a plan for euthanasia if an animal cannot successfully be treated. The project needs to monitor the animals once released whenever possible in order to ensure not only their immediate survival but also their viability (e.g., that social animals reunite with their group) (23). In fact, the 3Rs should be systematically applied throughout the wildlife research project, from planning of the project to publishing of data (23, 25).

For management purposes, the application of the 3Rs and evaluation of suffering and other welfare criteria within ethical assessments are not legally required. While the 3Rs are increasingly recognized in wildlife research (21), they are also applicable in wildlife management (6, 26). Crozier and Schulte-Hostedde (26) discussed animal welfare and ethical implications of wildlife disease management. The authors suggested indirect management practices on wildlife populations (e.g., fences to minimize contact, habitat management) rather than culling to prevent disease transmission between wildlife and domestic animals, and using the most humane culling methods on a minimal number of animals. Merbourg et al. (27) compared attitudes toward and methods used in rodent pest control and animal research. They proposed using methods to repel rodents from entering a specific area and using the most animal welfare friendly control methods.

Members of the AECs (or IACUCs [Institutional Animal Care and Use Committees] in America) are often not familiar with the specific issues of wildlife research (5, 22). This lack of wildlife expertise in the AECs is a problem that occurs in several countries. Sikes and Bryan (28) describe the situation in America and the unique issues when using wild animals for research. They state that the IACUCs should have special tools and competences to be able to fulfill the task of wildlife project review. The lack of expertise can unfortunately result in failing to ask the important questions to the investigators. Examples of such questions include asking how a transmitter is aerodynamically designed, rather than just asking how much the transmitter weighs in relation to the weight of the animal, or how the transmitter can affect movement and health of the animals (15, 29), or the short- and long-term risks on health and welfare from capture and handling (4). The research procedures in traditional laboratory settings affect animals confined in a controlled environment. In contrast to laboratory settings, it is not always feasible to monitor animals released back to the wild (20). Importantly, this may also have implications on a larger scale; short- and long-term effects of capture, handling and identification, relocation, selective removal, and unintentional disease transmission, may affect wildlife populations, environmental health and biodiversity, domestic animals and humans, i.e., One Health (5, 30, 31).

Reduced Possibilities to Control Management Activities

The County Administrative Boards (CABs) are the competent authorities for carrying out official animal welfare controls in Sweden. In order to be able to perform these controls, the CABs need to be aware of what kind of animal activities, including research, are being carried out within the county. The gray area between research and management of wild animals complicates the official animal welfare control in Sweden. For the capture of wild animals, an authorization from the Swedish Environmental Protection Agency is required. Procedures carried out on animals (injections, blood sampling, anesthesia, surgery, etc.) can be permitted based on species preservation, i.e., management. If the procedure includes collection of data that can be used for a scientific purpose, it also requires permission from the Swedish Board of Agriculture in combination with an ethical approval from an AEC. The ethical approval is communicated to the CAB. If permission from an AEC to use wild animals in a research-like management situation is lacking, the CABs have no way of knowing that activities involving animals occurs. Such activities involving capturing, handling, sampling and marking of wild animals are not controlled by the CAB.

According to the Swedish Animal Welfare Act, animals in the care of humans must not be exposed to unnecessary suffering. Procedures that have been approved by an AEC are not considered to cause unnecessary suffering. However, animals subjected to invasive procedures (such as anesthesia) that have not been approved by an AEC, are considered to be suffering unnecessarily, unless the procedure has a veterinary justification for the individual animal. It can be argued that wild animals subjected to invasive management procedures when in temporary human care should fall under the Animal Welfare Act. In line with this reasoning, not only are the management activities unknown to the CAB, but they may also directly conflict with the Animal Welfare Act. The aforementioned example shows the difficulties when the legislation is unclear, and it opens up for different situation-based interpretations.

CONCLUSIONS AND RECOMMENDATIONS

Unclear and sometimes conflicting legal requirements and policies complicate the definition of a dividing line between wild animal research and management in Sweden, like in several other European countries (7). Hence it is difficult to determine into which category—research or management—an animal belongs, and if an ethical review of the animal procedure is needed. It is crucial that the competent authorities conduct a gap analysis between different legislations, e.g., in Sweden the legislations concerning animal welfare, hunting and fishing, and make them compatible. Wild animal management as such should be defined in the legislation and be subjected to animal welfare requirements similar to wildlife research.

The dividing line between research and management is hard to interpret. All procedures involving wildlife in research as well as management should undergo an ethical harm-benefit assessment for approval. The approval is not only beneficial from an animal welfare perspective, but will also facilitate the use of collected data, regardless of which category the handling of the wild animal has been defined as during the procedure. Within the current ethical project assessment and approval system, the knowledge of wild animal welfare and ethics is limited and needs to be improved (5). We therefore suggest that the assessment should be performed by one single AEC specialized in wildlife, with expertise in animal welfare, animal ethics, wildlife population health and One Health. This would ensure a similar ethical and welfare assessment for all wildlife. A completely new ethical committee could be created for this purpose. Alternatively, one of the existing AECs could specialize in wild animal practices by incorporating researchers with field experience, ethologists, biologists, lawyers, and public health experts.

We also suggest increased and improved official animal welfare controls of wildlife research and management procedures through harmonized legislation and facilitated by a mandatory authorization of animal procedures, based on ethical review.

Suggested changes and improvements would increase stakeholders' and public insight into, and understanding of, research and management procedures, and how these activities align with a harmonized legislation.

AUTHOR CONTRIBUTIONS

JL, KC, ES, JO, and MS all contributed equally to the problem description and discussion, and manuscript revision. All authors read and approved the submitted version.

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Sociality and Wild Animal Welfare: Future Directions

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Emergent evidence of aspects of sociality, such as social structure and social learning, across many vertebrate taxa, warrant more detailed consideration of their influence on welfare outcomes for wildlife. Sociality can be dynamic across organismal development, it can: provide protection through safety in numbers; may influence breeding outcomes via mate choice and alloparental care; can influence foraging success through transmission of social information and co-operation; and it can provide opportunities for the spread of novel behavior. Social learning itself provides an important mechanism for resilience in changing environments, but also has the potential to increase vulnerability or facilitate the spread of maladaptive behaviors. The welfare consequences of vertebrates living in social groups are explored using Wilson's 10 qualities of sociality as a framework, and the implications of human activities are discussed. Focus to date has been on the importance of social networks for the welfare of farmed or captive animals. Here I consider the importance of social networks and sociality more generally for the welfare of wildlife and explore Mellor's five domain model for animal welfare within the context of wildlife sociality.

Keywords: sociality, animal welfare, social learning, animal culture, social structure, vertebrates, five domains model, wildlife

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INTRODUCTION

Sociality is a measure of the degree to which animals interact or form long-term or transient associations and is prevalent across a broad range of vertebrate and invertebrate taxa. Animal welfare, on the other hand, is a multidimensional field, measured through a range of criteria from health and comfort, to the ability to express natural behaviors (1). While some natural behaviors may be considered, many aspects of sociality are often overlooked in animal welfare assessment and this is particularly the case for wildlife, where social settings may be complex.

Wild animal conservation and individual and group welfare are deeply intertwined (2). While the social environment is undoubtedly of significance to both the conservation and welfare of many species, quantifying the welfare implications of aspects of sociality can be challenging in the wild. The social environment has been described as being comprised of non-random and heterogeneous social interactions (3, 4). The social environment of vertebrate taxa is highly diverse, ranging from: the complex third order alliances of male bottlenose dolphins (*Tursiops* sp.) (5); to matriarchal African elephant societies (*Loxodonta* sp.) (6); to the hierarchical group dynamics of flocking birds (7). For long-lived, wide ranging species, such as blue whales (*Balaenoptera musculus*), there are also important spatio-temporal considerations for interpretation of behavior and associations (8).

Aspects of sociality, such as social structure and social transmission of information, across many vertebrate taxa, warrant a more detailed exploration of their influence on individual and group welfare outcomes for wildlife. Quantifying the welfare of wild animals presents a number of unique challenges. Wildlife welfare is often framed in terms of physiology or individual behavior. Nevertheless, better understanding of the processes of social behavior may provide important insights for the welfare of wildlife. While the focus of this review is vertebrates, there are some notable invertebrate taxa, such as cephalopods (9), which might also benefit from similar consideration.

Wilson's 10 qualities of sociality (10) have previously been suggested as a framework for evaluating the importance of sociality for individual and group welfare for cetaceans (whales and dolphins) (11). Here I attempt to expand these ideas to examine how sociality may be important for the welfare of a range of vertebrate taxa: exploring the risks and benefits of sociality to animal welfare; investigating the relationship between sociality and the impacts of human-induced rapid environmental change (HIREC) (12) on sociality and animal welfare. I then examine this new perspective within the context of the five domains model (13) of animal welfare.

SOCIALITY AND LIVING IN GROUPS

There are a number of potential ecological and animal welfare benefits from living in groups which include: predator defense, cooperative foraging, mating opportunities, and reduced vulnerability to infanticide (14). However, there are also risks and costs associated with group living, such as: increased risk of spread of disease, or increased conspicuousness to predators and competition for resources (3). Living in groups can also influence individual reproductive fitness, gene flow and spatial distribution (10, 15) and it has been argued that the buffering effects of social support may be relevant to farm animal welfare (16). There are likely many facets of sociality which have implications for both individual and group welfare in wildlife.

E.O Wilson listed 10 "qualities" of sociality (10) which are used to understand and classify conspecific groups. These characteristics of animal societies have also been used to provide a framework for evaluating the importance of sociality for individual and group welfare in cetaceans (whales and dolphins) (11). Here this framework is used to examine Wilson's 10 qualities of sociality within the context of wildlife welfare, more generally (**Table 1**).

RISKS AND BENEFITS OF SOCIALITY

Within the vertebrate taxa there are a variety of social structures, types of association between individuals, and

TABLE 1 | Wilson's 10 "qualities" of sociality (10) and welfare considerations for wild animals [adapted from Brakes (11)].

Quality	Welfare considerations
Group size	Welfare benefits may include predator defense, co-operative foraging, mating opportunities, and reduced vulnerability to infanticide (14). Here "group" is defined as "animals that actively achieve or maintain spatiotemporal proximity" (after 13). However, some of these welfare benefits may also be obtained in aggregations, which are not the result of social interaction but instead result from patchy resource distribution.
Demographic distribution	Populations and social groups may to some extent be robust to fluctuations in demographic distribution (from a welfare perspective), but this may depend on the extent and duration of parental and alloparental care and the social role of older individuals in predator defense, resource acquisition or as repositories of social knowledge (6, 17).
Cohesiveness	Wilson (10) suggested that the proximity of individuals may be used as an index of sociality. Today the more common measure is the rate of interactions (18). If the rate of interactions correlate with social behaviors, such as cooperative foraging, then it may follow that successful feeding could be correlated with interaction rate.
Patterns of connectedness through communication	Communication is central to sociality. Many vertebrate species exhibit complex patterns of connectedness through communication; these can be vocal, visual, tactile, or chemical. Some aspects of communication, such as bird song, can be socially transmitted, and the transmission itself may be dependent on aspects of the social network of the population, which may also extend between species (19). Measuring patterns of connectedness through communication may not always be straightforward, e.g., there is evidence that dolphins may eavesdrop on the echolocation of others (20). In cases where communication involves the transmission of social information, this may be relevant to wildlife welfare, for example where it relates to resource acquisition, such as food patches.
Permeability of movement between social groups	The movement of individuals between groups may act as vectors for the spread of disease or information. In addition, permeability has implications for the transmission of information between social groups, e.g., information on predators or resource acquisition.
Distinct social units	Potentially relevant to the emergence of unique socially learnt behaviors and cultures. Resilience to environmental change may depend on a variety of aspects of sociality, such as group composition (6) and how likely individuals are to innovate, or for innovations to be transmitted in the face of external pressures (21, 22).
Differentiation into social roles	Female pilot and killer whales exhibit a post-reproductive phase, indicating an import role within their social groups (17). This is supported by evidence that post-reproductive female killer whales boost the fitness of kin (23). The removal of individuals with key social roles, such as matriarchs, may have welfare repercussions for their social group (24, 25).
Integration of behavior	Whitehead (18) argues that measuring synchrony may be one way to examine integration of behavior. The welfare implications of synchronous behavior have not yet been extensively examined, but synchrony likely influences energy expenditure while traveling and hunting. It may also be useful to explore how fluctuating asymmetry (FA) (26, 27) varies in relation to synchronous and other integrated behaviors.
Information flow	May be relevant to resilience, particularly in relation to innovative foraging techniques, resources patches, and safe habitat (28, 29)
Time devoted to social behavior	The welfare implications of the proportion of time devoted to social behavior depends on the cost and benefits to the individual of spending time exhibiting that behavior, which may be contingent on the other qualities of sociality identified by Wilson (10).

TABLE 2 | Summary of the importance of social living for wild animal welfare [after Brakes (11)].

Positive	Negative
Resilience to environmental change and adaptation through social learning and the spread of novel behavior	Conservative cultures may hinder adaptation and resilience Potential for spread of maladaptive, or undesirable behavior through social learning
Individuals may act as repositories of social knowledge for the social group	Vulnerability from removal of repositories of social knowledge or individuals with specific social role
Potential for alloparental care in some species	Vulnerability of some cohorts and dependents if "carers" are removed Potential for increased competition for mates
Foraging cooperation Sharing information on food sources, either directly or through local enhancement	Foraging competition
Predator defense and alerting conspecifics to danger	Conspicuousness to predators Generally high probability of disease transmission in higher density groups

transmission pathways for social information. As a result the relationship between sociality and welfare across vertebrate taxa is multifaceted (see **Table 2**). Undoubtedly, sociality provides benefit to individual welfare, for example in predator defense, alloparental care, or by increasing foraging success through the transmission of information about food sources or other types of public information, or through co-operative foraging. But sociality also has associated risks, such as the increased probability of the spread of disease, or conspicuousness to predators. These risks and benefits can change according to the environment and may also be dynamic across the developmental stages of an organism.

While the risk of spread of disease and parasitic burdens associated with living in social groups has been extensively studied, sociality has, nevertheless, evolved independently in many taxa, demonstrating that these risks are overall offset by the benefits of sociality.

Social Support Hypotheses

The potential benefits of group living are varied (**Table 1**), but social support may specifically provide beneficial effects to the recipient, irrespective of whether or not the recipient is being challenged; or social partners may modulate or downregulate the impact of stressors on the recipient's homeostasis [a process known as stress buffering (30)]. Stress buffering has been investigated for farm animal welfare and it has been suggested that farmers could exploit animals' natural ability to benefit from their social group to obtain better welfare outcomes (16). Arguably, for some highly social species of wildlife it may also be the case that better management can be achieved through strategic use of elements of animal sociality to enhance welfare outcomes.

Social Learning, Animal Culture, and Welfare

Social learning—"learning that is influenced by observation of, or interactions with, another animal (typically a conspecific) or its products" (31)—has been observed across a broad range of vertebrate taxa (32) and can be important for conservation efforts (21, 33, 34). Social learning can act more rapidly than the intergenerational process of Darwinian selection (21) and some facets of sociality may also hold important insights for wild animal welfare. For example, social learning can provide mechanisms for resilience to ecological or anthropogenic stressors, such as reduced prey abundance [for example through diversification of foraging strategies (22, 35, 36)]. In contrast, it can also result in the transmission of socially learnt conservative foraging specializations, such as those found in killer whales (*Orcinus orca*), resulting in the species being less, rather than more, resilient to fluctuations in prey abundance (21).

Social learning also has the potential to facilitate the spread of maladaptive behaviors, which can evolve much more rapidly than genetic selection can counter them (21, 37). This is particularly relevant to animal welfare in human-wildlife conflict situations, both in relation to the spread of behaviors that lead to human-wildlife conflict (38) and in relation to facilitating resolution of these conflicts (39, 40). In all cases, a better understanding of the processes of social learning may help mitigation efforts and improve welfare outcomes for wildlife.

Social learning can also result in more persistent behavioral traits developing into "animal cultures." Whitehead and Rendell (41) define culture as: "information or behaviors—shared within a community—which is acquired from conspecifics through some form of social learning." But the interplay between animal culture and individual or group welfare within wild vertebrates may be complex. Cultural behavior may shape both social relationships and social structure (42), or even act as a marker of group identity (41, 43). Although social network analyses have been used to examine the welfare implications of disrupting these social systems (44) (see section Tools for Assessing Sociality and Wildlife Welfare), most studies have focused on farm or captive animals and the implications of these aspects of sociality for wild animal welfare warrant further exploration.

HUMAN IMPACTS ON SOCIALITY AND WILDLIFE WELFARE

The impact of human activities on wildlife and habitat is ubiquitous across virtually all ecosystems and HIREC is now a widely acknowledged phenomenon (12). From deforestation, to climate change and ocean acidification, wildlife around the globe is challenged by rapid environmental change, but aspects of sociality may provide opportunities for resilience to this rapid change, or increase vulnerabilities (45). It is timely to examine how sociality may influence wild animal welfare and responses to HIREC.

HIREC has the potential to influence all behavioral domains associated with social behavior, from breeding to communication, foraging and migration. A method to classify this vast array of threats from an individual welfare perspective is to consider acute and chronic implications for sociality and welfare (**Table 3**).

TABLE 3 | Acute and chronic implications of HIREC for sociality and welfare.

Threat	Acute implications	Chronic implications
Deforestation	Disturbance	Displacement
Hunting	Separation of social groups during hunting, potentially resulting in fragmentation	May result in the removal of individuals that have a specific social role (24)
Bycatch and entanglement	Acute suffering associated with being caught in fishing gear	Long-term suffering of individuals who remain entangled in fishing gear for days, weeks, or potentially months, with unknown implications for social interactions
Pollution	Potential to interfere with or mask the transmission of social information (e.g., noise) and/or result in the loss of key individuals	Anthropogenic pollution (e.g., noise, light, chemical pollution etc.) may influence the welfare of entire social groups in a chronic manner, potentially leading to displacement, and/or fragmentation
Harassment or displacement	Loss of cohesion within the social group in short-term	Longer-term loss of cohesion within the social group, particularly if harassment or displacement is persistent
Anthro-dependance[a]	Dependence on a food source provided by humans e.g., crop raiding, which may result in culling	May lead to loss of knowledge of non-anthro-dependant foraging strategies within social groups
Climate change	Potentially multiple implications including disturbance and displacement	Potentially multiple implications including disturbance and displacement
Ocean acidification	Unknown	Unknown

[a] *Dependence on human activities.*

COGNITION, SOCIALITY, AND WILDLIFE WELFARE

Understanding and predicting how individuals behave in response to HIREC may be important for evaluating aspects of sociality relevant to wildlife welfare. For example, understanding how individual innovations arise may be relevant for predicting—and setting up optimal conditions for—the spread of novel behavior through social learning. Wildlife behavioral responses are governed by cognitive processes ranging from perceptual processes to learned behavior. Understanding these cognitive processes and the effect of HIREC associated stress, may also assist in reducing human impacts on wildlife (46). It has been argued, using the same rationale, that if cognition underlies a behavior that is relevant to welfare, then understanding these cognitive processes may help in achieving better welfare outcomes for species such as cetaceans (11) and this is arguably also the case for other wildlife.

Greggor et al. (46) argue that "*cognitive theory can thus help predict how best to manipulate and exploit attentional biases, innate responses, and learning tendencies to enhance conservation efforts*." For example, they argue that mitigation methods will only be effective if they are reliably perceived by the target species (e.g., preventing birds colliding with human-made structures) and that this perception is rapidly learned. The same argument can been made for a range of wildlife mitigation activities, including: acoustic "pingers" on fishing nets designed to prevent dolphins from becoming entangled and boundaries designed to prevent crop raiding. The success of some mitigation methods may also be contingent on the social transmission of information, which in turn is contingent on other aspects of sociality such as social structure.

TOOLS FOR ASSESSING SOCIALITY AND WILDLIFE WELFARE

Asher et al. (47) argued for expanding the scope and development of new quantitative methods for the analysis of various aspects of behavioral organization as indicators for animal welfare, including: fractal analysis, temporal methods, social network analysis (SNA), and agent-based modeling and simulation. Social network analysis has now begun to emerge as a tool for assessing animal welfare. Kleinhappel et al. (44) argue that SNA is as yet, underused in the field of animal welfare and suggest a number of opportunities for using these methods, particularly in relation to the welfare of captive animals. However, SNA also has important application for assessing the welfare of wild populations.

SNA can be used to detect and describe the patterns and quality of interactions among individuals, with implications for physical health (e.g., disease transmission), psychological health (e.g., stress and social buffering), and social well-being (e.g., group stability) (48). These types of analyses have been used to investigate animal welfare in captive settings [e.g., for captive elephants (49) and primates (47)] and also have value in wild settings. For example, Godfrey et al. (50), demonstrated the link between parasite infection patterns and the connectivity of individual lizards within a population. It has further been postulated that SNA could be used to track behavioral changes and predict and prevent disease outbreak within groups (44).

EXTENDING THE FIVE DOMAINS MODEL TO INCORPORATE SOCIALITY IN WILDLIFE

There are several models that might be applicable for expanding our consideration of wild animal welfare in relation to sociality.

Hinde's framework for classifying aspects of sociality (51) might for example provide a basis for attempting to maintain optimal conditions of sociality from a welfare perspective within wild populations. However, trying to ensure optimality in the wild is both challenging to define and difficult in practice.

A more realistic approach may be to use the five domains model of animal welfare (13). While generally applied to domestic and captive animals, where some degree of compromise in welfare circumstances is implicit, the five domains model may be a more practical framework for managing welfare issues arising from human impacts on wild animal sociality. It is suggested here that the five domains model may be useful to avoid directly aversive situations resulting from poor management of the sociality of wildlife, for example through the removal of repositories of social knowledge (25). Instead, it may be better to try to manage wild environments so that socially complex systems can thrive and avoid situations that will hinder their development. The five domains model itself resulted from recognition of the need to provide positive experiences for animals (beyond the five freedoms framework) (52) and this approach may be useful for exploring how we can monitor and potentially assist social systems to flourish in the wild.

The objective of the five domains model is to "draw attention to areas that are relevant to both animal welfare assessment and management" and focus on the "presence or absence of various internal physical/functional states and external circumstances that give rise to welfare-relevant negative and/or positive mental experiences, i.e., affects" (13). In formulating the five domains model, Mellor "carefully and cautiously" considered the affects of the first four domains on nutrition, environment, health and behavior, on the fifth domain of mental state.

Considering some of the issues raised in this review, here I have attempted to explore some of the possible implications of sociality for wildlife welfare within the context of the five domains model (**Table 4**). This list is not intended to be exhaustive, but instead is a first exploration.

