PERCEPTIONS OF HUMAN-ANIMAL RELATIONSHIPS AND THEIR IMPACTS ON ANIMAL ETHICS, LAW AND RESEARCH

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Editorial: Perceptions of Human-Animal Relationships and Their Impacts on Animal Ethics, Law and Research

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Editorial on the Research Topic

Perceptions of Human-Animal Relationships and Their Impacts on Animal Ethics, Law and Research

Non-human animals live in ecosystems that are increasingly impacted by the growing human population, and have now developed relationships that mostly or partly depend on human societies. Although some of these relationships are positive and enable non-human animals to enjoy anthropized environments, most relationships with humans are negative and prove to be disastrous for non-human animals. Individuals are suffering and biodiversity is being lost at an unprecedented rate. However, human behavior varies, and people from non-industrialized societies behave differently from those living in WEIRD societies (Henrich et al., 2010). This includes their attitude toward animals, as shown in different approaches such as totemism or animism (Descola, 2019). Human perceptions of animal species in terms of their presence and function, and the potential co-use or sharing of their personal environment, depend on multiple sociocultural and biological factors. Humans usually make discriminations between animal species based on these perceptions. Donaldson and Kymlicka (2011) recently classified non-human animals into three categories according to their proximity with human beings, the role they fulfill and their distribution range, namely Wild, Domesticated and Liminal. Wild animals form their own communities and benefit from rights of sovereignty; domesticated animals are fully involved in human societies and may benefit from citizenship. Indeed, domesticated species have developed quite remarkable sociocognitive skills over the thousands of years they have coexisted with humans (Bhattacharjee et al.). Finally, liminal species are wild but live in the midst of human settlements and may benefit from resident status.

USING HUMAN COGNITIVE BIASES IN ANIMAL ETHICS

Discrimination between animal species is called speciesism, a term introduced in the 1970's by the psychologist Richard R Ryder (Sueur, 2019). Beside Kymlicka and Donaldson's categorization, a prime distinction was based on the phylogenetic proximity with human species (Miralles et al., 2019). In general, people show a greater preference for warm-blooded vertebrates than

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for invertebrates, but also show preferences for some species within a given taxon, for example preferring bees to wasps. Discrimination is also based on culture, as shown in the case of differences in diet and the traditional consumption of pork but not dog meat by Europeans, despite these two species being comparable at multiple levels such as body size, longevity or intelligence. Sueur et al. (2020) performed a survey to understand how humans displayed anthropomorphism toward animals, and showed that men and older participants are less likely to attribute human-like mental states to animals. Similarly, people who work with animals or have at least one pet at home demonstrated less anthropomorphism. Conversely, they found that members of animal protection associations attributed more intentions and mental states to animals than non-members. The emotions we feel for animals have important consequences for their welfare and for their conservation (Castillo-Huitrón et al.). While large predators and reptiles may trigger anger, fear, and disgust in some societies, they can produce emotions such as personal value-related happiness in people belonging to other ethnic groups. However, the excessive representation of some species on TV shows or in cartoons may create a biased perception of these animals, resulting in unintended detrimental effects on conservation efforts (Courchamp et al., 2018). Many humans express sadness about the threatening situations that animals are currently facing.

The way people perceive these animals, for instance in terms of how we coexist and interact with them, progresses as our societies, individual behavior and scientific knowledge evolve. For instance, the subject of slaughter sets the debate about defining an acceptable treatment of animals at an extremely low level, and the ethics around slaughtering have considerably evolved over at least the last half century in our western societies. Animal farming and meat consumption cause not only animal suffering but also global warming (Koneswaran and Nierenberg, 2008) and also play a role in the emergence and amplification of infectious diseases (Espinosa et al., 2020). Recently, there has been considerable investment in developing cell-based meat, an alternative meat production process that uses muscle cells cultivated in a bioreactor, thus eliminating the need to raise and slaughter animals. Heidemann et al. discuss the animal ethics impacts of cell-based and plant-based meat on human-animal interactions from animal welfare and rights perspectives, focusing on industrial meat production scenarios. Their hypothesis is that the insertion of cell-based meat in the global meat market may alleviate farm animal suffering and potentially restore resources for wild fauna by freeing up the land (one third of all fields) that is currently devoted to livestock. From a conservation perspective, empathy is subject to significant biases. This inflexible adherence to moral rules can result in a "do nothing" approach, as observed in the Australian case of biodiversity loss and the suffering of preys due to the proliferation of cats (although the perception of cats in Australia is now changing: see Riley, 2019; Woolley et al., 2020). Consequently, Griffin et al. consider that the Compassionate Conservation philosophy, which is based on empathy, should not be enshrined as a legalized guiding principle for conservation action as it could be detrimental to some species.