Play and the Five Domains Model

The stated objective of the five domains model is to provide opportunities for positive welfare (13) and it follows that one such opportunity might be granted through play in wildlife. Play is variable across species, has a variety of definitions (54, 55) and its proximate mechanisms and ultimate functions are not well understood. Play can indicate good welfare conditions, but can also be an indication of stressful situations, for example resulting in reduced parental care (56). Play has a variety of roles and it has been argued that play is usually the first behavior to disappear when welfare is compromised: when animals are stressed, anxious, hungry or unwell (57, 58). It has been suggested that play may be a reliable indicator of psychological and physical well-being (56). However, using play as a definitive indicator for optimal or good welfare can be confounded by several factors including: the heterogeneity of play; the fact that play can be a coping strategy; factors with no obvious relation to animal welfare can influence intrinsic playfulness within individuals; and the fact there are circumstances in which negative welfare can actually result in more play. Thus, play cannot definitely be considered an indicator of optimal or good welfare (59). But play can also be dynamic across life stages and arguably may be important for positive mental state in some species (see **Table 4**). For example, it has been argued that play may be socially contagious and therefore capable of spreading good welfare in groups (56).

Play behavior may also be of value in relation to innovation. In addition to having a potentially positive influence on mental states, there is potentially reciprocity between the social aspects of play, innovation and how innovation may then spread in wild populations. Bateson (57) argues that numerous functions for play have been proposed but they are not mutually exclusive and there are indications that those individuals who play most are most likely to survive and reproduce.

Potentially, the reciprocity between play and vital rates may manifest through the social transmission of innovative behaviors. Although fitness outcomes are not always synonymous with welfare outcomes, associations and bonds forged through play may influence the spread of information across a network and the

TABLE 4 | Potential interface between sociality and wild animal welfare as it relates to the five domains model (13) of animal welfare.

Nutrition	Environment	Health	Behavior	Mental state
Social information on food patches	Predator defense	Higher risk of spread of disease	Local enhancement via conspecifics (for example on critical breeding or feeding habitat, or sources)	Behavioral resonance[a], potentially resulting in positive emotions and closer affiliations
Safety in numbers during foraging	Thermal advantage associated with group living	Increased risk of transmission of parasites	Social learning of: communication; individual foraging strategies; or co-operative foraging behavior	Spread of emotional contagion, both positive and negative (e.g., fear in response to predators)
Social learning of novel foraging strategies	Response to HIREC: resilience and vulnerability to acute and chronic threats (see **Table 3**)	Better opportunities for mate choice	Role of individuals within their social group e.g., repositories of social knowledge	Social behavior providing opportunities for play and learning (see section Play and the Five Domains Model)
Co-operative foraging behavior		Potential for alloparental care of offspring	Potential for social learning of maladaptive behavior	

[a]*Strong and involuntary propensity to automatically synchronize with and imitate behavior of others (53).*

trial and error aspects of play may help individuals accumulate latent information, which may facilitate innovation as their environment changes. Thus, it can be argued that play may be an important part of the behavioral repertoire of some wildlife for maintaining resilience.

CONCLUSION

The interplay between sociality and the welfare of wildlife is multifaceted. The widespread evolution of sociality, social learning, and in some instances even animal culture, among vertebrate taxa is evidence that overall the benefits of social living out-weight the costs. Nevertheless, the individual and group welfare issues associated with the processes of social living are undoubtedly important for the consideration of wild animal welfare.

Previous explorations of the interface between sociality and animal welfare focus predominantly on domestic or captive animals: an entirely different paradigm from evaluating the implications of sociality on free ranging vertebrate organisms. There are many avenues for further research in this field (16), including for example, capitalizing on the mechanisms of social learning for the restoration and rehabilitation of wildlife populations (53, 60). But perhaps the most pressing are instances where human activities significantly disrupt social systems and can influence individual and group welfare (24, 25).

The principle objective of the five domains model is to move beyond an animal welfare focus of survival, toward individuals thriving. In order to meet the objective of thriving wild vertebrate populations, it is essential to incorporate aspects of sociality into their welfare assessments.

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The author confirms being the sole contributor of this work and has approved it for publication.

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Leukocyte Coping Capacity: An Integrative Parameter for Wildlife Welfare Within Conservation Interventions

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Wildlife management, conservation interventions and wildlife research programs often involve capture, manipulation and transport of wild animals. Widespread empirical evidence across various vertebrate taxa shows that handling wildlife generally induces a severe stress response resulting in increased stress levels. The inability of individuals to appropriately respond to rapidly changing environmental conditions during and after manipulations may have deleterious and long-lasting implications on animal welfare. Therefore, mitigating stress responses in the frame of conservation interventions is a key animal welfare factor. However, we have a poor understanding of the metrics to adequately assess and monitor the dynamic physiological changes that animals undergo when subjected to stressful procedures in wild or captive conditions. A growing number of studies provide good evidence for reciprocal interactions between immune processes and stress. Here, we review the existing literature on a relatively new technique—Leukocyte Coping Capacity (LCC), a proxy for stress quantifying oxygen radical production by leukocytes. We discuss the strength and weaknesses of this immunological approach to evaluate stress, the individual capacity to cope with stress and the resulting potential implications for animal welfare. Additionally we present new data on LCC in captive roe deer (*Capreolus capreolus*) under long-time anesthesia and free-ranging Asiatic wild asses (Kulan; *Equus hemionus kulan*) were LCC was used to assess stress levels in animals captured for a reintroduction project.

Keywords: stress, leukocyte coping capacity, endocrine-immune interaction, animal welfare, wildlife management, conservation interventions

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STRESS AND ANIMAL WELFARE

With increasing human impact on natural ecosystems, the need for "hands-on" wildlife conservation and management is on the rise [e.g., (1–3)]. Conservation interventions frequently require capture, manipulation and transport of individuals, but the concomitant and potential long-lasting effects on the target animals are often overlooked (4–7). Only few studies have investigated the impacts of conservation activities on wildlife health and welfare (8–10).

The broad definition of "Animal welfare" involves the well-being of animals based on the underlying psychological and physiological ability of the individual to cope with changes in its immediate environment (11–13). Difficulties or the inability to cope with environmental pressures can lead to stress and hence potential negative impacts on animal health and well-being as well as decreased resilience (14–16). Moberg (17) proposed that determining to which extent an animal is impacted from stress due to changes in its biological functions, thereby entering a pre-pathological state, is the only defensible measurement of well-being in animals (17, 18). Accordingly, the definition of potential stressors and the further development of methods to measure and assess stress responses are crucial for the evaluation of wildlife welfare (19–21).

The term "stress" is a notoriously ambiguous concept in biology and medicine. After the earlier definitions of the term by Cannon (22) and Selye (23) which were broadly based on the "non-specific responses of the body to any demand for change" [see (24), for a comprehensive review on the definition of stress] Sterling and Eyer (25) and later (16, 26) introduced the concept of "Allostasis." This concept can be summarized as the process of "achieving stability of the internal milieu (homeostasis) through change." This definition accounts for daily and circannual physiological adjustments that constantly occur during the life cycles of animals. More recently the allostasis concept was extended within the reactive scope model, which integrates the importance of species developmental strategies and their potential long-lasting impact in priming and programming later life stress responses (24).

Beyond the mere definition of stress, which due to the complexity and multi-dimensionality of the phenomenon may be hard to frame, the main physiological systems for coping with stressors are relatively well-studied. There are two major mediators orchestrating the stress response in vertebrates: (i) catecholamine's controlled by the sympathetic nervous system (SNS) and (ii) glucocorticoid stress hormones [GCs; corticosterone in amphibians, reptiles and birds, cortisol in most fish and mammals—(27)] modulated by the Hypothalamic-Pituitary-Adrenal axis (HPA-axis). Activation of the SNS triggers the release of catecholamine's within milliseconds after the onset of a stressor for immediate responses such as the "fight or flight" response [Cannon (22), recently reviewed by Romero and Wingfield (28)]. The HPA axis response is slower (within minutes) and acts on various physiological pathways to adjust essential bio-regulatory mechanisms in response to stressors, such as extreme weather conditions, predator exposure, or shortages of food (15, 29). This is primarily achieved by up-regulating key body functions, including cardiac-, respiratory- and brain-activity as well as energy mobilization at the expense of other processes such as growth, reproduction, immunity or the balance between oxygen radicals and the antioxidant system (29–31).

In general shorter-term/acute stress responses are thought to have an adaptive fitness value, whereas longer-term/chronic exposure to stress are generally associated with persistent immune modulation and an increase in susceptibility to diseases (17, 26, 29, 32). However, nature, duration and magnitude of stressful events are likely to be fundamental in determining the biological benefits or costs of exposure to stress (29, 33). There is growing evidence suggesting that the long-term and repeated exposure to moderately challenging stressors is associated with positive, rather than negative, organismal outcomes, improving survival and delaying the onset of reproductive senescence (34, 35). It is therefore key to assess and quantify how and to which extent differing stressors such as those provoked during wildlife and conservation management activities (i.e., capture, handling, transport, relocation) impact on individual responses and consequently on animal welfare (36, 37).

MEASURING STRESS

Stress responses vary vastly among species as well as within individuals of the same species (28, 38–40), are modulated by season, time of day (41) and can be triggered by a great variety of stressors (42). Moreover, stress responses involve several physiological processes in parallel and are therefore difficult to measure and to assess, particularly with the small sample sizes typical in field studies of wildlife species (43). Currently physiological stress responses in wildlife are assessed with a variety of techniques (20) including measuring GCs in various tissues (44–46), changes in blood chemistry and hematology (47) and behavioral alterations, such as exploratory or avoidance behaviors (48). Measuring GCs has generally been adopted as a standard procedure to estimate individual stress levels. However an elevation of GCs does not necessarily always indicate a state of stress or discomfort, as baseline and stress GCs levels can fluctuate hugely among an individual's life history stages (49, 50). Therefore, the use of GCs as a single metric to gain a comprehensive understanding of individual stress conditions is limited (50). While there has been an over-reliance upon GCs, other pathways of the stress response, such as endocrine-immune interactions as proxies for stress and animal welfare, are surprisingly understudied. In order to better understand the causalities and complex mechanisms within the stress response and its implications for animal welfare, it is imperative to integrate different approaches to better assess and interpret the phenomenon of stress (43, 51).

IMMUNE MARKERS AS A POTENTIAL PROXY FOR STRESS AND ANIMAL WELFARE

Several studies provide solid evidence for the strong and reciprocal interaction between immune processes and stress (52–54). It is now widely accepted that the immune system and the neuroendocrine system form an integrated and evolutionary highly conserved element of physiology across phyla (55, 56). Therefore, direct and indirect stress-induced effects on quantitative and functional immune parameters can serve as additional markers to assess stress and wildlife welfare. The best established and most commonly used immune parameter applied across all five vertebrate taxa is the stress-related change in immune cell distribution (i.e., leukocyte profiles). Higher stress levels are associated with an increase of neutrophil granulocytes (heterophils in bird and reptile species) and a decreae of lymphocytes in the bloodstream and hence an increase in neutrophil to lymphocyte ratio [N:L; (57)] [for review see (47, 58)]. Singh (59) lists acute phase response protein levels, natural serum antibody levels, the phagocytic capacity of Natural Killer cells, γδ- receptor positive T-lymphocytes, and stress-induced changes in inflammatory cytocine levels (interleukines and tumor necrosis factors) as innate immune markers which can be used to infer welfare outcomes. Another interesting immunological marker for stress is neopterin, a pteridine derivate synthetized by monocytes and macrophages upon inflammatory cytokine stimulation. Serum neopterin levels in pigs significantly increased after a 30 min transport phase and could be a useful marker to quantify acute/short-term stress-induced cellular immune stimulation (60). Another promising immune marker appears to be Immunoglobulin A (IgA) and in particular its secretory form (SIgA) the major antibody of mucosal immune defense in mamals and birds. The review by Staley et al. (21) reports that long-term examinations of IgA levels reveal consistent patterns with a suppression of SIgA after periods of psychological or physical chronic stress. In contrast, situations with good or enhanced welfare, lead to increased SIgA levels suggesting that this marker can be a suitable immunological proxy for animal welfare.

LEUKOCYTE COPING CAPACITY AS A PROXY FOR STRESS

Polymorphonuclear leukocytes (PMNLs), i.e., primarily neutrophil granulocytes in mammals (61) and heterophil granulocytes in birds (62), are the first line of innate immune protection in vertebrates. They become activated when binding to surface peptides of pathogens or by the stress-related activation of their α- and β-adreno- (63, 64) and glucocorticoid receptors (65). Once activated, PMNLs perform the so called 'oxidative burst' and produce superoxide free radicals as the basis for a suite of anti-pathogenic reactive oxygen species (ROS) generated upon the NADPH oxidase enzyme complex (66). An example emphasizing the biological significance of this innate immune reaction is chronic granulomatous disease (CGD), an inherited immunodeficiency in humans, where PMNLs are not able to generate ROS upon stimulation. CGD and an insufficient oxidative burst response in general, are characterized by recurrent bacterial and fungal infections and a set of inflammatory complications with not uncommonly, lethal outcome (67, 68).

In wildlife the initial stress-induced oxidative burst of PMNLs acts as immediate protection against invading pathogens in the case of injury by a predator (69, 70). However, the capability of PMNLs to produce further ROS after the initial (stress induced) burst is curtailed to protect the organism from over-activation of PMNLs while reducing free radical damage of surrounding tissues (71, 72). Therefore, during short-term stress PMNL ROS production denotes an immediate stress response which is rapidly curtailed (71, 72). On the other hand, if stress conditions persist, this innate immune response is diminished to depleted with detrimental impacts for the health, welfare and survival of the individual (70, 73–75).

McLaren et al. (76) developed a method called Leukocyte Coping Capacity (LCC), using PMNLs and the change in their reactivity as bio-indicators for measuring stress events (76). PMNLs have over 150 different receptors which are sensitive to varied stress signals in the organism, including plasma endocrine factors, changes in blood biochemistry and red cell hemodynamics, changes of cytokine levels and mediators released by the HPA axis and the SNS (72). This synchronous sensitivity to several stress mediators and an array of stress-related physiological changes emphasizes PMNLs as excellent indicators in evaluating stress levels (77). The technique relies on the observation that PMNLs of stressed individuals have a reduced capacity to produce ROS in response to a secondary (chemical) external stimulus (78). Thus, low LCC levels in an individual indicate a decreased innate immune response and increased stress levels.

Despite the sensitivity of PMNLs to an array of constituent mediators of the stress response, the physiological relevance of the method is promising for the following reasons: (i) PMNLs remain in their natural environment, i.e., in whole blood, allowing dynamic, and three dimensional interactions with other surrounding blood cells (e.g., macrophages or erythrocytes) as well as cell–cell interactions within and among different leukocyte cohorts, (ii) the method does not necessitate centrifugation known to change cell reactivity and also avoids "plating out" cells on glass slides as in other approaches to determine PMNL activation [Nitro blue tetrazolium test—Montes et al. (79)], minimizing the disruption of important cell signaling pathways and maintaining PMNL responsiveness and integrity, (iii) the response can be followed in real-time via direct quantitative chemiluminescence readings (80), (iv) the interaction between the immune- and stress systems is evolutionary highly conserved and therefore the LCC technique can be applied potentially across all wildlife species (78, 81, 82). For further information on details of the LCC protocol see **Supplementary Material S1**.

The method provides several additional technical advantages: (i) a relatively small amount of blood (i.e., 20 μl) is needed to perform the assay, making it applicable for small vertebrate species, e.g., rodents, passerine bird or bat species; (ii) the procedure is rather simple, minimizing sources for error, and (iii) the response can be measured via a portable Chemiluminometer (e.g., Junior LB 9509, EG & G Berthold, Germany) providing immediate results, which is a great advantage in field studies in free-living animals.

Confounding Factors and Constrains

Measuring stress with the LCC protocol is still relatively novel. There are several aspects which require further experimental testing to establish the diagnostic efficacy of the methodology. It should be noted that studies investigating the relationship of LCC to more commonly used proxies for stress (e.g., heart rate, N:L ratio, blood glucose or circulating cortisol levels) did not find correlative relationships (77, 83, 84). This lack of correlation may be explained by large individual variation in stress responses as well as by differing physiological strategies to cope with stress and/or the diverging operative time frames of pathways and mediators involved into the stress cascade (39, 40, 43). An additional explanation may be the synchronous sensitivity of PMNLs to several stress related changes (77). During infection and disease a multitude of immunological factors are altered. Neutrophil "priming" agents such as chemoattractants (e.g., bacterial peptides/proteins), inflammatory cytokines (e.g., tumor necrosis factor alpha) or Toll-like receptor agonists (e.g., endotoxins) all have the potential to increase PMNL ROS production (72, 85) and potentially bias LCC dynamics. Gonadal steroids (e.g., androgens and estrogens) may have direct effects on the ROS production of PMNLs and alter LCC responses during times of reproduction, although previous studies on this topic provided contrasting results (86–88). Future studies will need to assess stress hormone, and gonadal steroid effects on the LCC response in order to better elucidate functional endocrine-immune interactions that could be linked with animal welfare. We also need further studies to elucidate the down-stream mechanisms triggering PMNL activation and relevant time windows in which these pathways do operate. However, there are no clear physiological profiles of ensured welfare within a species or even between individuals. Hence future studies should aim for a systematic, multivariate approach including several parameters of physiological and behavioral nature to gain more insight toward the validity of potential tools such as LCC to assess stress and welfare (89–92).

Capture and handling of wildlife species often involve anesthesia of individuals with varying protocols which are constantly adapted for animal safety and welfare reasons (93, 94). Anesthetic agents have the potential to decrease PMNL oxidative burst capacity in humans. This decrease has been shown for opioids (morphine), thiopental, propofol, midazolam, volatile anesthetics (i.e., halothane, isoflurane, and sevoflurane) and local anesthetics (lidocaine, bupivacaine). In contrast ketamine and synthetic opioids (fentanyl, remifentanil, and alfentanyl) did not alter PMNL ROS production (95, 96); for review see Kurosawa and Kato (97). However, despite some studies in humans [e.g., (98, 99)] and one in a fish species (100), studies on the effect of anesthetic agents on PMNL function in wildlife are to date lacking.

Studies Inferring LCC as a Valid Proxy to Assess Stress in the Context of Welfare

A review on phagocyte photon emission in response to stress and disease noted that the capability of PMNLs to emit ROS reflects the pathophysiological state of the host and that the magnitudes of stress as well as the presence of pathogens and disease processes can be estimated (81). A later study in Atlantic salmon (*Salmo salar*) revealed that fish subjected to a 2 h period of confinement stress had a reduction in oxygen free radical production in isolated PMNLs and therefore a lower oxidative burst capacity and a debilitated innate immune response (78). In **Table 1**, we review a sample of studies inferring LCC as a valid proxy to assess stress and animal welfare. McLaren et al. (76) used the LCC method to examine the effects of transport from a capture site to a field laboratory in wild badgers (*Meles meles*). The study showed that transported individuals (ca. 10 min on a trailer pulled by an all-terrain quad) exhibited a detectable reduction in LCC levels when compared to individuals sampled directly at the capture site. These data indicate that transport is likely to be a compounding stressor beyond the capture event (76). A study on bank voles (*Clethrionomys glareolus*) and wood mice (*Apodemus sylvaticus*) indicates that handling *per se* is likely to alter LCC responses. Handled animals (only for 20 s) showed remarkable reduction in LCC in comparison to non-handled animals (102). In non-anesthetized European Roe deer (*Capreolus capreolus*) LCC levels were negatively impacted by the time of human presence at the capture site prior to the actual handling procedure, suggesting that human presence at the trapping site prior to handling should be minimized (84). The LCC technique was used to investigate the stress response caused by capture and subsequent abdominal surgery of free-ranging brown bears (*Ursus arctos*) and to evaluate whether variation in LCC co-varied with other proxies of metabolic and physiological stress, such as heart rate, N:L—ratio, blood glucose and circulating cortisol concentrations (83). Their main result revealed that LCC values following capture were lower in solitary bears when compared to females with cubs and lower in bears in poorer body condition when compared to those in good body condition. LCC levels did not seem to be influenced by the actual surgical procedure under anesthesia (83). A recent study comparing blood glucocorticoid levels, hematology, LCC, scrotal, and perineal temperature, scrotal lesion, and a pain score in two groups of male calves (*Bos Taurus*), a ring castration and a sham castration control group, suggests LCC as an innovative tool for stress and pain assessment (105).

Within a reintroduction program for conservation purposes Moorhouse et al. (103) analyzed the impact of housing conditions, handling procedures and radio-collaring in captive bred water voles (*Arvicola terrestris*) via LCC measurements. The authors found a larger decrease in LCC levels between week 1 and 2 for individuals that were radio-collared while this was not the case in non-collared individuals, suggesting that radio-collaring could be an additional stressor, at least in this species. In this experiment one group of individuals were housed in outdoor enclosures and the other group in indoor laboratory cages. LCC values of both groups decreased constantly over the 6-week study period, but interestingly, animals housed indoors and individually in laboratory cages showed lower LCC values despite the fact that they usually do not live in large groups and are territorial in the wild (103). This result partially contrasts results from (101), who examined short-term social stress by means of body weight change and LCC to test the effects of group size in captive-bred water voles destined for release within a reintroduction program. LCC scores were negatively correlated with group size, suggesting that individuals held in larger groups experienced higher relative levels of stress and therefore showed a greater decline in LCC (101). Moorhouse et al. (103) interpreted the overall continuous decrease in LCC values as the cumulative result of repeated-handling induced stress. The latter study and Gelling et al. (101) also suggest

TABLE 1 | Overview of studies inferring LCC as a valid proxy to assess stress and welfare in animals.

Species	Context	Change in LCC	Remarks	References
Badger (*Meles meles*)	Capture, transport, handling	↓ Transport	Transport was identified as additional stressor prior to handling	(76)
Scandinavian brown bear (*Ursus arctos*)	Capture via helicopter, surgery	↓ Capture	Variation in LCC was best explained by social status	(83)
		↑ During anesthesia	Bears in better body condition coped better with capture and handling	
Water vole (*Arvicola terrestris*)	Captive housing, social stress	↓ Group size	Individuals held in large groups showed greater declines in LCC	(101)
Bank vole (*Clethrionomys glareolus*)	Trapping and short handling	↓ Handling	Even a short period of 20 s of handling induces a decrease in LCC	(102)
Wood mice (*Apodemus sylvatikus*)			Note: potential bias by the use of isoflurane during handling	
Water vole (*Arvicola terrestris*)	Captive conditions, handling,	↓ Captivity	Indoor-housing caused a greater decline in LCC compared to outdoor- conditions	(103)
	Radio collaring	↓ Indoor housing	Continuous decrease of LCC over the entire experiment (6 weeks)	
		↓ Collaring	LCC of collared individuals decreased more within the first week of the exp.	
European roe deer (*Capreolus capreolus*)	Capture and handling	↓ Prior to handling	LCC levels were negatively correlated with the time of human presence prior to the handling procedure prior to the handling	(84)
House sparrow (*Passer domesticus*)	Capture and handling	↓ Capture, handling	Capture induced a decrease in LCC	(51)
		↑ During confinement	LCC of birds kept in a cotton bag recovered during a 30 min period	
		↓ Females	Females showed significantly lower LCC levels in response to the stressor	
Rhesus macaques (*Macaca mulatta*)	Captive conditions	↓ Caged housing	Caging system caused significantly lower LCC responses compared with open rooms	(104)
Kulan (*Equus hemionus*)	Capture for reintroduction	↓ In agitated indiv.	Suggests LCC has the potential to identify high risk candidates	Huber et al. this study
European Roe deer (*Capreolus capreolus*)	Long-term anesthesia monitoring	↑ Until 80 min and ↓ thereafter	Suggests LCC as a useful tool for anesthesia monitoring	Huber et al. this study
		↓ In winter	Marked seasonal difference in LCC with lower levels in winter	
Cattle (*Bos taurus*)	Ring castration	↓ Ring castration	Lower LCC in ring castrated calves during the degenerative phase of scrotal tissue	(105)

that the preferred social structure needs to be considered in order to reduce stress levels and enhance wildlife welfare within conservation projects. Honess et al. (104) likewise applied the LCC method (referred to as "neutrophil activation test") to assess differences in stress levels between different housing conditions in a breeding colony of rhesus macaques (*Macaca mulatta*). Individuals were housed either in a caging system (reinforced stainless steel two-tier laboratory cages) or open-rooms. Animals in the caging system exhibited significantly lower LCC responses when compared to animals held in open rooms, indicating that cage housing is associated with diminished immune function as well as higher stress levels and therefore impaired welfare (104). The LCC method was recently tested in an avian species, the house sparrow (51). It was shown that after an initial decrease LCC levels increased during a 30 min time period after the captive birds where confronted with the acute stressor of a standardized capture and handling (106). LCC levels during the acute stress response were compared to circulating concentrations of GCs (i.e., corticosterone) and markers of oxidative stress in two different seasons, winter and spring, respectively. All three methodologies detected significant changes due to the acute stressor but they were not correlated with each other. There were marked seasonal differences in GC response, with higher levels in spring in both sexes. Had the study measured the classical approach of measuring total GCs, the most obvious conclusion would have been that individuals confronted with the same stressor experienced a higher short-term stress response in spring when compared to winter, with no difference between sexes. On the other hand, simultaneous LCC measures revealed similar stress responses during both seasons with marked sex differences in relative stress levels and thus in the ability to cope with the stressor. There was no change in oxidative stress levels at the expense of a decrease in anti-oxidative capacity (measured as the ability of serum to neutralize hypochlorous acid) 30 min after the acute stress event. Combining the three methodologies allowed, to some extent, for a more holistic appreciation of the stress response: the elevation of GC levels and the neutralizing effect of antioxidants on ROS in the circulation facilitated the reestablishment of homeostasis in the organism (Allostasis). This recovery was illustrated by

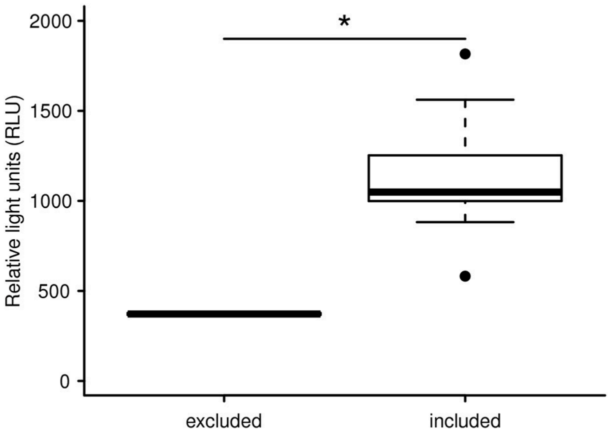

FIGURE 1 | LCC peak levels (expressed in relative light units) of free ranging Asiatic wild ass after capture and handling within a reintroduction project in Kazakhstan. The LCC of two overly agitated individuals are significantly lower compared to 10 animals not showing signs of increased agitation. The two severely stressed kulan were excluded from the transport and translocation for animal welfare reasons. The asterisk indicates a significant difference of $^{*}p = 0.013$.

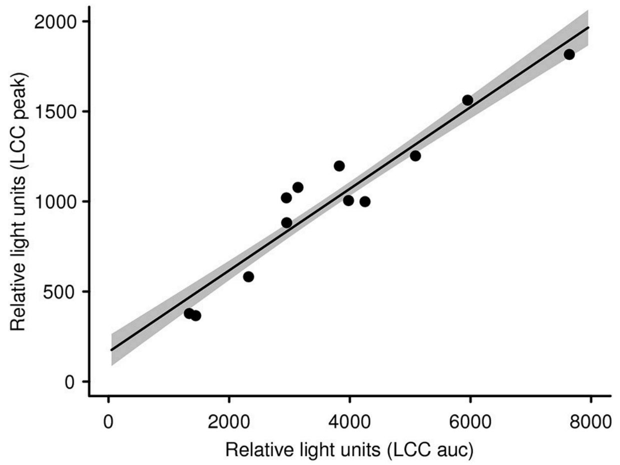

FIGURE 2 | LCC peak levels in kulan are significantly linked with and therefore representative for the whole LCC curve (i.e., area under the curve; see also **Figure S1**). The gray shaded area represents the standard error of the slope.

the increase in LCC within a 30 min time period and reflects the restoration of the capacity to cope with repeated or novel stress (76). Results from this study clearly highlight the necessity of increasing the scope and number of physiological systems within the stress-endocrine-immune interface which need to be investigated concurrently in future studies to better assess and understand the complexity of coping mechanisms related to stress and the impacts on welfare.

In our perspective the above mentioned literature suggests LCC as a useful tool within wildlife management or conservation interventions (i.e., capture, handling, and transport, housing conditions). In order to further assess the validity of LCC to identify stress eliciting factors future studies should incorporate different intensities of identified or suspected stressors in a systematic approach (e.g., short- vs. long-human presence prior to handling) and include LCC in addition to other measures of stress and welfare (e.g., hormone levels, SIgA, behavioral scores). Such studies would be very important in order to optimize exposure to the tested stressors, thereby increasing animal welfare and furthering our understanding of the extent to which different stressors alter LCC responses.

Latest LCC Data From Two Ongoing Wildlife Projects

With the aim of evaluating capture and handling procedures and to further expand the LCC approach to different vertebrate species, we measured LCC in 12 kulan (*Equus hemionus*) captured in Kazakhstan during a translocation project. In brief, kulan had been driven into a capture corral, rested overnight, then anesthetized via remote darting and subsequently sampled, radio-collared, and boxed for translocation the following day (107). Two kulan out of 12 had to be released from the transport boxes prematurely due to severe stress and danger from self-inflicted injury. By comparing the LCC peak values of these 2 prematurely released individuals vs. the 10 transported kulan, we were able to identify a significant difference between the two groups (**Figure 1**). This finding suggests that LCC measures on-site in the field may be a powerful animal welfare tool allowing the identification of overly excited individuals (potentially severely stressed), which have an increased risk of injury and mortality. Especially in situations where a subset of animals is selected for further handling or transport, LCC data might guide (i) the selection of the least stressed individuals, (ii) the exclusion of the most stressed individuals, and (iii) in expediting appropriate interventions for those individuals which most likely have an insufficient ability to cope with capture and handling. This study also confirmed findings from a previous study in roe deer (*Capreolus capreolus*) in which LCC peak values were shown to be a robust proxy for the entire LCC curve [**Figure 2**; (84)].

To expand our knowledge concerning LCC dynamics and stress during long-term anesthesia (over a 120 min period) we analyzed data from 9 anesthetized captive European roe deer males. It was our aim to test recovery from initial capture and handling-induced stress (i.e., an increase in LCC) during the subsequent anesthesia, as observed in anesthetized brown bears (83). We found that season and sampling time significantly affected LCC levels in roe deer independently. LCC values during summer were markedly higher compared to two winter seasons (**Figure 3**). Supporting the work by Martin (32) these results suggest possible seasonality effects on the immune system. This highlights that seasonal impacts on the general capacity to cope with stressors as well as the cost to the immune system must be considered in study design. Ideally future studies will avoid or at least minimize capture and handling of roe deer during the winter in order to reduce stress levels and thereby improve welfare outcomes. We further identified a significant increase of LCC with increasing sampling time (i.e. the progression of anesthesia) suggesting

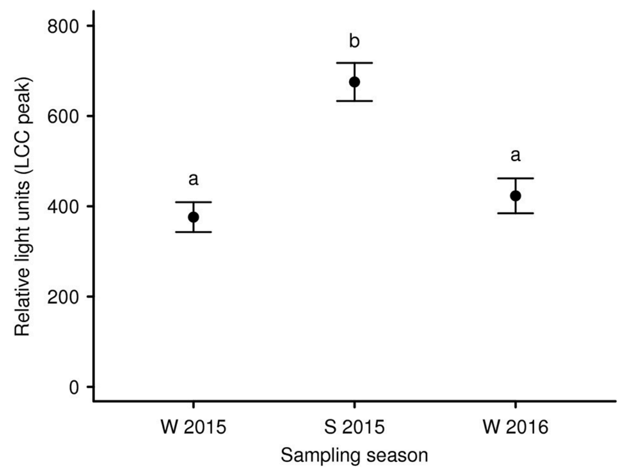

FIGURE 3 | Mean LCC levels (± s.e.m.) of 9 European roe deer males during a 120 min period of anesthesia and split by seasons (W 2015: winter 2015; S 2015: summer 2015, and W 2016: winter 2016). Blood samples were taken as soon as the animals were in lateral or sternal recumbency due to anesthesia (T0) as well as 40 min (T40), 80 min (T80), and 120 min (T120) thereafter. Throughout all seasons the same 9 individuals were sampled. Different letters indicate significant *post-hoc* pairwise contrasts ($p < 0.05$ after Tukey's multiple comparison adjustment).

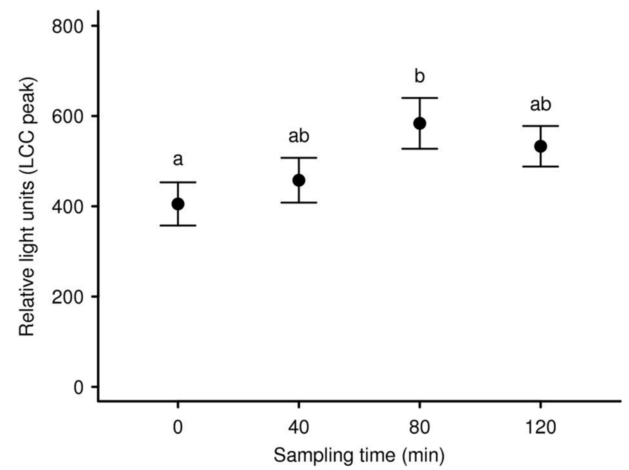

FIGURE 4 | Mean LCC levels (± s.e.m.) of 9 European roe deer males during a 120 min period of anesthesia separated by sampling/bleeding time. The first sample was taken as soon as the animals were in lateral or sternal recumbency due to anesthesia (T0) as well as 40 min (T40), 80 min (T80), and 120 min (T120) thereafter. Throughout all seasons the same 9 individuals were sampled. Different letters indicate significant *post-hoc* pairwise contrasts ($p <$ 0.05 after Tukey's multiple comparison adjustment).

a gradual recovery of innate immune function and capture stress during anesthesia (**Figure 4**). However, subsequently LCC values decreased non-significantly in all animals from T80 to T120. This result provides some evidence that LCC may be a useful tool for anesthesia monitoring detecting a possible threshold (a decrease after an initial increase in LCC levels) for ending the anesthesia to prevent the onset of cumulative negative impacts.

For full details on the two projects described here, including the LCC protocol, statistical analyses and results see **Supplementary Materials S1, S2**.

CONCLUSION

There are several approaches such as shifts in hormone concentrations, blood parameters and behavior to assess stress and its implications for wildlife welfare (20). However, these common measures generally do not always provide robust and reproducible results, largely due to the challenges associated with the complexity of the neuro-endocrine systems (92). Moberg (18) stated that the biological cost of mounting a stress response is the key to determine the welfare implications of potential stressors and therefore would be more relevant when compared to other measures of stress such as physiological or behavioral changes (17, 18). The LCC technique provides a window to assess the biological costs associated with the impaired capacity of PMNLs to mount an oxidative burst after a stressful event. A reduction of LCC directly reflects increased stress levels and reduced (innate) immune function. This denotes a "pre-pathological" state which engenders costs, may be predictive for a breakdown in biological functions and is subsequently a promising indicator of animal well-being (76, 83, 84, 108). Due to the fact that LCC captures some of the complexity of action and reaction of PMNLs to a multitude of stress signals within and among animal species and their environment this method provides holistic insights into the trade-off and associated costs between stress response and immune function. However, a combined approach using two or ideally more stress parameters provides a far more comprehensive approach when evaluating stress and animal welfare impacts.

Our review suggests that measuring LCC has the potential, amongst others, to develop in the short-term into a helpful tool to disentangle the stressful components of capture, trapping and handling procedures in wildlife. Given the implications that animal welfare perception has on the acceptance of wildlife conservation and management interventions, information provided by new techniques, such as LCC, will allow researchers to better evaluate and communicate the impact of their work while adjusting and refining procedures and protocols accordingly.

ETHICS STATEMENT

This study on the European roe deer was carried out in accordance with the recommendations of the German Ministry for Environment, Health and consumer protection and all experimental procedures were approved by the ethical committee of the German Ministry for Environment, Health and consumer protection (AZ: 2347-4-2015). The Kulan project (ecological assessment) was approved by the Committee of Forestry and Wildlife (CFW) of the Ministry of Agriculture of Kazakhstan, Document Number: KZ41VCY00098965.

AUTHOR CONTRIBUTIONS

NH and JP initiated the LCC study on long-term anesthetized European roe deer and designed as well as conducted the experiment together with FG. PK is the head of the Kulan reintroduction project in Kazakhstan and initiated the evaluation of capture and handling procedures in cooperation with CW and NH. NH conducted all LCC measurements. Data analysis and preparation of figures was done by SV and VM. NH wrote the manuscript with contribution of VM. CW, PK, and VM revised the manuscript. All authors participated in revisions and approved the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fvets.2019.00105/full#supplementary-material

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Implanted Radio Telemetry in Orangutan Reintroduction and Post-release Monitoring and its Application in Other Ape Species

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Designed as a new method to facilitate the reintroduction and post-release monitoring of orangutans and other apes, implanted radio-telemetry (IRT) was developed and first deployed in 2009. Since that time, it has been necessary to collate and review information on its uptake and general efficacy to inform its ongoing development and that of other emerging tracking technologies. We present here technical specifications and the surgical procedure used to implant miniaturized radio transmitters, as well as a formal testing procedure for measuring detectable transmission distances of implanted devices. Feedback from IRT practitioners (veterinarians and field managers) was gathered through questionnaires and is also presented. To date, IRT has been used in at least 250 individual animals (mainly orangutans) from four species of ape in both Asia and Africa. Median surgical and wound healing times were 30 min and 15 days, respectively, with implants needing to be removed on at least 36 separate occasions. Confirmed failures within the first year of operation were 18.1%, while longer distances were reported from positions of higher elevation relative to the focal animal. IRT has been a transformational technology in facilitating the relocation of apes after their release, resulting in much larger amounts of post-release data collection than ever before. It is crucial however, that implant casings are strengthened to prevent the requirement for recapture and removal surgeries, especially for gradually adapting apes. As with all emerging technological solutions, IRT carries with it inherent risk, especially so due to the requirement for subcutaneous implantation. These risks must, however, be balanced with the realities of releasing an animal with no means of relocation, as has historically been, and is still, the case with orangutans and gorillas.

Keywords: great apes, technology, orangutan, post-release monitoring, rehabilitation

INTRODUCTION

Most ape species are subject to population pressure across their range due to diminishing habitat quality and/or human wildlife conflict and hunting (1–7). As a direct result of these threats, the Javan gibbon (*Hylobates moloch*) is Endangered, while the three species of orangutan (Sumatran: *Pongo abelii* and *P. tapanuliensis*; Bornean: *Pongo pygmaeus*) and the western lowland gorilla (*Gorilla gorilla gorilla)* have become critically so (8). Habitat loss, poaching and displacement has also led to increasing numbers of displaced apes, as well as the proliferation of rehabilitation facilities in Africa and Asia. These facilities typically operate with the goal of managing otherwise healthy orphaned animals through pre-release training and reintroduction programmes.

In the context of species conservation, reintroduction is the only logical step that rehabilitation centers should be making. Yet the practice carries with it welfare and disease risks for both released and resident wild animals (9–11). Post release monitoring is the most effective method of assessing how to reduce these potential risks, as well as providing the means to better understand the process of adaptation, assessing the suitability of a given pre-release rehabilitation protocol and release site, and to formulate criteria for assessing reintroduction success. Despite this, its application among several species has been limited (12). Post-release monitoring is severely restricted by an inability to relocate animals regularly, as is often the case for wide-ranging apes which may also show limited social interactions or vocalizations, e.g., orangutans. Reintroduction successes and failures may thus remain unknown for the vast majority of animals.

Radio telemetry has the capacity to transform our ability to conduct adequate monitoring and data collection, through the development of methods specifically designed to locate individuals after release. Among its key benefits are the unequivocal identification of individuals and the facilitation of data collection (13), and the ability it conveys to reintroduction specialists to intervene to promote welfare or prevent potential conflict situations involving released animals. Its biggest impediment among apes, however, has been the absence of appropriate species-specific attachment systems for these dexterous, intelligent, and strong animals (14–16). Decisions not to employ available tracking devices may also be influenced in some cases by their prohibitive cost per individual released, weight, and the historically poor fix rates of commonly used GPS devices because of canopy closure and topographic conditions (17, 18). While radio collars have proven successful in monitoring prosimians [*Galago alleni:* (19); *Galago senegalensis*: (20)], some monkeys [*Ateles geoffroyi:* (21, 22); *Aotus azarai:* (23)], and reintroduced chimpanzees [*Pan troglodytes:* (24–26)] it has not been possible to fit them on orangutans because of their small heads, relatively wide necks and soft throat pouches (27).

In response to these issues, the Research Institute of Wildlife Ecology in Vienna developed new subcutaneous radio telemetry transmitters and a corresponding surgical implantation method in 2009. Since then, implanted radio telemetry (IRT) has been adopted by numerous ape reintroduction projects such that the collation of information on its application is now necessary to inform its continued development and use in facilitating post release monitoring. This is particularly necessary given that tracking technologies are constantly evolving and improving (28). Here we describe (1) the technical specifications of equipment used; (2) the surgical implantation method; and through surveys with end users we also review (3) general device uptake; (4) observed distances and ranges of implants; and (5) practitioner perceptions and recommendations. In our discussion, we also identify the key issues and challenges associated with implanted devices and we compare these with more established applications of radio telemetry. The scope of this technology is potentially vast across many different genera so we intend not only to bring IRT to the wider attention of biologists but also to assist all those interested in further developing wildlife tracking technologies.

MATERIALS AND METHODS

Miniaturized Radio-Telemetry Transmitters—Technical Specifications

To be suitable for sub-cutaneous implantation each device comprises a miniaturized circuit board, battery and VHF transmitter housed in inert and secure ceramic circular casings to protect against liquid ingress (**Figure 1**). Two small circular VHF transmitter implants have been developed with different battery options: a smaller iteration with a 280 mAh battery ($d =$ 28 mm, $h = 10$ mm, 14 g), and a larger iteration with a 540 mAh battery ($d = 28$ mm, $h = 12$ mm, 17 g). Based on diameter alone, this makes both implants marginally smaller than a United States 50 cent coin. Since 2009, 481 transmitters were sold up to the end of December 2016, most of which carried the larger battery (362) vs. the smaller (119). Each device emits a pulse of 0.01 s duration at 1.5 s intervals. The electronic circuit is housed in a computer numerically controlled (CNC) engineered, inert ceramic casing, hermetically sealed with specially formulated epoxy glue.

The on/off timing schedule of each transmitter is pre-programmed during production in response to how many hours

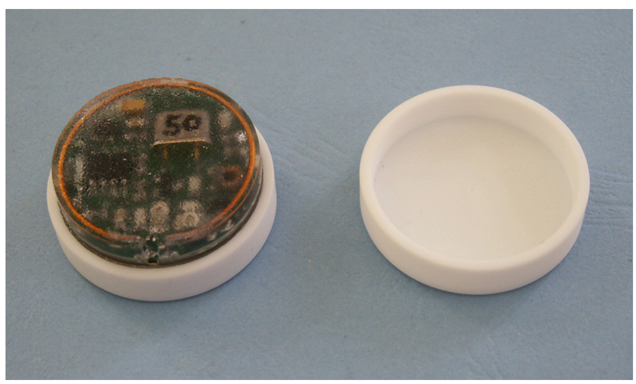

FIGURE 1 | An open transmitter showing its circuitry and ceramic casing.

per day the research team requires transmission. The start time of this schedule is determined by the user via magnetic switch. The unit is controlled by a very low-power-timer-circuit that allows for a life span of several years. Shorter daily transmission periods result in longer battery lifespan; an 8-h daily transmission schedule provides an estimated battery life of 33.6 months. Various frequency bands are available. To track the signal of the implants, a standard tracking receiver and adequate directional antenna covering the frequency range is required.

Implantation Surgery and Recovery

Following induction of surgical anesthesia transmitters are implanted in a surgically created subcutaneous pouch in the cranio-dorsal cervical area. After hair-trimming and standard aseptic pre-operative surgical preparation of the skin, a 4cm paramedian incision is made ∼4 cm distal to the base of the occipital bone. This is followed by blunt dissection of the subcutaneous tissues caudal and lateral to the initial incision to facilitate subcutaneous dorsal parasagittal-midline insertion of the transmitter. Subcutaneous tissues are sutured to secure the transmitter before the skin is closed with absorbable monofilament suture material using an interrupted intra-dermal suture pattern. The transmitter is implanted specifically with the plane of the transmission face facing the suture line to maximize detection efficacy. Treated animals are then maintained in smaller enclosures until the wound is fully healed. Wound healing times are subject specific, but can reasonably be expected to complete within ∼2 weeks post-surgery. The healing process is regularly evaluated by veterinarians and any healing abnormalities are treated accordingly. Placement of the transmitter lateral to the spinous processes in this position reduces the likelihood of traumatic damage post operatively.

Questionnaire and Device Outcome Table for End Users

A questionnaire and a device outcome table were designed for primate reintroduction practitioners who have used IRT with non-human primates to assess general use and effectiveness. These documents were emailed to practitioners between July 2013 and March 2017, with the nature and purpose of the questionnaire clearly explained. Consent to participate was implied upon completion of the questionnaire. The device outcome table provided quantitative biodata on animals implanted, surgery and recovery times, implant battery lives and outcomes. The questionnaire provided data on the current perceptions of IRT from field practitioners. Questions were mostly close-ended multiple choice to facilitate completion and quantitative analysis, although some sections required descriptive detail. Due to the relatively small number of projects that are using this technology, descriptive statistics and frequencies were used in analyses of the questionnaires.

Distance Testing Protocol

To give an indication of the signal range capability of implanted transmitters, instructions were given to four field projects to measure the angle through which audible transmitter signals could be detected at increasing 50 m intervals from the focal animal while it remained stationary (typically while resting, foraging, or in an acclimatization enclosure). Participants were asked to conduct this signal test under three conditions where possible: (1) at similar elevations to those of the focal animal; (2) from downhill positions; and (3) from uphill positions. Data were recorded for 13 different implanted animals until the point at which each signal became undetectable. Each person conducting the tests was asked to have their earphones plugged in with maximum gain to increase signal detectability. All tests were conducted in clear weather. Each 50 m interval, as well as the elevation of subject animals and of the person conducting the test were measured by hand held GPS units (Garmin CSX).

For each 50 m testing interval all differences in elevation between the animal and the receiver were pooled and categorized, with values ≥300 m forming one group due to diminishing sample sizes. Two independent groups for comparison were then created to test the following three hypotheses: (1) either side of the median elevation differential: when values were split down the middle would either group produce significantly better signal range compared to the other? (2) either side of the mean elevation differential: would a more pronounced division of samples which isolated the largest differences in elevation produce a significant difference in audible signal range? (3) positive vs. negative positions: does being either uphill or downhill from the animal result in better signal range? Non-parametric Mann Whitney *U* analysis was conducted on each of these three comparative groups due to non-normal data distribution. A simple linear regression was also conducted across the entire sample to predict the effect of increasing distance on audible signal range. Statistical analyses were conducted in IBM SPSS Statistics 23.

Distance Testing Site Descriptions

Distance testing data were collated from four ape reintroduction projects; two with Bornean orangutans *Pongo pygmaeus* (Tabin Wildlife Reserve, Sabah, Malaysia & Bukit Batikap Protection Forest, Central Kalimantan, Indonesia) one with Sumatran orangutans *Pongo abelii* (Jantho Pine Forest Nature Reserve, Aceh, Indonesia) and one with Javan gibbons *Hylobates moloch* (Gunung Tilu Nature Reserve). Each is an undulating, hilly rainforest at low elevation <500 m asl, except for Gunung Tilu which is montane forest at 1,300–1,800 m.

Ethics Statement

Procedures in Malaysia, Indonesia, Gabon and the Congo were carried out according to the requirements of national animal welfare and animal use legislation by registered and qualified veterinarians in registered institutions, IUCN Guidelines for Reintroductions and Other Conservation Translocations. No additional permits were required.

The main issue is that in most of the countries we work, there are no specific national animal welfare and animal use legislation beyond the permit to work on the animals and this is covered by the stringent permits of the registered institutions [Indonesia, Gabon, Congo] or government institutions [Malaysia].

TABLE 1 | Biodata of implanted apes per species.

Species name	Surgeries			Age @ first implantation (yrs)				Bodyweight at implantation (kg)		Date range	Project locations
	#	% ♂	% ♀	N	Mean	SD	Range	N	Range		
Pongo pygmaeus	206	37.9	62.1	173	13.3	5.1	5–25	161	11–91	2009 - ongoing	Sabah, Malaysia; Kalimantan, Indonesia
Pongo abelii	80	51.2	48.8	75	9.1	4.1	5–22	70	11.5–62	2010 - ongoing	Sumatra, Indonesia
Gorilla gorilla gorilla	3	33.3	66.6	3	17	9.8	6–25	3	50–170	2013–14	Gabon; Republic of the Congo
Hylobates moloch	2	50	50	2	14.5	2.5	12–17	2	5.2–6	2015	West Java, Indonesia

% ♂, percentage of males implanted; % ♀, percentage of females implanted; SD, standard deviation from the mean.

RESULTS

Device Outcome Table Results

Response Rate and Species Represented

A total of 11 different ape release projects were identified by the first author as having adopted IRT. We received nine fully completed questionnaires representing the views of all but one of the groups that have historically employed IRT; one organization ran multiple projects. The device outcome tables were returned by respective projects in varying degrees of completion. Two species of orangutan (*Pongo pygmaeus* and *Pongo abelii*); western lowland gorilla (*Gorilla gorilla gorilla*), and the Javan gibbon (*Hylobates moloch*) are represented in our dataset, and, at the time of writing, remain the only species of primates in which IRT has been investigated in a field setting.

Biodata and Uptake

Since their initial development in 2009 until March 2017, a minimum total of 291 surgeries have resulted in transmitters being implanted into 256 individual apes. The variation in weight of focal animals ranged from 5.2 to 170 kg. For the lightest ape implanted in our dataset, the larger implant therefore represents 0.33% of the animal's total body weight. Additional biodata of implanted animals are presented in **Table 1**.

Implantation Surgeries and Healing

From the data available detailing surgical implantation procedures ($n = 155$), as measured from the first incision to closing of the wound, over three quarters (78%) were completed under 45 min with a mean of 26 ± 8.4 min. The median duration across the entire group was 30 min, with a range of 5–88. Post-surgical healing durations ($n = 169$), as measured in days until the wound was deemed entirely healed by project veterinarians, had a wide documented range of 3–127 days, but a relatively low median value of 15 days, within which more than half of animals (57.4%) had fully healed by primary intention after initial stitching. In a small number of cases practitioners reported wounds opening in the days and weeks after surgery. This process was in some cases caused or exacerbated by a few anecdotal reports of persistent interference with wounds and stitches by orangutans, especially so by more feral individuals that had spent less time in rehabilitation facilities. In these cases where the wound edges were no longer held together, wounds were re-sutured or left to heal by secondary intention i.e., granulation tissue matrix filling the wound defect, therefore rendering them more susceptible to complications (infections, seroma) in the healing process.

There were an additional 26 surgeries where implants were removed and immediately replaced with new devices during the same procedure. Predictably, the surgical times ($n = 9$; median = 45; range: 30–120) and healing durations ($n = 14$; median = 32; range: 7–45) typically lasted longer compared with the implantation procedures above, due to the additional work involved during surgery and increased trauma to the soft tissue around the implantation site, respectively.

Implant Removals

Transmitters were removed from focal animals on 36 separate occasions. Details of the seven most complex clinical cases, as reported by the respective project leaders and veterinarians, are presented in **Table 2**. Additionally, seven implants prematurely failed and were found with cracks in their ceramic casing at the time of removal. Implant developers identified that there had been a faulty batch of devices produced with some hairline fractures in their ceramic casings, so a further five transmitters were removed and replaced as a precautionary measure.

Implant Status and Confirmed Outcomes

At the time of writing, device life cycle data were available from 210 transmitters. Within that figure, audible signals were detected in the 6 months immediately preceding the latest field update in 21.4% of cases ($n = 45$). Failed devices were confirmed by sightings of the animal without signal being present. The right censoring that we employed, therefore, reflects a high probability that in the majority of cases the remaining outcomes can be considered final, with animals either dispersing, dying, or monitoring effort ceasing beyond a certain point (full results presented below in **Figure 2**).

Confirmed implant failures decreased as a proportion of total device outcomes with each successive half year period, as the proportion of censored outcomes correspondingly increased. This is most likely due to the majority of animals being monitored intensively only in their first several months after release, until resources are focused on other, more recently released, apes. We should therefore acknowledge here that the high failure rate reported from year one final outcomes,

TABLE 2 | Implanted transmitter removals.

Species and focal animal biodata	Reason for removal, implant status and additional comments
1) *Pongo pygmaeus* 9yo female	Eight weeks post-surgery the orangutan received multiple bite wounds by a conspecific at implant site while awaiting release. She was retained in clinic for observation and treatment but within 1 week the wound started to dehisce and a fragmented ceramic shard became visible grossly. Implant was fractured with its seal broken. Nine small fragments were retrieved along with the main part of the transponder. The surgical site was grossly contaminated with discharge, necrotic tissue and a dark material believed to be battery contents. There was considerable localized irritant reaction together with secondary infection and tissue necrosis. Another implant was placed 6 months later adjacent to the original surgical site—there was minimal residual fibrosis and surgery was uneventful, healing by first intention within 5 days.
2) *Pongo pygmaeus* 8yo male	After the orangutan had been free roaming in the pre-release forest school, he was brought back to a cage in preparation for release. It was then noticed that the transponder was not transmitting. Efforts were made to reactivate the transponder with several different magnets but with no success. When removing the transponder, it was found that the device had cracked into pieces and within the surgical wound some necrotic tissue was found, possibly due to battery leakage. A replacement was fitted on the same day as the faulty implant was removed, with healing time taking longer than average at 41 days.
3) *Pongo pygmaeus* 7yo female	The orangutan removed the surgical stiches and the surgical wound had to be re-sutured 2 weeks after the initial procedure. Sutures were again pulled out by the animal. The wound could not heal by first intention healing and it was infected, so it was decided to remove the implant almost 4 weeks later to allow the wound to heal by second intention. The implant was not replaced.
4) *Pongo pygmaeus* 5yo male	This was a wild young orangutan therefore it was difficult to check his wound after the 49-min implantation surgery. Six days after surgery an infection was spotted so the orangutan was sedated to clean the wound and remove the implant. During the procedure, the orangutan had a cardio-respiratory arrest and died.
5) *Pongo pygmaeus* 8yo male	Months after successful implantation, the orangutan was seen falling out of a tree. Two days later a heavy branch fell across its shoulders, after which the device became inactive. A small crack in the ceramic casing was visible before it splintered completely under the pressure of pincers during removal. The implant was replaced 14 months later.
6) *Pongo abelii* 6yo male	Orangutan was engaged in some rough and tumble play with a conspecific less than 1 month after the device was fitted when the transmitter stopped functioning. Upon removal, the implant was found to have fractured into several different pieces and there was a severe localized reaction and infection at the transmitter site. Device was not replaced.
7) *Pongo abelii* 9yo male	Animal was very active during recovery, banging its neck and back against the cage such that the wound required re-stitching four times. The skin surrounding the implant site had lacerations and the transmitter protruded about 5 mm. A day later the station manager found parts of the fragmented transmitter on the cage floor, with the animal playing with and sucking other fragments. We suspect the OU took the transmitter from the lacerated skin and bit it. Two fragments of transmitter casing were found but some other parts (including the battery) were not located. The wound was opened and cleaned before another implant was placed a day later.

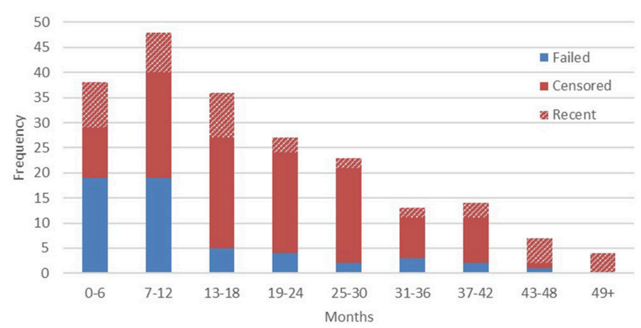

FIGURE 2 | Confirmed vs. censored device outcomes per 6 month interval.

when regular monitoring is more common, would indicate that additional transmitter failures likely go undetected among the censored population, especially given the wide ranging habits of exploratory orangutans. Conversely, our data demonstrate that in a small number of cases (11.9%, $n = 25$) implants also function beyond the end of their expected device lifetime (33.6 months on a typical 8 h transmission schedule), so similarly long transmissions may also go undetected. To date, the longest reported transmission was recorded 57 months after implantation. The animals represented in years four and five post-release are likely individuals who have settled within relatively stable home ranges close to the research base, thus enabling regular signal detection within the typical range of IRT.

Questionnaire Responses

Reliance on IRT

Practitioners were asked "*how many days per month do you sight each released individual?*" The most common response given was 0–3 days per month ($n = 5$), representing 56% of respondents. When asked to highlight the factors responsible for limiting direct observational data collection, the two most common responses given (both $n = 7$) were "*topography of release site*" and "*limited maximum distance and range transmission of implants.*" When asked if they felt able to record behavioral data at the same intensity without implants eight out of nine respondents answered "no".

Managing Faulty/Failed Implants

When asked if they would be concerned with leaving a faulty device within the body of an animal, 56% of questionnaire respondents answered yes. Of these responses, 80% stated explicitly the potential for faulty implants to cause injury to the host animal (i.e., battery leaks and splinters because of cracked casings, potential to migrate within the host organism). In cases where transmitters are known to have failed prematurely, respondents were also asked if they would consider retrieving and replacing them if the animal had already been wild released.

Just over half of respondents (56%) said they would attempt to retrieve the faulty implants, with the single most common reason cited being *"signs of damage to the implant,"* although it was also noted by multiple respondents that this would be contingent on their ability to relocate and recapture these animals. For those that said they would not retrieve faulty implants, the most common reason cited was concern about clinical/surgical risks (e.g., anesthesia/darting etc.).

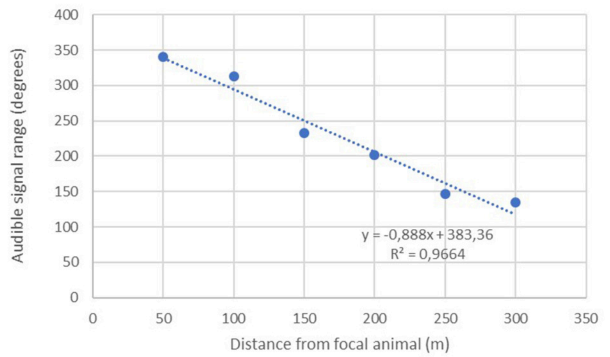

FIGURE 3 | Mean audible signal range measured at increasing 50 m intervals away from focal animals.

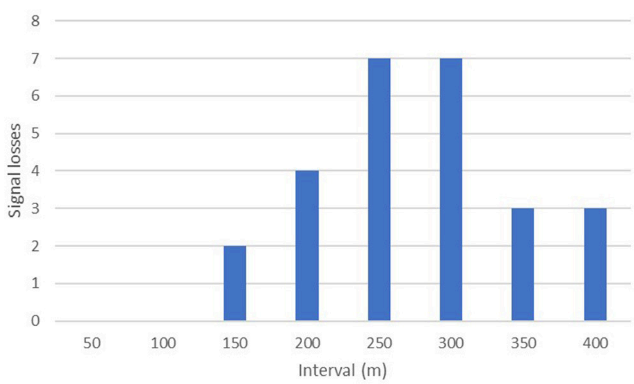

FIGURE 4 | Signal drop outs plotted at their final distance testing interval.

IRT Reuse and Practitioner Perceptions

One hundred percent of questionnaire respondents said they would use IRT again. Respondents were also asked to describe their general thoughts on IRT, the biggest issues they have faced when using this technology in the field, and how they would like to see the implants developed in the future. Results are presented in **Appendix A1**.

Distance and Range Testing of Subcutaneous Implants

A linear regression was conducted to assess the extent to which increasing distance predicted the remaining audible signal range of the implanted transmitters ($n = 26$). Results show a significant inverse relationship with audible range typically decreasing by about 44.39 degrees with each additional 50 m interval traveled away from the focal animal (**Figure 3**).

The maximum distance testing interval reached during our formal tests was 400 m; a figure obtained by just three separate implants. However, anecdotal reports from several projects suggest much greater distances can be obtained in special circumstances i.e., when there is little landmass between focal animal and the receiver. Seventy-seven percent (40/52) of our tests up until the 100 m distance interval yielded audible signal ranges in all directions throughout 360°. No signals were lost across the entire sample until we moved past the 150-m interval, with the majority of signal drop outs (14/26) occurring between 250 and 350 m (**Figure 4**).

When the sample was divided by the median value for each interval into two independent groups consisting of <median ($n = 67$, mean rank = 72.19) and ≥median ($n = 77$, mean rank = 72.77) no significant differences were found: $u = 2558.500$, $z = -0.086$, $p = 0.931$. Similarly, the more pronounced division of samples either side of the mean value for each interval (<mean: $n = 92$, mean rank = 74.92; and ≥mean: $n = 52$, mean rank = 68.21) resulted in no difference: $u = 2169.000$, $z = -0.950$, $p = 0.342$. However, when the test was applied to evaluate whether positive values i.e., being uphill from the focal animal ($n = 96$, mean rank = 77.50) would yield stronger signals compared with negative values (**Table 3**) i.e., being downhill from the focal animal ($n = 48$, mean rank = 62.50) we found a significant difference across the entire sample: $u = 1824.000$, $z = -2.084$, p

TABLE 3 | Uphill vs. downhill range and signal loss characteristics relative to the position of the focal ape, per distance testing interval.

	Level/uphill receiving position					Downhill receiving position				
	N	**Mean signal range and SD**	**Elevation differential**	**Drop outs**	**Drop out differential**	***N***	**Mean signal range and SD**	**Elevation differential**	**Drop outs**	**Drop out differential**
50 m	20	335.4 ± 77.2	7.5	0	–	6	354.8 ± 9	−11.7	0	–
100 m	19	312.7 ± 100.8	10.6	0	–	7	311.9 ± 89.2	−23.9	0	–
150 m	17	263.4 ± 105.3	17.1	2	21.5	9	175.1 ± 99.9	−24.0	0	–
200 m	15	214.9 ± 123.5	23.2	3	40.7	9	178.4 ± 94.1	−28.0	1	−55.0
250 m	11	136.8 ± 85.9	24.6	2	37.0	9	157.8 ± 41.7	−28.2	5	−24.4
300 m+	14	141.6 ± 117.4	22.6	9	23.6	8	123.8 ± 81.6	−26.3	4	−38.8

= 0.037. Our tests show that signals are therefore stronger when the receiver is uphill from the focal animal.

DISCUSSION

General Implications of IRT

The use of IRT, particularly with orangutans, has been transformational as prior to its development, post-release monitoring entirely depended on enough animals remaining within a given release site for long enough to enable reintroduction outcomes to be known (29–31). Researchers had no methods available to improve individual location in the field and there was virtually no information on reintroduction outcomes as a result (16). Over the coming years we can expect that the true value of IRT will be shown through greater data collection and the dissemination of post release outcomes that should guide reintroduction practitioners in adopting more successful release strategies. By facilitating focal follows, IRT has also enabled interventions that have saved the lives of struggling animals thus improving welfare for those individuals greatly. When functioning correctly, the long device lifespan of almost 3 years negates the need for disruptive re-captures of gradually adjusting rehabilitants to replace batteries, re-adjust attachments, or to retrieve transmitters, as seen among other species (32–34).

Having an implant, however, is just one factor involved in locating apes after their release. Release site location and its topography, monitoring effort and the ratio of research assistants to animals released, the number of animals awaiting release, and project financing all dictate the relative difficulty with which released apes can be relocated. Despite the widespread uptake of IRT many animals are still lost or disperse relatively early into their release, as demonstrated in our analysis of device outcomes. Variation in the number of animals released between projects, in particular, means that it is certainly easier for smaller projects to directly observe each animal on a regular basis compared with those conducting large group releases into the hundreds of animals. So, while carrying an implant doesn't necessarily result in the regular observation of *all* animals, this technology has nonetheless greatly advanced the field of ape reintroduction by dramatically increasing the number of animals that theoretically *could* be relocated.

Comparisons With External Application of Radio Telemetry

A common recommendation found in the literature is that a tracking device should aim to be no more than 5% of an animal's bodyweight (35, 36). At around 0.3% of total bodyweight for the smallest ape in our dataset, the size and weight of implanted transmitters most likely result in negligible effects on locomotive patterns, general behavior, and body condition. There may thus be substantial scope for increased use among a wider range of smaller species, including those outside the primate order. Heavier external devices that exert their weight on just one limb are probably more likely to affect an animal's activity patterns, as demonstrated by relatively small differences in radio collar weight interfering in the grazing behavior of zebras (37), and the mortality of migratory caribou (38). While the positional behavior of most species must be carefully considered before a tracking device is employed, therefore, IRT in apes is largely free from this requirement.

Our distance testing protocol present for the first time a method for the systematic testing of radio telemetry applications. At around 250–350 m, the modal maximum distances at which implanted signals are detected in this study are broadly similar to previous telemetry incarnations for locating galagos *Galago alleni* (19). Anecdotal reports from field teams would suggest that despite the relatively short distances we found during formal testing, signals are also regularly detected from long distance, although typically under rare topographical conditions such as within relatively open basins or across gullies with few central hills or vegetation to block signals. That we found stronger signals from elevated positions relative to the focal animal is consistent with previous research (39), and has important implications for release site choice and design, such as the identification of telemetry "sweet spots" including elevated ridges and trails, as recommended by the IUCN (10).

Aerial signal detection was not possible within this study but would most certainly enable considerably longer detection ranges for VHF-GPS implants (40). Flying unmanned fixed wing drones high above canopy level in grids would enable huge areas of land to be covered and for areas with strongest signals to be identified. This alone would represent a huge advance in post release monitoring by helping projects to more adequately assess the movements of a larger proportion of animals, particularly so for wide ranging species. This may also lead to well performing apes being almost entirely monitored remotely. For now, though, it is important to note that both staff training in good telemetry techniques and employing implant-frequency-specific antennas are essential when working with such low-output VHF transmitters.

To date, the requirement for sub-cutaneous implantation has severely constrained device functionality by limiting the maximum size of transmitters and their components. These are low output VHF capable devices, without store on-board data logging, accelerometers, GPS receivers, RFID sensing, satellite data retrieval, nor remote tracking capabilities. Their functionality thus falls dramatically short of most off-the-shelf collars produced by established wildlife telemetry companies that typically allow end users to either remotely track animal movements through two-way satellite communication, or to download stored positional data in the field within a certain range of the focal animal. With several large release programmes unable to directly observe individual animals on a regular basis due to a lack of resources or changing research priorities, there is a clear need to incorporate more sophisticated data logging and remote monitoring methods, as highlighted by end users in our survey. There is hope that the International Cooperation for Animal Research using Space (ICARUS; https://icarusinitiative.org) may provide the necessary data-download technology for similar small GPS implants in the near future (41). Spatial analysis provided by GPS capable devices would also provide improved mortality data, as currently IRT can only facilitate the homing of animals that stay within the relatively short range of its VHF transmitters.

IRT Faults and Risks

Perhaps the greatest drawback of IRT is that animals must undergo anesthesia and surgery to place the device along with a post-operative recovery period to monitor wound healing. Several cases of self-inflicted trauma to surgical wounds, especially by wild translocated orangutans and otherwise more feral individuals resisting treatment may explain the wide variation in healing between some individuals. Other confounding factors, including surgical technique, suture materials used, and post-operative veterinary care provided may also explain the wide variation we present in healing times. During the initial years of these implantation efforts regular training workshops were carried out to guarantee standardized best-practice surgical techniques during implantation. Over the years trained veterinarians left projects, were promoted or otherwise lost to performing surgeries, such that surgical techniques diverged from the original standards and may have suffered in consequence. The reality of rehabilitation center working schedules and practices may also result in limited veterinary continuity, no guarantee of expert tuition or prior experience, and several different vets being required to carry out the procedure. It is important, however, to note that, although slightly different in application, intra-abdominal VHF implantation surgeries have also led to documented problems, including hemorrhage and infection among relocated river otters (42), and the rejection of a subcutaneous implant in a harbor seal almost a year after surgery (43).

Apart from a few documented cases where direct damage (e.g., bites, repeated self-inflicted blunt trauma, and heavy bumps or branch falls) was directly witnessed by project staff, most causes of faults are yet to be identified. Compounding the difficulty of diagnosing prematurely failed implants is the fact that relocating and capturing the animal in question, as well as removing the damaged implant can be a highly disruptive undertaking, especially considering the sensitivity of many rehabilitated apes to the adaptive process of reintroduction (16), and the inherent risks associated with even simple surgeries i.e., darting, anesthesia, and infection. The death of one orangutan during an implant removal surgery, while only an indirect result of IRT and its methodology, nonetheless supports this view. It must also be noted that an unknown number of devices may have failed and not be known to have failed within the large censored population reported here. These device failures may result in host animals never being relocated, while having to carry cracked implants for the rest of their natural life. The relative newness of this technology means that the true impact of leaving faulty implants within long-lived animals may never be known, so project leaders must decide if the risks presented here are balanced by the potential benefits of long-term post-release detection.

During the course of everyday orangutan locomotion and activity it is difficult to envisage a scenario where direct pressure is sufficiently exerted on the back of an individual's neck to result in a cracked casing. However, it may be that damage is caused, and certainly worsened, when animals are sleeping on their backs in nests, or when using their necks as a fulcrum for doing roly-polys, an occasional form of terrestrial locomotion used by some animals. The 18.1% total device failure rate within 1 year of activation reported here, while high, is nonetheless considerably lower than implanted equipment failures reported in Brown bears (44), although this is likely due to the considerably more complex procedure required to implant both the transmitter and an external antenna. Similarly, evidence from the deployment of new and emerging satellite technologies in a range of large mammals (45) suggests that researchers should keep in mind the very high risk of equipment failure; the same can be said, albeit to a lesser extent, for IRT.

While it is a key strength of IRT that all components are housed within one small unit, the cracked casings present in our study suggest an urgent need to investigate adaptations to make the implant housing more secure and inert. This was partly addressed several years ago when implant developers changed casing thickness from 0.8 to 12 mm after discovery of the first faulty batch of implants found with hairline cracks. Since that time, however, cracks have consistently been found in removed implants, so if casings cannot be made to survive intact within the body of an ape for 40–50 years without dramatically reducing signal transmission, then a new implant design must be considered to remove all risk of injury to focal animals. Assuming an animal is adequately monitored and survives until the end of an expected device lifespan, if it is then dying several years later, potentially with dependent offspring, due to unknown or as yet undocumented deleterious effects of its implant, this loss is magnified within the longer-term context of any reintroduction project. Minimizing the risk of anything that might jeopardize an individual's long-term survival is therefore vital on both welfare and conservation grounds. We note, however, that risk is by no means unique to the implantation method; all external radio telemetry attachments should be field tested to ensure the absence of deleterious effects (46). The reported death of at least two red howler monkeys from a screwworm larvae infestation that developed under their radio collars (47), and changes to the demographic integrity of newly collared owl monkeys returning to their social groups are evidence of this (13). It's worth also remembering that other damaging effects caused by radio telemetry applications may remain unreported (48).

Conclusion and Recommendations

The importance of being able to regularly relocate reintroduced individuals is highlighted by the fact that both rehabilitated and wild translocated primates are most vulnerable immediately following release (24, 49). Radio telemetry therefore has a vital role to play in improving the long-term survival of individuals released. Implanted radio telemetry is directly responsible for the proliferation of scientific data collection on a widely reintroduced, yet Critically Endangered species, about which so little was previously known. With large sums of money channeled into great ape rehabilitation programmes worldwide, these data are now helping donors and conservationists to identify whether they are getting value in the strategies used, and outcomes produced, through reintroduction. Additionally, the generally positive perception of IRT among its practitioners demonstrates the clear and ongoing need for effective and reliable tracking methods for hard-to-monitor species like the orangutan.

Given the rapid pace of technological development and miniaturization of battery power sources in particular, implanted VHF transmitters may indeed be rendered superfluous within a few years. Notwithstanding, they currently remain the only viable, and robustly tested, option for the monitoring of orangutans. It is universally accepted that the current iteration of the implant must be improved to prevent faults and increase functionality. Most urgently, transmitter casings must be made more secure and shatter-proof. Its risks for some animals, namely splintered ceramics, assumed battery leakage, self-inflicted trauma and stress, and long-term post-operative recovery periods must, however, be balanced with the alternative of releasing animals with no monitoring device. If reintroduction is to serve its primary conservation function of re-establishing viable populations of threatened species, then all data on post-release outcomes and behavior are vital to promote survivorship. IRT is one such tool that has been developed to facilitate data collection. We hope that the results discussed here will lead to the improvement of this and other emerging technologies designed to facilitate the post release monitoring of hard-to-monitor species, not just those within the primate order.

ETHICS STATEMENT

Procedures in Malaysia, Indonesia, Gabon and the Congo were carried out according to the requirements of national animal welfare and animal use legislation by registered and qualified veterinarians in registered institutions, IUCN Guidelines for Reintroductions and Other Conservation Translocations. No additional permits were required.

The main issue is that in most of the countries we work, there are no specific national animal welfare and animal use legislation beyond the permit to work on the animals and this is covered by the stringent permits of the registered institutions [Indonesia, Gabon, Congo] or government institutions [Malaysia].

AUTHOR CONTRIBUTIONS

JR and CW conceived and designed the study. GF, TP, MA, BG, and RS contributed to the conception and design of the study. JR wrote the manuscript and conducted statistical analysis. SH and NH wrote sections of the manuscript. JR, SH, AF, IS, MN, KL, AW, and PP acquired, categorized and provided data for the work. All authors contributed to manuscript revision, read and approved the submitted version.

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APPENDIX

Appendix A1 | Practitioner perceptions of the benefits and limitations of IRT and their recommendations for future development.

Benefits of IRT	***Limitations of IRT***	***Desired improvements/recommendations***
"Couldn't identify that orangutans were adapting well/success rates only possible with this technology—many orangutans have disappeared and been re-found months later in different locations. Needed it for various interventions: provision of supplementary feeding; repatriation for medical treatment; prevention of crop-raiding. I wouldn't want to do reintroduction without telemetry for these latter reasons—early diagnosis of problems, and intervention, only possible for this many OU's with telemetry."	*"Topography and natural obstacles, e.g., dense vegetation, can distort and dampen the signal, leading to the short range of the radio signal and poor signal reception."*	*"The incorporation of GPS/satellite technology would be a big help, so we could record where they had been traveling; and pick up signals from further distances. Would be nice to have positional data sent so can go direct to location to observe."*
"Currently there is no better radio telemetry method for monitoring orangutans, and PRM without the use of radio telemetry has proved very difficult."	*"If a device fails prematurely, it's unclear why it has stopped functioning. Given that a number of the devices have had cracked casings while still inside orangutans that have been released, a prematurely failed device may potentially pose a direct danger to an animal's well-being."*	*"Ideally, if small implants (like now) could transmit GPS signals so one could monitor their whereabouts from outside the forest."*
"Great advance in tracking technology" and "Observers who are monitoring released animals can find and identify individuals more efficiently."	*"Faulty receivers: 1) broken or weak signals from some units; 2) apparent interference between transmitters—the picking up of one signal when a different OU is nearby. Sometimes we are right in front of an orangutan and the receiver does not record their signal; even though the next day with a different receiver unit we pick it up."*	*"More powerful transmissions with a wider VHF signal range in mountain and dense forest."*
"The scheduling capability of IRT means I can modify monitoring protocols and transmission schedules based on available resources and individual progress."	*"Skill and discipline in using the receivers, combined with tedious entangling of the antenna in the rain forest." "Given that the implants are expensive and that a fair number of implants have already become broken or have failed, it is currently neither cost-effective nor time-effective to utilize the chips in all animals."*	*"Is it possible to have stronger signals without interfering with wellbeing/health?"*
"It does make relocating an animal much easier, especially in the first several months post release before ranging habits have stabilized."		*"Implants with increased battery lives and the ability to switch on and off remotely would be very useful, to preserve battery life and change the transmission schedule, according to logistics or the time of year."*
"The devices I implanted sub-cutaneously were a good size and caused no significant surgical problems but, of course, the smaller the better, i.e., easier to implant."		*"Better/more durable casings, longer/more efficient battery life, and greater signal range."*
"It's easy to pass an orangutan that is right under your nose until they have established routines and ranging patterns, and then the result of the re-introduction remains unknown, and possibly the investment of over 5 years of rehab is lost (or at least is difficult to justify)."		*"Ensure that no device will fail."*
		"Smaller size to enable easier implanting with less tissue reaction."

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Less Is Better. Avoiding Redundant Measurements in Studies on Wild Birds in Accordance to the Principles of the 3Rs

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The Principles of the 3Rs apply to animal use in research regardless where the research is conducted. In wildlife research, particularly research on wild birds, 3R implementation lags behind research using laboratory, farm, or pet animals. Raised 3R awareness and more field-adapted techniques and protocols are expected to improve the situation. Unpredictable access to animals entices the wildlife researcher to make the most of each caught animal, leading to potential over-use, and violation of the 3Rs. In this study, I statistically screened an existing set of Bean Goose biometric data for the presence of redundant measurements. The results show that it was possible to distinguish between the *fabalis* and *rossicus* subspecies (the original aim of the measurements) with fewer measurements (2 vs. 17). Avoidance of the redundant measurements was estimated to reduce both handling time and welfare impact with c. 80%. A robust scheme, supported by an R-script, is presented for continuously weeding out redundant measurements. This scheme is potentially applicable for measurement protocols in any wildlife study, and thus, contributes to the implementation of the principals of the 3Rs in wildlife research in general.

Keywords: principle of the 3Rs, redundant measurements, anser fabalis, R script, welfare, bird studies

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INTRODUCTION

Unlike in research using laboratory and farm/domestic animals, access to animals in wildlife research is often highly unpredictable. No matter how skillful and well-informed the staff is, it takes favorable circumstances and a stroke of good luck to e.g., dart a moose or catch a migrant bird. Once the animal is finally available, the researcher is tempted to make utmost use of the occasion, and thus, measure and sample "as much as possible." When challenged, the use of the individual animal beyond the core purpose of the study could easily be motivated with e.g., data sharing and bio-banking in an *a posteriori* manner. How does such opportunistic sampling behavior match the legal and moral requirements of the use of animals in research?

The Principles of the 3Rs are at the core of modern regulations of the use of animals in research and education (1–3). Originally formulated by Russell and Burch (4), the Principles of the 3Rs ("the 3Rs") prescribe a continuous process aiming to *Replace* live animals with other study systems (e.g., cell cultures or computer models), to *Reduce* the numbers of animals used without jeopardizing the quality of the research and, finally, *Refine* the conditions for the individual animals truly needed for the experiment. The 3Rs apply independently from legal definitions of "animals used in experiments and teaching" and thus, the requirements for approval by an Ethical Committee on Animal Experiments ("ECAE"). In addition to positive effects on animal welfare, the implementation of the 3Rs is known to improve research quality through better planning and the development of novel methods and practices [e.g., (5)].

The 3Rs are now firmly rooted and routinely implemented in laboratory research (6, 7). Also in research based on the use of farm and domestic animals, the 3Rs are rapidly gaining momentum (8). In both fields, a predictable research environment facilitates a strict application of methods and protocols, high-quality care taking and housing, and properly organized and educated staff. The main body of the EU and Swedish national regulations for animals used in research were developed for these research environments, but they also apply to wildlife research (2, 9). In their review of the implementation of the 3Rs in wildlife research, (10) sorted out the challenges and possibilities for bringing wildlife research in par with practices in the laboratory and the farm. They concluded that raised 3R-awareness and field-adapted methods and protocols were important factors for successful implementation.

In most wildlife research, the animals are the object of study rather than a means to study other phenomena (e.g., toxicity or medical treatment). For this reason, the wildlife researcher has an inherently genuine interest in the well-being and functioning of the included individuals. How well this interest is materialized depends on the species-specific veterinary knowledge and skills of the research team, as well as the organization and the toolbox of the operation. In ornithology, unpaid volunteers and amateur researchers do most of the fieldwork (11–13), and their competence in the field of animal welfare, the 3Rs and research planning is often insufficient.

The numbers of wild birds subjected to scientific experimentation are unknown. For e.g., Sweden, which has a special definition of animals used in scientific experimentation (14), the official statistics for animals used in research (15) do not separate numbers for different research environments. Together with colleagues, I have estimated the number of wild birds used in research in Sweden to be c. 10,000 annually. To this number, c. 300,000 birds subject to "normal" ringing should be added (16). Bird ringing does not require ECAE approval in Sweden and most other countries.

Bird ringing not only involves catching and putting a metal ring around the leg of a bird, but also collecting data on weight, wing length, molt patterns, fat scores, etc. These all add to the overall time the bird is held captive and the level of human-induced stress the individual bird is exposed to. Handling times and levels of invasiveness are assumed to be valid proxies for negative impacts on welfare and fitness [e.g., (17–19)]. Consequently, a reduction of handling time and/or avoidance of particularly invasive treatments would improve the well-being of the wild birds used in research. From a 3R point of view, the fringe benefit of each additional measurement or treatment must be shown to out-weigh the negative effects.

Large avian herbivores (e.g., swans, geese, and cranes) wintering in the agricultural landscapes of temperate Eurasia and

TABLE 1 | Origin of the sampled individual.

Subspecies	Finland	Germany	Norway	Sweden	Sum
Fabalis	1	15	1	63	80
rossicus	–	118	38	26	182
Sum	1	133	39	89	262

TABLE 2 | Full and abbreviated variable names and a short description of their biological meaning.

Variable	Abbreviated	Description
Culmen	A	Distance from tip of bill to forehead
Lower mandible	B	Length of the lower mandible
Bill tip to nostril	C	Distance between the tip of the bill and the nostril
Bill plus head	D	Length of bill and head
Head length	E	Length of head from the base of the bill
Head width	F	Width of head across the "cheeks"
Nail length	G	Length of the nail on the bill
Nail width	H	Width of the nail on the bill
Bill height	I	Height of the bill at its base
Bill height nail	J	Height of the bill right behind the nail
Bill height nostril	K	Height of the bill right in front of the nostril
Bill width	L	Width of the bill at its base
Height lower mandible	M	Maximum height of the lower mandible
Tail	N	Length of tail
Tarsus	O	Length of the tail
Toe nail	P	Length of the tarsus
Teeth	Q	Number of teeth in the upper mandible (one side)

TABLE 3 | Basic statistics.

Variable	Min	Max	Range	Mean	SD	Median
Culmen	45.2	67.2	22.0	57.5	4.4	57.7
Lower mandible	42.9	65.9	23.0	55.3	3.6	55.9
Bill tip to nostril	25.1	39.1	14.0	30.5	2.0	30.6
Bill plus head	96.0	129.0	33.0	115.4	6.4	116.0
Head length	57.8	72.8	15.0	65.5	2.8	65.4
Head width	26.7	43.5	16.8	38.0	2.1	38.2
Nail length	12.5	21.3	8.8	16.1	1.3	16.1
Nail width	10.0	16.3	6.3	13.7	0.9	13.8
Bill height	27.0	35.4	8.4	30.8	1.6	30.9
Bill height nail	9.5	15.0	5.5	12.2	1.0	12.2
Bill height nostril	14.0	21.7	7.7	18.0	1.5	18.1
Bill width	20.2	29.8	9.6	26.6	1.3	26.7
Height lower mandible	6.6	10.4	3.8	8.7	0.9	8.7
Tail	90.0	152.5	62.5	123.3	11.3	124.8
Tarsus	60.4	89.1	28.7	77.1	4.9	77.1
Toe nail	64.9	104.0	39.1	86.2	6.9	86.6
Teeth (N)	20	30	10	23.7	–	23.0

All measurements in mm except the number of "Teeth" on the upper mandible (integer). N = 262 for all variables. Min = minimum value, Max = maximum value, Range = Max – Min, SD = standard deviation.

North America have increased dramatically in numbers over the last decades (20, 21). The Bean Goose *Anser fabalis* is one of the few exceptions to this general trend, with a stable population at best (21, 22). The Bean Goose has a complex and long-debated population structure (23–28) and several subspecies and sub-populations are in marked decline (29, 30). Throughout its range, the Bean Goose is subject to both regulated and illegal hunting and, when in conflict with agricultural interests, protective shooting, and scaring (14, 31–33). For successful international management and conservation of all relevant components of the Bean Goose population there is a great need of discrimination criteria and range delineation data (30, 34). Various on-going research projects try to provide this information [e.g., (35–37)]. The data set used in this study was generated as part of this endeavor.

I will explore the presence of redundant measurements in this existing set of Bean Geese biometrics data. The outcomes of the statistical analyses will then be discussed in the light of animal welfare and the implementation of the Principles of the 3Rs. From this, I will conclude on a 3R-adapted strategy for the development of measuring and sampling protocols for research with unpredictable access to wild birds. Because non-academics play an important role in ornithological research, this strategy will be designed to fit even this category of researchers.

MATERIALS AND METHODS

The Dataset

The existing measurement dataset had been collected by Dipl.Biol. Thomas Heinicke, Germany, from live geese during various catching operations in Germany, Finland, Norway and Sweden 2007–2012 (**Table 1**, full data set as **Supplementary Material**). These independent operations each had a full range of relevant permissions, including animal research ethics approval. The core aim of the data collection was the discrimination between Taiga and Tundra Bean Geese (*Anser fabalis fabalis* and *A. f. rossicus,* respectively). Based on the expert knowledge of Mr. Heinicke, the geese were classified as either *fabalis* or *rossicus* from a combination of body structure (habitus), location, and season. The measurements were intended to be descriptive at first, but decisive when used in future goose studies (38, 39). The measurements were part of protocols that, depending on the catching operation at hand, also included e.g., weighing, aging, sexing, marking, and DNA sampling. For the sake of this study, the measurement data were taken "as are" and

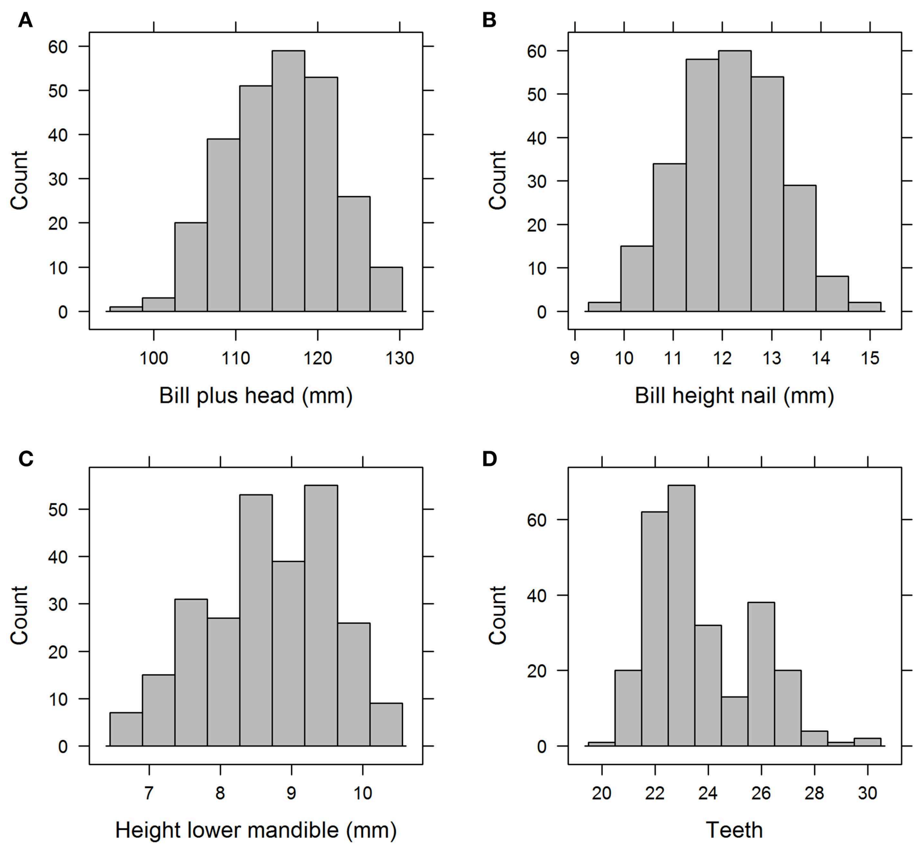

FIGURE 1 | Histograms of a selection of the 17 variables, "Bill plus head" **(A)** and "Bill height nail" **(B)** with unimodal distribution vs "Height lower mandible" **(C)** and "Teeth" **(D)** with bimodal distribution.

without scrutiny of measuring technique and instrumental error. In addition, the subspecies classifications (182 *rossicus* and 80 *fabalis*) were taken as ground truth. All measurements were made with a mechanical caliper to the nearest 0.1 mm, except the tail length, which was measured with a ruler to the nearest multiple of 0.5 mm [c.f. (40)]. Numbers of tomia (further referred to as "Teeth" in accordance to common vocabulary among field-ornithologists), were determined by visual inspection.

The dataset contains 17 potentially explanatory variables (**Table 2**) and one response variable (*fabalis* = 1, *rossicus* =0). Variable names are given in brackets in the text. For improved readability, the full variable names were replaced by single letter names (A-Q) in the output of some analyses (e.g., correlation matrix). The creation of new (composite) variables from existing ones (e.g., "Bill shape" = "Bill height" / "Culmen") may seem appealing, but composite variables require special statistical considerations and thus, were largely avoided. The only exception was "Nail shape" = "Nail length" / "Nail width," because the shape of the nail (clypea) on the bill was considered to be a strongly discriminating feature and recorded separately as a categorical variable (and thus unsuitable for most analyses used here). Potentially, this dataset allows for a huge amount of combinations of existing variables, with and without interactions. Because the aim of this study was the reduction of measurements and thus variables, rather than finding the best models, I chose to include only a few variable combinations at the final stages of model selection.

TABLE 4 | AICc scores for all 17 single variable logistic models.

Variable	AICc
Culmen	235.4
Lower mandible	268.1
Bill tip to nostril	324.6
Bill plus head	245.8
Head length	315.7
Head width	324.5
Nail length	274.6
Nail width	295.4
Bill height	325.7
Bill height nail	303.8
Bill height nostril	207.3
Bill width	313.4
Height lower mandible	135.6
Tail	224.9
Tarsus	211.7
Toe nail	189.7
Teeth	19.0

The lower the AICc, the better the model fitted the data.

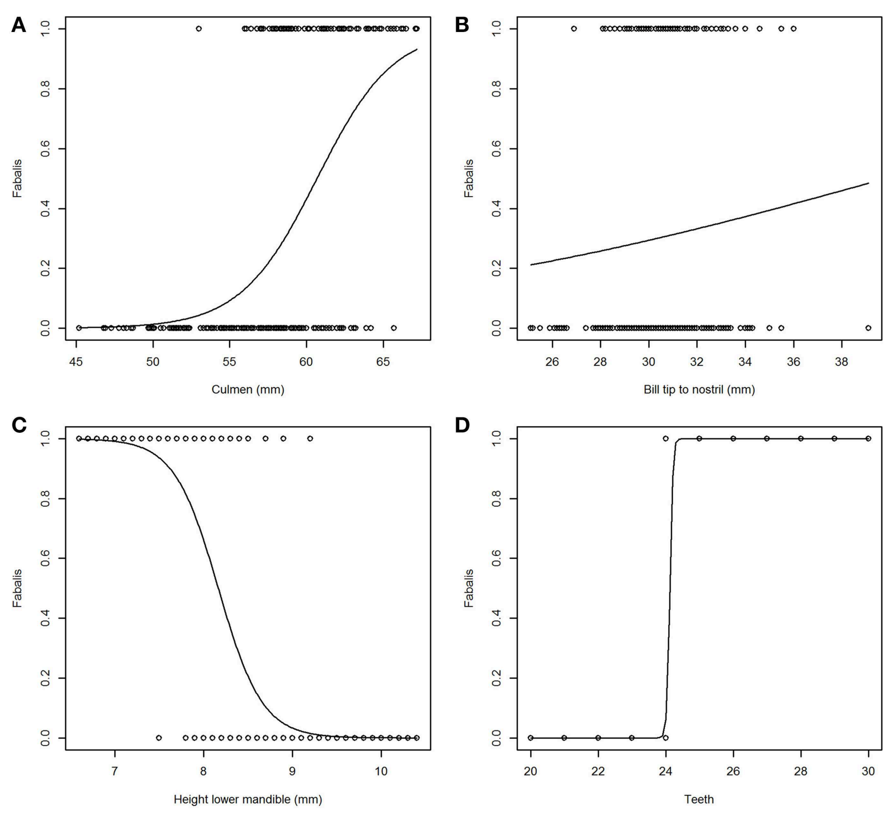

FIGURE 2 | Incidence plots from a selection of logistic models for subspecies (*rossicus* = 0, *fabalis* = 1). Predicted responses go from poor in "Bill tip to nostril" **(B)** to distinct in "Teeth" **(D)**. Variables "Culmen" **(A)** and "Height lower nmandible" **(C)** show intermediate, contra-directional responses.

Statistical Analysis

I screened the full set of potentially explanatory variables for subspecies determination by stepping through a number of statistical analyses on single, pairwise, and multiple variables (R functions in brackets, R script in **Supplementary Material**).

Individual Variables

After listing the basic statistics for individual variables, I visually inspected their frequency distributions ("histogram") and incidence plots of their logistic models for subspecies discrimination ("glm, family = binomial").

Pairwise Variables

First I plotted the observations against all variable pairs ("pairs") and the correlation matrix ("cor" and "corrplot"). To exemplify the effect of the number of measured individuals, I also produced the correlation matrix analysis on a small ($N = 20$) random sub-set of the data. I then used partitioning of the observations on pairs of variables ("kmeans," a simple form of cluster analysis) to visualize how well variable pairs could distinguish the subspecies.

Multiple Variables

I used discriminant analysis ("lda") and AICc-based model selection of the logistic models ("aictab") for multiple variable analyses. In the latter, I also included a selection of composite and multi variable models. Based on the results of the model selection process, I checked the quality of discriminant models for strongly reduced numbers of potentially explanatory variables ($n = 5$ and $n = 2$). Although Principle Component

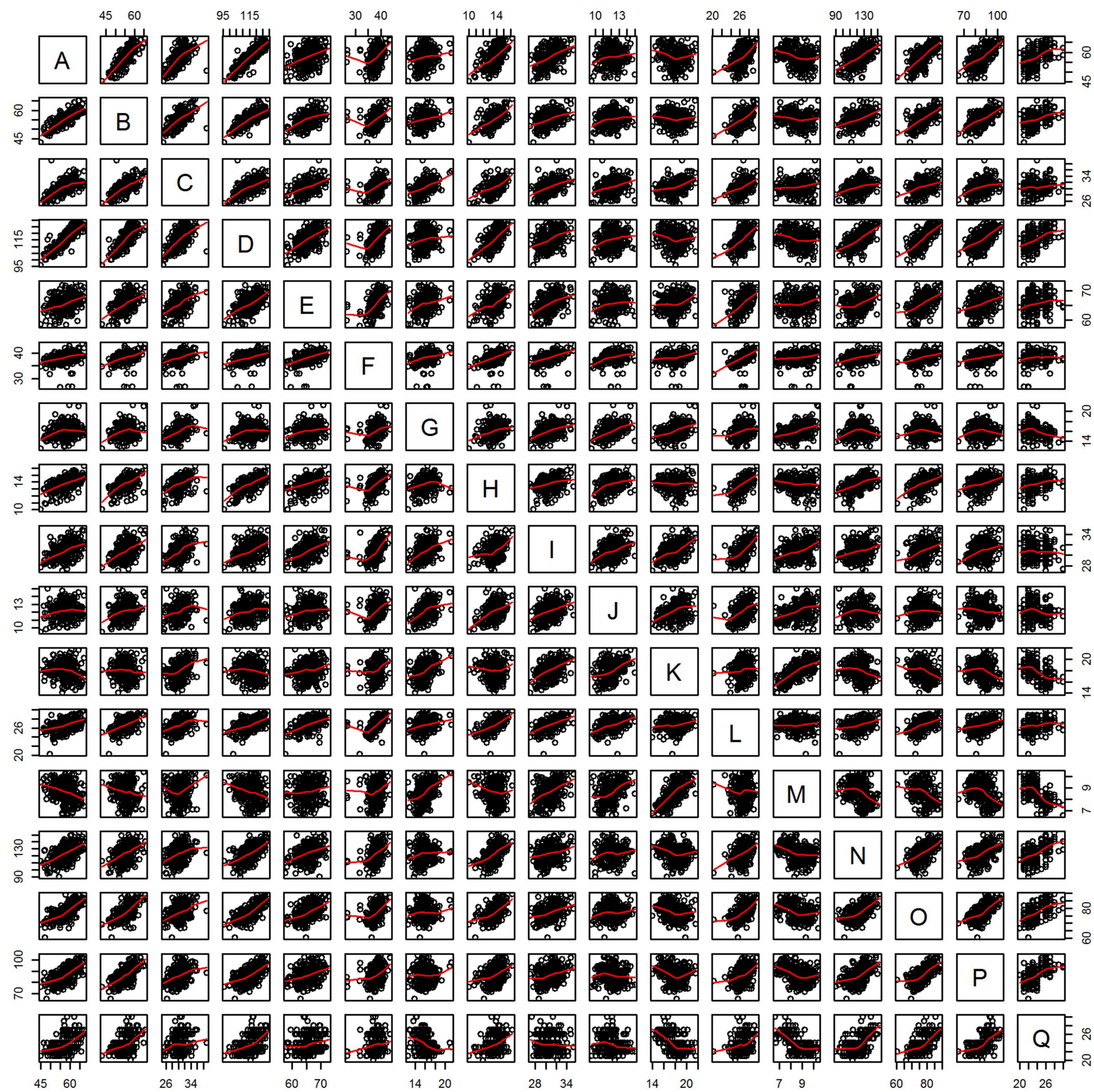

FIGURE 3 | Panel plot of observations against pairs of variables. Trend lines in red. See **Table 2** for variable name acronyms.

Analyses (PCAs) are popular for multivariate analyses and can produce visually appealing output, I chose to avoid PCA because they require pre-treatment of the input variables and their output is difficult to interpret [e.g., (41)]. In addition, PCAs aim to conserve rather than challenge existing variables, and thus, are less suitable for the purpose of this study.

All statistical analyses were made in R 3.4.4 x64 (42), with additional packages AICcmodavg (43), corrplot (44), lattice (45), lme4 (46), MASS (47), and Matrix (48), and supporting packages these depend on.

Animal Welfare

Based on personal experience from participating in most of the catching operations behind the dataset, I took times for taking the various measurements on a mock-up goose. I also estimated the times used for additional procedures of the most extensive protocol (**Table 8**). Times for catching and storage (in bags) were not included, because these vary dramatically with circumstances; many of which are beyond the control of the research team. All estimates assume the team to be well-trained and well-equipped for outdoor conditions. Estimates also assume that a dedicated staff member takes notes and other members take care of the logistics (e.g., photo-documentation and releasing the birds). Consequently, all estimates of handling times are conservative. In addition to handling times, I subjectively scored the level of invasiveness of each procedure on scale 1–10, with 10 being the highest level.

RESULTS

The basic statistics (minimum, maximum, range, mean, standard deviation, and median) of all explanatory variables are presented in **Table 3**. The frequency distribution of a selection of four variables are shown in **Figure 1**. The upper

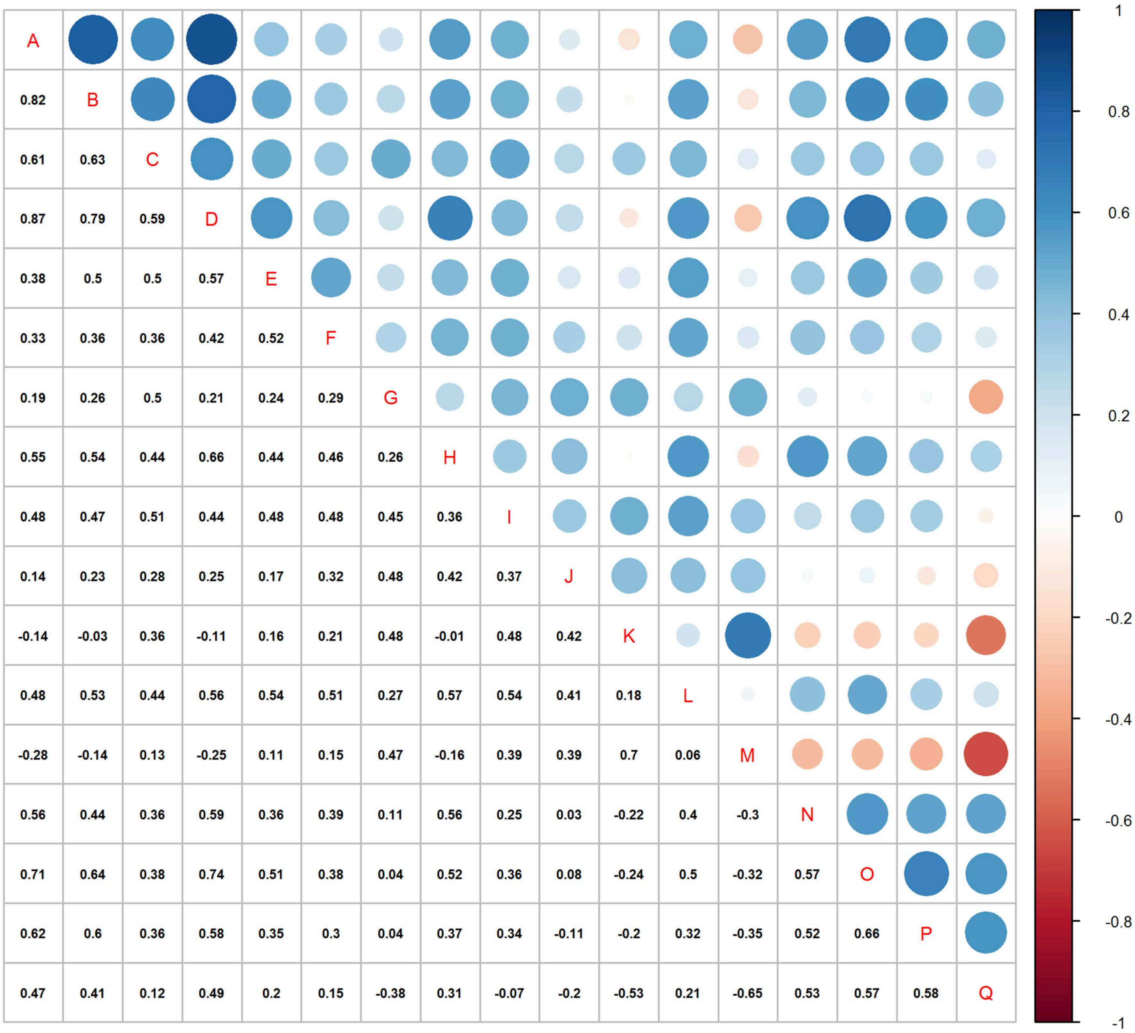

FIGURE 4 | Correlation matrix for all 17 variables in the analyses. See **Table 2** for variable name acronyms.

two histograms ("Bill plus head" and "Bill height") show unimodal distributions indicative of normal distribution across the entire sample. The lower two ("Height lower mandible" and "Teeth") show bimodal distributions indicative of sub-grouping of the individuals based on these characteristics.

Incidence curves for logistic models based on four individual variables are presented in **Figure 2**. **Figure 2A** shows a clear but not abrupt relationship between "Culmen" and subspecies (*fabalis* birds have longer culmen) in contrast to **Figure 2B** with virtually no effect of "Bill tip to nostril" (in *fabalis* and *rossicus* birds the distances are very similar). For "Height lower mandible" (**Figure 2C**), the curve dips fairly steep indicating a firm strong relationship with subspecies (*rossicus* birds have greater height = more pronounced "grin"). The variable "Teeth" (**Figure 2D**) reveals a very strong relationship with subspecies expressed as a sharp break at 24 teeth (*fabalis* birds have more teeth than *rossicus*). The model based on "Teeth" had by far the lowest AICc value (19) and thus, fitted the data best (**Table 4**). The "Height

TABLE 5 | Assignment of individuals to subspecies class by the kmeans models against the ground truth classification.

	Fabalis—ground truth	
A		
Fabalis–model	0	1
0	75	75
1	107	5
B		
Fabalis—model	0	1
0	182	1
1	0	79

A = scores by model based on "Culmen" and "Height lower mandible", B = scores by model based on "Teeth" and "Height lower mandible".

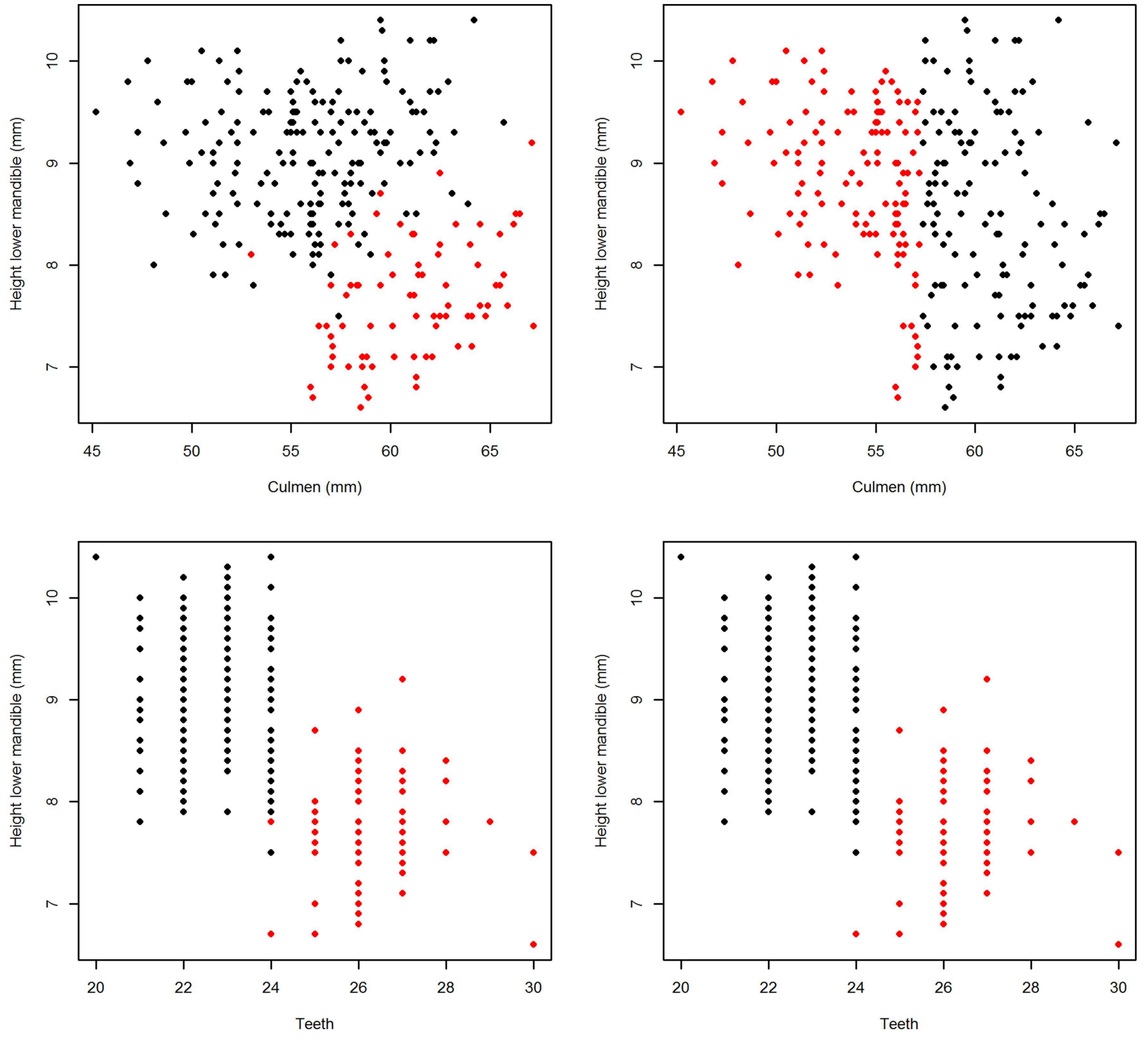

FIGURE 5 | Plots of individual Bean Geese (*fabalis* = red, *rossicus* = black) on pairs of variables. (Left) original subspecies classification (ground truth). (Right) classification by the "kmeans" function.

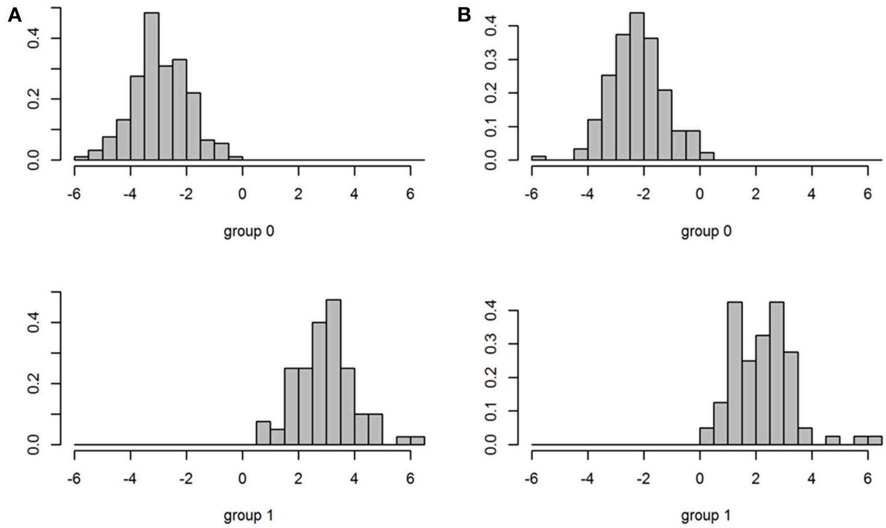

FIGURE 6 | Plots of discrimination between subspecies (Group 0 = *rossicus* and Group 1 = *fabalis*) for models based on all 17 variables **(A)** and only two variables **(B)**.

lower mandible" model came second (AICc = 136) while all other models had AICc > 189.

The Pairs plot (**Figure 3**) shows that observations are either aggregated along a trend line (indicative of correlation) or seemingly randomly dispersed across the plot area (indicative of absence of distinct grouping). In a plot with this many variables, the details of the distribution are not visible, though. For more detailed analysis, separate plots of variable pairs ("plot(x, y)") are suggested (not included here, but described in the R scripts in **Supplementary Material**).

The correlation matrix (**Figure 4**) shows strong correlation between many of the variable pairs (high correlation coefficients and large dots). Most (85%) of the correlations were positive and 3.7% had >0.7 coefficients (8.1% > 0.6).

Two pairs of plots of the results of partitioning are presented here (**Figure 5**). For combination of "Culmen" and "Height lower mandible" the real and modeled distribution of the two subspecies are clearly different (upper panels). For the combination of "Teeth" and "Height lower mandible" the patterns of real and modeled distributions are almost identical (lower panels). The kmeans model based on the first pair of variables assigned only 30.5% of the individuals correctly while the second was accurate in 99.6% of the cases (**Table 5**).

The *fabalis* and *rossicus* subspecies were well separated by the discriminant model based on all variables (**Figure 6A**). The linear discriminant coefficients (LDs) were highest for "Height lower mandible," "Teeth" and "Nail length" (LD1 = −0.76, 0.62, and −0.36, respectively). Twelve (70%) of the variables had coefficients <0.1 and thus, contributed little to the discrimination process (**Table 6**). After removing all LD1 < 0.1 variables, the remaining five variables still separated the subspecies nicely. Even with only "Height lower mandible" and "Teeth" included, the overlap between the subspecies was very small (**Figure 6B**). In the latter model, the coefficients were equally strong, but of opposite sign (−0.88 and 0.88, respectively).

In the formal AICc-based model selection process for the single variable logistic models (**Table 7A**), the "Teeth" variable virtually absorbed the entire AICcweight and thus, left very little credit for the other models. After adding four logistic models based on one composite variable ("Nail shape") and three variable combinations, "Teeth & Height lower mandible" and "Teeth & Nail shape" proved to fit the data better than the "Teeth" variable alone (**Table 7B**). The difference between the top three models and the next was large (ΔAICc > 116).

The original 17 measurements took an estimated 209 s (3.5 min) to perform (**Table 8**). Based on the statistical analyses in this study, the number of measurements could have been reduced to only two ("Height lower mandible" and "Teeth") without significant loss of discriminating power in subspecies identification. This reduction would have brought down the estimated time needed to take the necessary measurements to 37 s, 18% of the original time (**Table 8**).

Across the full protocol of Bean Goose catching, overall time for handling an individual bird was estimated to 647 s (10.8 min). Based on the results of this study and the use of genetic sex markers, the completion of the protocol could be reduced by an estimated 66% (**Table 8**).

DISCUSSION

In this dataset, two variables proved sufficient to distinguish between the two subspecies, the core objective of the data collection. The other 15 variables contributed virtually nothing and thus, should be considered redundant in this context. If these had been omitted from the measurement protocols, the 262 Bean Geese behind this study would have experienced an estimated reduction of 82% in time. Novel research is needed to reliably

TABLE 6 | Linear discriminant coefficients for model based on all 17 **(A)**, five **(B)** and two variables **(C)**.

	LD1
A	
Height_lower_mandible	−0.765
Teeth	0.624
Nail_length	−0.356
Bill_height_nostril	−0.249
Bill_width	0.120
Bill_height	0.098
Bill_height_nail	−0.093
Head_width	−0.086
Lower_mandible	0.067
Head_length	0.064
Toe_nail	0.062
Culmen	0.057
Bill_tip_to_nostril	−0.054
Tail	0.031
Bill_plus_head	−0.023
Nail_width	0.020
Tarsus	0.013
B	
Teeth	0.805
Height_lower_mandible	−0.753
Bill_width	0.303
Bill_height_nostril	−0.239
Nail_length	−0.101
C	
Teeth	0.880
Height_lower_mandible	−0.878

TABLE 7 | AICc-based model selection for the 17 original single variable models **(A)** and the extended variable set **(B)**.

	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
A						
Teeth	2	19.0	0.0	1	1	−7.5
Height lower mandible	2	135.6	116.6	0	1	−65.8
Toe nail	2	189.7	170.7	0	1	−92.8
Bill height nostril	2	207.3	188.3	0	1	−101.6
Tarsus	2	211.7	192.7	0	1	−103.8
Tail	2	224.9	205.9	0	1	−110.4
Culmen	2	235.4	216.4	0	1	−115.7
Bill plus head	2	245.8	226.8	0	1	−120.9
Lower mandible	2	268.1	249.1	0	1	−132.0
Nail length	2	274.6	255.6	0	1	−135.3
Nail width	2	295.4	276.4	0	1	−145.7
Bill height nail	2	303.8	284.8	0	1	−149.9
Bill width	2	313.4	294.4	0	1	−154.7
Head length	2	315.7	296.7	0	1	−155.8
Head width	2	324.5	305.5	0	1	−160.2
Bill tip to nostril	2	324.6	305.6	0	1	−160.3
Bill height	2	325.7	306.7	0	1	−160.8
B						
Teeth & Height lower mandible	3	11.7	0.0	0.89	0.89	−2.8
Teeth & Nail shape	3	16.4	4.7	0.09	0.98	−5.1
Teeth	2	19.0	7.3	0.02	1.00	−7.5
Height lower mandible	2	135.6	123.9	0.00	1.00	−65.8
Nail shape	2	182.4	170.7	0.00	1.00	−89.2
Culmen & Bill height	3	186.7	175.0	0.00	1.00	−90.3
Toe nail	2	189.7	178.0	0.00	1.00	−92.8
Bill height nostril	2	207.3	195.6	0.00	1.00	−101.6
Tarsus	2	211.7	200.0	0.00	1.00	−103.8
Tail	2	224.9	213.2	0.00	1.00	−110.4
Culmen	2	235.4	223.7	0.00	1.00	−115.7
Bill plus head	2	245.8	234.1	0.00	1.00	−120.9
Lower mandible	2	268.1	256.4	0.00	1.00	−132.0
Nail length	2	274.6	262.9	0.00	1.00	−135.3
Nail width	2	295.4	283.8	0.00	1.00	−145.7
Bill height nail	2	303.8	292.1	0.00	1.00	−149.9
Bill width	2	313.4	301.7	0.00	1.00	−154.7
Head length	2	315.7	304.0	0.00	1.00	−155.8
Head width	2	324.5	312.8	0.00	1.00	−160.2
Bill tip to nostril	2	324.6	312.9	0.00	1.00	−160.3
Bill height	2	325.7	314.0	0.00	1.00	−160.8

K = number of model parameters. AICc =, ΔAICc = difference in AICc's between the best and the current model, AICcWt = AICc weight, Cum.Wt = accumulated AICcWt, LL = loglikelihood value.

quantify the welfare impact of reduced measurement protocols, but the invasiveness scores of individual measurements (**Table 8**) suggest that some reductions are likely to have a greater impact than others.

The role for subspecies identification of the number of tomia ("teeth") in the upper mandible and of the maximum height of the lower mandible (referred to as "grin" by field ornithologists) were commonly known before the sampling started [e.g., (49)]. The other variables were either proxies for size (*fabalis* is generally larger than *rossicus*, but so are males relative females) or indicators of complex features, e.g., "elongated bill" in *fabalis* vs. "short and distinct" bill in *rossicus*. Characterizing these shapes would often require the construction of composite variables (e.g., "Culmen"/"Bill height"). Composite variables often have complex error structures and thus, are statistically problematic (41). The perception of "jizz" (an overall, vague appearance/impression often used by birdwatchers) is difficult to frame with a simple set of measurement data. This example shows that the measurements taken failed to do so.

The dominance of "Teeth" and "Height lower mandible" was visible through the full chain of analyses. They were the only ones with a bimodal frequency distribution and showed the steepest curves in the incidence plots of the single variable logistic models (**Figures 1**, **2**, respectively). Obviously, the use of logistic models is inappropriate for response variables with more than two classes. In these cases ANOVA or other classes of models should be used. The other components of the chain of analyses presented here would still be valid for non-binomial response variables.

TABLE 8 | Estimated duration (seconds) for actions in this study and in protocols for Bean Goose catching operations, with potential reductions based on the results of this study.

			Times (seconds)			
					Protocol	
Procedure	**Type**	**Invasive**	**Study**	**Reduced**	**Full**	**Advised**
Startup	Handling	4			30	30
Ringing	Handling	6			60	60
Bill color (% orange)	Visual inspection	1			5	5
Bill shape-color code	Visual inspection	1			8	
Shape of nail (round/oval)	Visual inspection	1			5	5
Shape of the nostril	Visual inspection	1			5	
Bill plus head	Measurement	4	15		15	15
Head length	Measurement	3	12		12	
Head width	Measurement	3	12		12	
Bill width	Measurement	3	10		10	
Culmen	Measurement	3	7		7	
Bill tip to nostril	Measurement	3	8		8	
Nail length	Measurement	3	7		7	
Nail width	Measurement	3	7		7	
Length lower mandible	Measurement	3	10		10	
Bill height	Measurement	3	8		8	
Bill height nostril	Measurement	3	9		9	
Bill height nail	Measurement	3	9		9	
Height lower mandible	Measurement	4	12	12	12	12
Teeth	Count	5	25	25	25	25
Tarsus	Measurement	4	30		30	
Toe nail	Measurement	3	8		8	
Wing length (flat wing)	Measurement	6			25	
Tail	Measurement	5	20		20	
Length bill – sternum	Measurement	6			30	
Total length	Measurement	7			80	
Photos of the head	Handling	2			25	25
Aging	Visual inspection	4			5	5
Sexing	Visual inspection	10			120	
Feather sampling	Sampling	8			20	20
Finishing	Handling	4			20	20
		Total	209	37	647	222
		Percent	100	18	100	34

Invasive = subjective invasiveness score of the procedure.

Due to the high number of potentially explanatory variables, the "pairs" plot was not very informative (**Figure 3**), but a closer look at the plots for single pairs would have revealed more structure in the plots for the truly informative variables than the rest. The correlation matrix (**Figure 4**) showed that many variables were positively correlated. Strong positive correlations are indicative of redundant variables. Many of these correlated variables were associated with the size of the birds. In a PCA or Factor analysis, many of these variables had probably been bundled into a common PCA or Factor. In the light of this study, this would confirm that most of the bundled variables should have been omitted from the protocol. The use of plots and tables from "kmeans" showed that a combination of two variables could distinguish the subspecies adequately (**Figure 5**; **Table 5**).

For this dataset, the discriminant analysis separated the subspecies very well (**Figure 6**). The use of linear discriminant coefficients (**Table 6**) for the selection or omission of variables may be misleading if done in isolation (because the variables interact in the model). Here I used this technique as an integrated part of a screening scheme, which reduced most of the risks of sorting out important variables. With only two remaining variables, the subspecies separation was still good (**Figure 6**). In the final model selection step, the dominance of the "Teeth" variable stood out sharply among single variable models (**Table 7**). The effect of additional models confirmed this dominance and showed the potential of combining variables in model building. In this case, better models were constructed from the same duo of key variables and thus, did not motivate retaining other measurements. In cases when optimal models are important, more supporting variables (and thus more measurements) might be desirable, but the fringe benefit of keeping or introducing more variables needs to outweigh the negative impact on the birds exposed by the treatment.

From a statistical point of view, there are issues that could be brought up, especially if this variable screening strategy needs to be fully applicable to "problematic" datasets (e.g., datasets with diverse data quality levels or highly skewed variables), but this is beyond the scope of this study. My aim has been to demonstrate a simple, yet robust scheme for weeding out redundant variables and thus, omit unnecessary procedures in line with the Principles of the 3Rs. The supplemented R script can be used in this process.

This study was based on a single dataset of Bean Goose biometrics and further studies to demonstrate the potential of 3R implementation by reduced measuring are wanted. The levels of reduction in handling time shown in this example are highly encouraging and indicate significant 3R potential of reduced measurement protocols in wildlife research in general. Novel research is needed to reliably quantify the welfare impact of reduced measurement protocols, but the invasiveness scores of individual measurements (**Table 8**) suggest that some reductions are likely to have a greater impact than others. The search for redundant measurements will also raise 3R awareness in general, pointed out as a strong driver of improved animal welfare by Lindsjö et al. (10).

This study is also a good example of how existing data can be used to gain more knowledge; a case of combined *Replacement* and *Reduction* because no geese, only data, were handled for the purpose of this study. When applied in future studies on geese and other wildlife, the concluding recommendations will also lead to *Refinement*.

Similar schemes could also be developed for the *Reduction* of the numbers of geese and other animals used in wildlife research. Supplementary to the initial power analysis, the explanatory capacity of the collected data could be gradually evaluated and the inclusion of additional individuals halted when desired levels are reached.

RECOMMENDATIONS

I recommend a continuous process of challenging the necessity of measurements taken in wildlife research. Based on clear objectives and good knowledge of the research field, a minimized initial measurement protocol should be chosen. Once the set of measurement data grows (e.g., after each catching event), the dataset should be checked for weak or redundant measurements. Their place in the protocol should then be challenged. Arguments like "You never know how these data can be used in the future!" or "Colleague X may want to have these data." might be tempting to apply, but do no longer fit into the modern world of research using live animals. If these arguments are truly relevant, the related measurements should be included in the initial protocol.

I also recommend that ECAEs, when applicable, demand a step-by-step motivation of each planned measurement and the inclusion of a reduction scheme similar to the one presented here. Finally, I recommend complementary studies on the reduction of potentially redundant measurements in research on other taxonomic groups and in-depth evaluations of how and to what extent reduced measuring actually improves the well-being of animals used in wildlife research.

A summary of this study and the full recommendation to omit several commonly applied measurements will be presented in Goose Bulletin, the official bulletin of the Goose Specialist Group of Wetlands International and IUCN. When implemented by the international goose research community, the proposed measurement reduction strategy could ease the life of hundreds of Bean Geese and thousands of other wild geese caught and handled by researchers annually.

ETHICS STATEMENT

Data had been collected by Dipl.Biol. Thomas Heinicke, Germany, during fully approved goose catching operations arranged by national research groups in Germany, Finland, Norway and Sweden 2007–2012. None of the measurements were taken for the purpose of this study, and the taking of the measurements was not subject to legal requirements of ECAE approval at the time and location of sampling.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fvets.2019.00195/full#supplementary-material

[1] http://www.petralundbergsstiftelse.se/

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Ethical Considerations for Wildlife Reintroductions and Rewilding

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The recovery of many populations of large carnivores and herbivores in major parts of Europe and North America offers ecosystem services and opportunities for sustainable utilization of wildlife. Examples of services are hunting, meat, and skin, along with less invasive utilization such as ecotourism and wildlife spotting. An increasing number of studies also point out the ecosystem function, landscape engineering, and cascading effects of wildlife as values for human existence, biodiversity conservation, and ecosystem resilience. Within this framework, the concept of rewilding has emerged as a means to add to the wilderness through either supplementary release of wildlife species already present or reintroduction of species formerly present in a certain area. The latter involves translocation of species from other geographical areas, releases from captivity, feralization, retro-breeding, or de-domestication of breeds for which the wild ancestor is extinct. While all these initiatives aim to reverse some of the negative human impacts on life on earth, some pose challenges such as conflicts of interest between humans and wildlife in, for example, forestry, agriculture, traffic, or disease dynamics (e.g., zoonosis). There are also welfare aspects when managing wildlife populations with the purpose to serve humans or act as tools in landscape engineering. These welfare aspects are particularly apparent when it comes to releases of animals handled by humans, either from captivity or translocated from other geographical areas. An ethical values clash is that translocation can involve suffering of the actual individual, while also contributing to reintroduction of species and reestablishment of ecological functions. This paper describes wildlife recovery in Europe and North America and elaborates on ethical considerations raised by the use of wildlife for different purposes, in order to find ways forward that are acceptable to both the animals and humans involved. The reintroduction ethics aspects raised are finally formulated in 10 guidelines suggested for management efforts aimed at translocating wildlife or reestablishing wilderness areas.

Keywords: restoration, conservation, reintroduction, rewilding, ecosystem service, ethics, animal welfare

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INTRODUCTION

Human domination on earth has influenced the conditions for life and the long-term existence of all living organisms for thousands of years (1). This has resulted, e.g., in a 58% decline in population abundance of 3,706 species monitored between 1970 and 2012 (2). Large mammalian carnivores and herbivores have been notably negatively affected by human activities (3–7). The consequences of these declines are a trophic downgrading of the planet (8–10). However, there are exceptions to these negative scenarios for large mammals in many areas of Europe and North America. After a long period of decline, which started with the first appearance of our species, *Homo sapiens*, outside Africa (11), mostly as an effect of human hunting (12–14), there has been a dramatic recovery in wildlife in Europe and North America during the past 50 years [e.g., (15–18)]. This recovery is largely a result of protection from hunting, limitations on toxic waste release, changes in land management, and an increase in protected areas/reserves. Translocation of species, as introductions, reintroductions, or supplementary releases, has also contributed.

In Sweden, ungulate populations decreased to a minimum in the mid-nineteenth century since the Swedish king Gustav III decided in 1789 to open hunting rights to all landowners (19); fewer than 100 individuals for red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*), and probably fewer than 1,000 for moose (**Table 1**). Wild boar (*Sus scrofa*) became extinct. Fallow deer (*Dama dama*) may have occurred sporadically on some larger estates in the south of Sweden. Large carnivore numbers also plummeted during the early twentieth century (18). In addition, the Eurasian beaver (*Castor fiber*) became extinct (28) and the European otter (*Lutra lutra*) population came under pressure (29). In 1830, the formation of Swedish Association for Hunting and Wildlife Management (Sw. "*Svenska Jägareförbundet*") was a turning point for the overall conservation of populations of large mammals and birds in Sweden. However, it took almost 100 years before the populations of large ungulates started to make a substantial comeback in Sweden. A combination of careful management and selective hunting, whereby primarily juveniles and younger specimens were shot, and implementation of novel forest management routines resulted in large amounts of suitable forage in the landscape (30) and facilitated the recovery of, first, the moose population, which peaked in the 1980's, and, second, the roe deer population, which peaked in the 1990's. This population development is recognizable in the Swedish game bag statistics, compiled by the Swedish Association for Hunting and Wildlife Management (**Figure 1**). The wild boar was reintroduced [cf. (24)], and populations are still growing, along with red deer populations aided by supplementary release of non-native contingents (cf. (31)). Fallow deer are still expanding in both range and numbers, and during the past 10–20 years, populations of mouflon (wild sheep; *Ovis orientalis*) have started to appear in many places (P. Kjellander, 2007; unpublished results). Another large herbivore comeback worth mentioning is the Eurasian beaver, which numbers around 100,000 today thanks to a successful reintroduction effort that started in 1922 (25).

TABLE 1 | Approximate minimum and current estimates of population numbers of a selection of wildlife species in Sweden.

Species	Year	Number	References
Moose (*Alces alces*)	1840	Few (no estimates available)	(20)
	2016	240,000	(20)
Red deer (*Cervus elaphus*)	1840	<100	(21)
	2016	26,000	(22)
Roe deer (*Capreolus capreolus*)	1840	<100	(23)
	2016	300,000	(20)
Wild boar (*Sus scrofa*)	1976	0	(24)
	2018	350,000	H. Thurfjell, pers. comm.
European beaver (*Castor fiber*)	1922	0	(25)
	1995	>100,000	(26)
Wolf (*Canis lupus*)	1970	0	Swedish EPA
	2018	305	Swedish EPA
Brown bear (*Ursus arctos*)	1930	130	Swedish EPA
	2013	2,800	Swedish EPA
Lynx (*Lynx lynx*)	1920	Few (no estimates available)	Swedish EPA
	2018	1,200	Swedish EPA
Wolverine (*Gulo gulo*)	1960	100	Swedish EPA
	2017	522	Swedish EPA

*In addition to the large ungulates included below, 38,860 fallow deer (Dama dama) are shot on annual basis (**Figure 1**), indicating a population of 126,000 individuals (22), and mouflon (Ovis orientalis) occur locally in south and central Sweden, likely numbered in thousands (cf. P Kjellander, 2007, unpublished data). There is also a local population of 11 wild muskoxen (Ovibos moschatus) in the south part of the Swedish mountains (B. Warensjö, pers. comm.), and sporadically white-tailed deer occur at the northern border to Finland [cf. (27)].*

An important factor influencing the population growth of large ungulates and herbivores during the first half of the twentieth century was the absence of large carnivores. When ungulates (i.e., wild prey) became rare in the nineteenth century, large-scale carnivore predation on livestock became an increasing problem. This led to bounty hunts and organized population control of large carnivores, often with the intention to exterminate (20). The bounty for wolf (*Canis lupus*) ended finally in 1965, and since January 1966, this species has been fully protected (32). By 1965, the wolf had nearly disappeared and was declared extinct in Sweden in 1980 (32). Brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), and wolverine (*Gulo gulo*) populations also fell to a minimum at that time (18). The protection of large carnivores was introduced primarily following

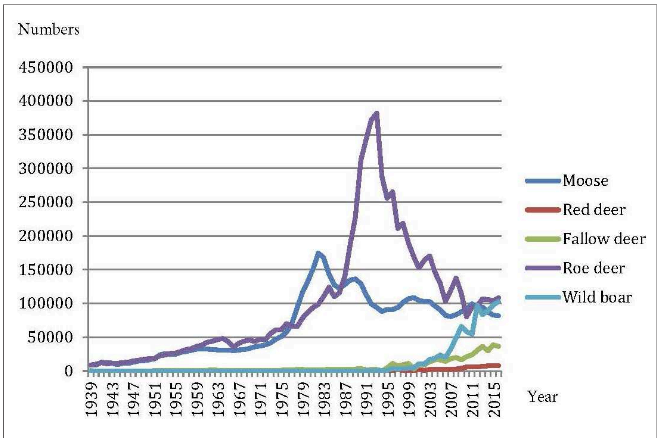

FIGURE 1 | Game bags of ungulates in Sweden from 1939–2016 (The Swedish Association for Hunting and Wildlife Management—Wildlife Monitoring, www.vildata.se; 2018-07-27).

actions from conservation organizations such as the Swedish Society for Nature Conservation (Sw. "*Naturskyddsföreningen*"), which was formed in 1909. By the time large carnivore protection was implemented, the populations of large ungulates to prey upon had recovered, providing an essential foundation for large carnivore population recovery. Thus, although large carnivore protection was not a major concern for hunters in Sweden, the synergetic effects of actions by hunters and conservationists benefited overall wildlife recovery. The recovery of forest-dwelling mammals in Sweden is documented in the Swedish Red List report (33), an interesting contrast to the rapid extinction rate globally (34).

The wildlife recovery in Sweden may be exceptional, which is why we use the Swedish example as a reference scenario in this paper. However, as indicated above, there are reports of similar recovery patterns in other parts of Europe [cf. (16, 35, 36)]. Despite ongoing negative trends for some species or groups of species in Europe, the overall trend in the Palearctic is a 6% increase in monitored vertebrates since 1970 (16). The "*Wildlife Comeback in Europe*" report by Deinet et al. 14 records positive population trends for a number of European species. Several of Europe's large carnivores are increasing in numbers over wide ranges [e.g., (18, 37, 38)]. Similarly, large herbivores are increasing in numbers, partly because of protection and regulated hunting, but also through active restoration initiatives and reintroductions [e.g., (39–41)]. Species such as European bison (*Bison bonasus*), moose, red deer, wild boar, European brown bear, gray wolf, Eurasian lynx, and Eurasian beaver are all showing positive population trajectories, and have done so for the past 50 years. The explanatory factors for these recent comebacks are of course different conservation actions and initiatives, but many of these large mammals have also benefited from ongoing land abandonment and urbanization in less populated parts of Europe, in particular Eastern Europe (42).

Similarly, in North America, many species of large carnivores and herbivores have made a recent comeback, strengthening in population size, distribution, and conservation status (17). The recovery of North American wildlife is often attributed to the 26th president of the United States, Theodore Roosevelt. He institutionalized and popularized conservation, and expanded federal protected lands by creating the United States Forest Service (43), an initiative that still permeates North American conservation and wildlife management (44). The stipulation that wildlife is a public trust and concern, and that hunting is an obligation governed by legitimate purposes, rather than a market-induced activity, has been referred to as the North American model of wildlife conservation (45). Species such as black-tailed deer (*Odocoileus hemionus* ssp. *columbianus*), white-tailed deer (*O. virginianus*), mule deer (*O. hemionus*), and black bear (*Ursus americanus*), which were on the brink of extinction in the late nineteenth century, now occur in vast areas of the United States and Canada; American bison (*Bison bison*) again roam large areas of the great plains; and moose, red deer, and pronghorn (*Antilocapra americana*) are widely occurring, as are large carnivores such as brown bear, gray wolf, and mountain lion (*Puma concolor*).

In this paper, we take the above-described situation as a point of departure for an ethical reflection of aspects relevant in reintroductions, translocation, and overall wildlife management. Our focus lies on considerations evoked by the current situation regarding ecosystem services, rewilding, and wildlife dependence each presented in a separate section. Further, we take an explicit ethical view on what is needed to ensure that wildlife management honors ethical standards and handles challenges inherent to translocations and introductions in a professional way. We suggest 10 ethical guidelines for management efforts aimed at translocating wildlife or reestablishing wilderness areas.

ECOSYSTEM SERVICES

The concept of "environmental services" was first introduced by Wilson and Matthews (46), renamed "ecosystem services" by Ehrlich and Mooney (47), and gained broader attention after the signing of the Convention on Biodiversity (CBD) in 1992 (48). The CBD refers to a set of measures to aid biodiversity conservation by emphasizing the intrinsic and actual value and importance of natural resources and ecosystem functions. The economic value of the world's collective ecosystem services was estimated at 125–145 trillion USD/year by Constanza et al. (49).

The classical subdivision of ecosystem services is into provisioning, regulating, cultural, and supporting services (50). Provisioning services are generally described as what humans need to subsist, like food, fresh water, wood, and fiber. The regulating services are wider, relating to impacts on climate, water systems, and disease dynamics, while the cultural services are naturally anthropogenic in their context, for example, esthetic, spiritual, educational, or recreational. The supporting services are fundamental ecosystem functions such as primary production, nutrient cycling, and soil formation. Many of the ecosystem services also relate to the 17 Sustainable Development Goals (SDGs) defined by United Nations (51), in particular SDG 13 (Climate action) SDG 14 (Life below water), and SDG 15 (Life on land), but also SDG 1 (No poverty), SDG 2 (Zero hunger), SDG 3 (Good health and well-being), and SDG 6 (Clean water and sanitation). Thus, the ecosystem services provided by large, wild animals are a critical concern for humanity at large.

Wildlife offers opportunities for provisioning ecosystem services such as meat, skin and fur, down and feathers, antlers and trophies, along with less invasive services such as ecotourism and wildlife spotting (52–54). Although provisioning services may be an underlying objective in wildlife management, recovered populations of large carnivores and herbivores in parts of Europe and North America also provide regulating services such as predation or grazing. Both these are important aspects of biodiversity conservation and ecosystem function, as recognized in a recent restoration strategy called rewilding (see below). In addition, or in combination, wildlife has an impact on supporting services such as nutrient, carbon, and water dynamics, and generally facilitates ecosystem resilience (55, 56). Wildlife may also function as climate change mitigators (55, 57–59). The cultural services that wildlife provide may be the most important, since presence of wildlife in a landscape adds to a notion of biological richness that provides comfort and beauty, but also a sense of food security and resource stability, as well as evoking interest in biodiversity and sustainable landscape management.

REWILDING

The concept of rewilding was first formulated by Soulé and Noss (60) and Barlow (61) as a positive trajectory for conservation and evolution that, in addition to protection of species, also included restoration of the degenerated ecosystem of other non-marginal species. It emerged from the gradual realization that humans throughout time, i.e., not only in recent centuries or millennia, but over tens of thousands of years, have depressed and exterminated many large species of birds and mammals [e.g., (11, 62, 63)]. Rewilding aims to enhance wilderness through supplementary release of wildlife species already present and through reintroduction of species formerly present. The latter can be achieved by translocation of species from other geographical areas, actual feralization (rewilding), or retro-breeding (into ancestral phenotypes or genotypes) of domestic strains for which the wild ancestor is extinct, such as cattle and horses. Recent developments in genetics and animal breeding offer biotechnical opportunities to retro-breed extinct species [e.g., (64–67)].

An important aspect of the rewilding initiative is to enable tourism that benefits both local inhabitants and visitors, i.e., sustainable ecotourism (35, 36). Ecotourism has potential as an economic revenue and may provide incitement for conservation, but there may be concerns for restrictions associated with hunting, agriculture, and forestry. Rewilding that aims for ecotourism may however be combined with hunting opportunities [cf. (52)]. According to recent figures from the Swedish Board of Agriculture, Swedish consumption of total (both domestic and wild) terrestrial meat (i.e., no aquatic animals) is 85.5 kg/person/year, of which wildlife meat comprises around 2 kg/person/year on average (68). Thus, wildlife meat is a significant amount of the overall meat consumption in Sweden. A reduction in per-capita meat consumption, accompanied by an increase in number of wildlife and subsequent (sustainable) harvest, may enable Sweden to source an even higher proportion of the meat consumed from wildlife, an interesting opportunity given the global challenges related to conservation of species, climate change, and food production. However, a society dependent on wildlife as a food resource raises ethical questions related to "harvest" through hunting, with obvious risks of unintended harm to a larger number of hunted specimens compared with farming of animals accustomed to humans. On the other hand, if wildlife were to provide an extensive amount of the animal protein needed in a sustainable system, ecosystems would potentially be more resilient to human presence. Further, the welfare and integrity of wild animal can be regarded as less compromised by humans than the welfare of intensively reared poultry, pigs, and ruminants. Moreover, as the numbers of bred and killed animals would decrease radically, far fewer animals would be affected by potential welfare impairments.

In addition, there is increasing interest in the opportunities for restoration of trophic levels, ecosystem function, and resilience that may accompany different rewilding initiatives, typically referred to as "trophic rewilding" [e.g., (9)], as a countermeasure to the trophic degradation eloquently described by Estes et al. (8). Svenning et al. (69) define trophic rewilding as "*species introductions to restore top-down trophic interactions and associated trophic cascades to promote self-regulating biodiverse ecosystems.*" There are numerous examples of reintroductions having positive impacts on ecosystems, such as the trophic cascades attributed to the reintroduction of wolves in Yellowstone National Park (70), the ecological impact of white rhinoceros in Kruger National Park (71), and the wetland creation resulting from introduction of beaver in Europe (72, 73) and North America (74, 75). Few experimental studies have addressed the implications of trophic rewilding thus far, but a recent study of the ecological impact of horses kept under feral conditions reported inhibition of shrubification (76) and benefits for plant and insect diversity (77).

The processes and initiatives that accompany rewilding attempts can generally be regarded as positive, in that they aim to restore the negative impact that human domination has imposed on life on earth, and is still imposing in many places. However, a rewilding process can also pose challenges, such as conflicts of interest between humans and wildlife in forestry, agriculture, traffic, or disease dynamics (e.g., zoonosis). These challenges are mainly economic (e.g., damage to forestry, agriculture, and horticulture), while others relate to human health and welfare (e.g., traffic incidents, disease dynamics). An additional consequence of the utilization of wildlife as a resource, irrespective of the specific form (e.g., hunting, ecotourism, ecosystem function), is how wildlife itself reacts to the rewilding process. Inevitably, some individuals will suffer and die during reintroduction efforts, but the extent may differ between methods, which justifies a proactive risk assessment.

WILDLIFE DEPENDENCE

Human domination on earth, the impact of which extends to all aspects of other living organisms, places humans in a responsible position as regards utilization of the ecosystem services provided by, e.g., wildlife, such as hunting, meat, skin, ecotourism, and wildlife spotting (78). Since humans are able to exterminate, preserve, or support most other life forms, and are capable of reflecting (and socially expected to reflect) upon their actions, they have particular responsibility for life on earth [e.g., (79–81)]. This logic underlies much of the CBD and conservation actions overall, and thus provides an ethical framework for conservation, and also for utilization of wildlife services.

The rewilding approach raises interesting, important, and, perhaps surprisingly, ethical and legal issues not foreseen or previously perceived within wildlife management. Under current legislation in many countries, humans are responsible for the welfare of domestic animals in their care (82, 83). This means that domestic animals, most of which are housed or fenced in, have the right to food and water, shelter from the weather, protection from predation, and also disease protection and treatment. In line with the legislation for domestic animals, but from an ethical point of view, a series of marginal situations arise in conventional wildlife management, for example, when humans protect wildlife from predation, provide supplementary feeding, interfere in reproduction, provide shelter, or shape landscapes to benefit certain species. Thus, restoration that aims to be beneficial for certain species or individuals also places the restorer in a potential caretaking position, where the level of ethical responsibility for the welfare of an individual animal might be difficult to discern.

Rewilding leads to additional ethical issues, as it blurs the boundary between wild and domestic even further (84). As reintroduction and rewilding in practice means introduction, or at least supplementary release, of individuals into new environments, humans compromise the welfare of these individuals in different ways. First, rewilding of domesticated animals (such as cattle or horses) may include transportation to a certain habitat and then leaving the animals to take care of themselves. Second, during translocation of wild animals, catching, handling, and transportation can impact welfare. Third, in potential cases of retro-breeding (i.e., introducing a number of individuals purposely bred as a "re-creation" of an extinct species, such as aurochs), the individuals are handled by humans, albeit in extensive farming conditions, before being left in the wild. In all three cases (introduction/supplemental release, feralization/rewilding, and retro-breeding), the animals involved cross the boundary between being human-reared and wild. If handled as domesticated animals, albeit briefly, wild individuals with no prior experience of humans risk experiencing stronger stress than domesticated animals (85, 86). Legislation and ethics may differ in how to reflect on this, but the welfare of the individual animal may still be impaired. One possible option is to handle welfare challenges in wildlife management by the same means as suggested for wildlife research, through application of the two of the 3Rs (replacement, reduction, and refinement), i.e., except for replacement strive for reduction of number of affected animals and refinement of methods and welfare impairment (87).

Many wildlife releases inevitably lead to suffering at different levels of the released specimen that has to encounter and adapt to a novel habitat, seek forage, and seek protection from weather and predation. If unsuccessful, released specimens may even die of starvation because they are unfamiliar with the new area, are preyed upon by local predators, or are harassed by existing members of the same or a related species. Others may be shot during regular hunting, either by accident or because of the incidental purpose of the release as a form of "put-and-take" or to achieve more sustainable long-term establishment that aims to increase population size for hunting purposes. Released specimens may also become infected with diseases transmitted from conspecifics or closely related species, or may experience stressful situations imposed by intrusive human observers (88). In addition, released specimens may have negative effects on the already present fauna and flora (89).

Reversing the argument, however, many of the species that rewilding and reintroductions aim to restore or reintroduce became extinct because of humans, so reintroduction may be the least we can do to compensate for previous mistakes. In order to enhance biodiversity and offer a multitude of life forms on earth a fair chance to reestablish, some individuals may need to experience hardship; that is, the envisaged consequences justify the means. This utilitarian reasoning, however, pinpoints a clash of ethical values between the fundamental claim of not imposing suffering on a specimen and the purpose of restoration of anthropogenically induced extinctions through the means of translocation, i.e., the ethical question is if the release can be seen as an acceptable compensation for the first mistake of making a species extinct. If so, it can, on the other hand, be argued that we inflict harm on the entity "species" twice: first by causing its extinction and then by re-establishing it in a manner that causes its members to suffer. In that view, we can be seen as trespassing a moral boundary twice. In any case, handling the instable entity of a species, there will inevitably be different individuals that are affected by extinction and by restoration. This raises the related issue of whether compromising the welfare of one individual can be compensated for by handling another specimen in a better way. An analogous issue that lies at the core of veterinary research ethics is whether harming one individual in the process of treatment can be regarded as acceptable if it potentially leads to increased welfare for future individuals of the same species or breed. This relates to the scope of agent responsibility, moral relations, and the ethical actions that can reasonably be expected. Palmer (90) argues in favor of applying different kinds of moral relationships to wild and domestic animals, partly depending on external factors such as culture or context, applying a laissez-faire approach to wild animals (not harming, but also not actively supporting), and obeying a moral obligation to care for domesticated animals. However, Palmer (90) shows that, as humans negatively influence the habitats of wild animals and their possibilities to survive and reproduce, humans might well-impose the ethical responsibility to assist them if necessary for their survival. This line of reasoning applies even more strongly to rewilded animals. It relates to the classical conflict between environmental ethics and animal ethics (91, 92) that concerns the value of a wild individual's life and whether it is relevant to consider ethically. Being alive may be considered a value in itself, and hence creation of a new "wild" individual is morally acceptable, or instead its ecosystem role is what matters morally. In the former, retro-breeding and establishment of suitable conditions for large numbers of offspring from rewilded species is an important aim. In the latter, the overall effect on the habitat and ecosystem becomes more important. In both cases, the welfare of the animals in question matters to themselves and challenges ideas of human responsibility.

REINTRODUCTION ETHICS

There are a few core challenges that need to be considered in the rewilding and reintroduction context. First, the objective of the effort and the potential suffering wild animals encounter in this process need to be related to the ultimate purpose of the measures taken. If beauty and pleasure for humans is the prime objective, the ethical considerations with respect to the individual animal may be weighted more strongly than if the prime reason for the action is species or ecosystem recovery, since pleasure and beauty are social values easily disrupted by the sight or awareness of animals in pain or with impaired welfare due to human actions. Similarly, if the objective is to generate more tangible short- or long-term provisional ecosystem services, such as meat or skin, it may be difficult to accept the suffering imposed by introductions or supplementary releases, as it would be a double instrumentalization of the animals, or clash with the view of hunting as a means to gain meat from animals having a good life until they die instantly. On the other hand, if the objectives are placed in a more holistic perspective, such as restoring, preserving, or saving a species, or generating ecosystem function or resilience, the suffering of specific specimens may be an acceptable cost, not on the individual level of course, but for one or many species or even ecosystems and biodiversity as a whole. We may consider this suffering "collateral damage," a necessary evil for a greater good.

Second, restoration and rewilding may be done in very different ways, but methods that minimize the suffering of the translocated specimens should always be used (again, this is in line with ethical considerations on using animals in research and the so-called 3Rs, replacement, reduction, and refinement). The term "soft release" is often used, meaning giving the animals a chance to adapt to the surroundings prior to release. Nevertheless, quantity may sometimes be preferable to quality, and we may need to consider the basic biological prerequisites of each and every species targeted for translocation before implementation in a plausibility analysis; e.g., the suffering of thousands may be argued to be still worthwhile if the benefits are for millions. Similarly, the suffering of individuals of one species may benefit an ecosystem with a magnitude of species. Here, however, the level of suffering is also relevant, as it will differ due to habitat, translocation method chosen, animal species, and individuals.

A plausibility analysis should also include a description of the consequences of both action and passivity. It could always be argued from an animal right's or deontological perspective that causing suffering to any individual to restore a locally or fully extinct species is unethical since it builds on instrumentalization of individuals. In combination with the view that "what has happened to the species has happened," this line of thought would argue that adding distress on new generations through restoration efforts simply is ethically unjustified, regardless of the species lost. If we decide to act, it can instead be based on a utilitarian weighting where we need to assess the risk of failure, and rate the level and amount of suffering imposed accordingly. Again, we need to address both the potential benefits to biodiversity on a local to global scale, and the potential for suffering by the individual animal.

Human responsibility may also extend long after a successful restoration, depending on the kind of wildlife restored and how humans may/can/will utilize them. Ultimately, however, we believe that we do the future of our world a disservice if we accept extinctions as permanent and rule out all restoration efforts. The future of biodiversity and species conservation depends on humans. This is, after all, Anthropocene, the Time of Man (93, 94), which calls for in-depth reflection on all actions with an impact on individual animals and ecosystems. As with all organisms, everything has consequences (e.g., the "butterfly effect"), but the consequences of human activities for other species are greatest.

In restoration and/or rewilding efforts that include introductions, reintroductions, translocations, supplementary release, or even different forms of re-creation of species [e.g., (66)], we suggest the following 10 ethical points to be considered in a plausibility analysis before decisions are made and action is taken. They can thus be seen as forming a guideline for the decision-making process in restoration and rewilding issues. It is important to note though that we claim no comprehensiveness of the points suggested, but think that if applied, an important step is taken to form general "reintroduction ethics," as it covers not only value clashes or diverse views regarding content but also how to formulate a strong ethical argument.

However, before we present our 10 points, a few words on how an ethical assessment is often made might be helpful to some readers. In general, ethics here refers to normative issues in applied ethics, i.e., the ambition to analyze what values and issues are at stake, and to formulate what is right or wrong in a certain context, based on the most solid argumentation in order to discern what would be a justified action, i.e., what is the most fundamental principle for the basis to decide what is ethically right to do. This justification can be based on either a principle like in utilitarianism (weighting good vs. bad consequences for all involved, choosing the act generating the overall good for as many as possible) or deontology (focusing on the act itself to be justified as a universal maxim ensuring respect for each ethically relevant entity), or a set of virtues as in virtue ethics, to be reflected upon and related to the specific context. In a well-established eclectic approach, four fundamental ethical principles (autonomy, non-maleficence, beneficence, and justice) are compiled, mirroring both utilitarianism and deontology (95). We suggest it useful to consider the following 10 ethical points:

1. *Description of the situation and problem formulation*. Here, a three step-process is useful. (A) An analysis of the situation is essential to create a clear and value-neutral description of the issues at stake, e.g., "Species x is not present in this area, whereas species y and z are," or "this situation causes much/little pain and suffering to x individuals." (B) The causative factors underlying the disappearance or levels of suffering then need to be considered. It is more difficult to remain value-neutral in this phase, due to the frequently large number of plausible and interacting causes and theories. If so, the different possible causes should be listed. (C) Finally, the actual problem should be formulated in a precise and concise way, e.g., "Due to low numbers of grazers in area x, grazing-dependent plants are disappearing."
2. *Alternatives*. What are the alternatives, e.g., maintaining the status quo or some form of action? If action, what measures can be taken? The answer here is related to the listed causes (1) and the purpose (3 below), and will be value- and perspective-dependent, but also limited to factual possibilities. Can we, for example, facilitate spontaneous recolonization from nearby areas? Can different parts of the landscape or terrain be

bridged in some way to increase access and spontaneous transgression? Or are there ecological equivalents available? The potential achievements from actions should be weighed against the counterfactuals, as described by, e.g., Corlett (96). Rather than evaluating success against a fixed baseline, the results of interventions to restore wildlife would then be compared with a counterfactual, i.e., what would have occurred without the interventions.

3. *Purpose*. What is the primary purpose behind any intended action? What arguments make this a valuable purpose and how is it weighed in an ethical framework considering alternatives?
4. *Object of concern*. Scrutiny of the intended species, its specific biological and behavioral needs, prerequisites for the action proposed, as well as the underlying reasons for its disappearance (as above). On a more ethical note, reflection on what the animal represents (on a scale from a commodity to an awe-inspiring creature valuable for its own sake), how to view the moral status of species and individual animals respectively, as well as the potential ethical and societal value of the existence, of having the species in the given area.
5. *Animal welfare*. Further, issues of welfare are relevant and one has to consider actual level of pain, frustration, and harm caused to the object(s) in question. Zoological and especially ethological knowledge and skills are called for here in order to ensure individual capacities are considered in its own right. This is important both to map current welfare of the animals in question and to foresee risks and impairments of welfare.
6. *Potential value clashes*. It is relevant to explore to what extent suffering and welfare matters ethically in relation to other values such as biodiversity or a stable population of a species much depending on (a) actual location and eventually housing of the animals, e.g., limiting their free movement (adaptation and survival possibilities); (b) whether upholding the welfare of wild animals should be less demanding than ensuring domesticated animal welfare levels; and, of course, (c) legislation (in some countries, wild animals are included in animal welfare law; in others, they are not).
7. *Chances of success*. An ethical cost (harm)–benefit analysis for achieving the specific goals of the proposed action should be performed. It is important to include both costs and benefits at the same level of detail, and to be open-minded in selection of factors not supporting one's own view.
8. *Unforeseen consequences*. Although action and risk of failure must sometimes be given priority over passivity and permanent loss, where possible and plausible, a consequence analysis should be conducted for specimens, targeted species, affected species, affected ecosystems, and affected people, before action is taken. The difference between classical conservation, which typically involves negative actions (e.g., preventing something from happening), and rewilding, which typically has a positive trajectory [e.g., re-establishing something; (97)], must be considered. The concept of restoration is in itself an anomaly; we cannot in fact restore a species to any ancestral state, but only form novel trajectories for evolution. This is a challenge for any analysis that aims to consider unforeseen consequences.
9. *Choice of method*. Given solid argumentation for a specific purpose and a certain action, careful selection of "best practice" is needed. For example, if hunting is a primary cause of decreased population, should hunting be regulated to uphold sustainable hunting practices? What, then, does "sustainable" mean for the affected species? Or should hunting be banned? If old-growth deadwood is scarce, what change is needed in forestry practice to ensure it will be provided in sufficient amounts over time? Here, again, the object of concern and its needs as well as potential harms (5) and (unforeseen) consequences (8) related to the method should be considered, in order to investigate the balance of intended benefits.
10. *Adaptivity*. As in research, trial and error is the only way forward. The points above (particularly 2, 7, 8, and 9) are crucial to ensure that potential risks are minimized, but we can never foresee all consequences of all actions; mistakes will be made, lucky coincidences may lead forward, methods can be improved, and actions can be made better. Constant evaluation and re-evaluation, even long after a successful project is undertaken, is a necessary part of any restoration or rewilding project. Hence, there will be a need to describe the situation and reformulate purposes throughout the rewilding process, in a continuous process.

We hope that the aspects advocated and suggestions and thoughts provided here offer guidelines for management efforts aimed at restoring wildlife or wilderness, or simply food for thought for future research efforts in this important field. Finally, we again emphasize that action is necessary to halter the loss of global biodiversity. Passivity is not a value-neutral choice. Since nature and conditions are constantly changing, choosing passivity means choosing further losses. As with the climate consequences of human activities, we have a responsibility to future generations of humans to preserve a rich, sustainable, and diverse planet. Rewilding can provide the benefits of food, experiences, and ecosystem function, and may very well be an important first step toward achieving such a planet.

AUTHOR CONTRIBUTIONS

C-GT and HR contributed equally to developing and writing the manuscript.

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