CONCEIVING NEW CONCEPTS IN ANIMAL ETHICS

Current scientific research allows the development of animal ethics, animal legislation and animal research. However, some elements are still difficult to disentangle within the context of these new rules: How and why should/do we categorize animals, even if it would seem unrealistic to think in another way? Like Bentham (1907), Dzwonkowska suggests that we should not look at non-human animals from a human-related perspective, but from a suffering-related one (Nussbaum, 2004), thus calling for radical responsibility. Radical responsibility is a form of moral responsibility that extends our moral obligations to the point where we are responsible "for the unintended (and often unnoticed) consequences of our actions and our failures to act" (Dower, 1989, p. 18). Here, Dower introduces the idea that radical responsibility concerns not only our actions, but our indirect footprint through actions taken for us by others.

When it is strongly supported by citizens, moral consideration for animals is sometimes transformed into law. Should we give different animal species the same moral status and rights or should their rights differ according to their sentience? The crucial question is whether all species should be included in these animal rights categories, or whether they should be limited to vertebrates alone, or even only mammals. To answer these questions, we need to harmonize the different elements - biology, law, sociology, ethics and philosophy – involved in the moral consideration and protection of animals. Human and non-human factors contribute equally to how we consider animals. Castillo-Huitrón et al. propose that the management of culturally important animal species (particularly those regarded as frightening, dangerous, harmful and disgusting) should be included in national education programs and massive media campaigns. Kletty et al. discussed how to address the ethical limits and the societal perception of implemented conservation measures when dealing with the protection of an endangered species. Like culture, ethics change over time. An animal species can evolve from the status of a pest to one of a conservation flagship in three decades, but good conservation management requires societal demand and the involvement of citizens for the programs to succeed.

It is important to assess these conservation education programs, which can also be used to test the conservation education hypothesis suggesting that people are more likely to defend conservation if they have been exposed to knowledge about endangered species and ecosystems. If a positive result is observed, these programs need to be secured. Bowie et al. introduced novel methods to assess a small-scale program in the Democratic Republic of Congo and confirmed that conservation education has improved relevant knowledge and the attitudes people show about environmental and social issues and toward

animals. Importantly, the authors discussed the important role children play in influencing their peers and family members to pursue pro-conservation behaviors.

The management of culturally important animal species closely follows the concept of Compassionate Conservation (Griffin et al.). The latter promotes "ethical" conservation practices, placing empathy and compassion and the moral principles of "first, do no harm" and "individuals matter" at the forefront of conservation practice. This means that environmental and animal ethics, which have often been opposed, must be combined (even if this can lead to dilemmas, as seen in the case of cats in Australia). The idea of combining environmental health with animal health has existed for about 10 years now and has a fundamental impact for human health, namely the so-called "One-health" concept (Destoumieux-Garzón et al., 2018). Human health, mental or physical, is impacted by the way we consider the environment and animals. When human health is endangered by the inappropriate use of biodiversity, it may result in a better protection of animals through measures such as wildlife trade and animal protection policies in China, which will likely be more strongly regulated in light of the recent SARS spread and Covid-19 pandemic (Bonilla-Aldana et al., 2020; Hemida and Ba Abduallah, 2020). Human fitness is measured in terms of health, and is only limited by the environment and human-animal interactions. Criscuolo and Sueur called this *evolutionary ethics*. Simple acts such as reducing meat consumption (Bègue and Treich, 2019; Espinosa et al., 2020) would have hugely positive impacts on animal ethics (reduction of animal suffering and use), environmental ethics (reduction of climate change and increase in biodiversity) and human health (reduction of cancer and cardiovascular diseases as well as a decrease in the number of new pathogens).

The moral consideration of animals also concerns animal research, regardless of whether our goals are fundamental or applied. A great amount of progress has been made regarding the 3Rs (Replace, Reduce, Refine) but researchers need to continue their efforts to reduce the number of animals they use and the suffering that animals endure. Specific guidelines exist now for research in the wild (Costello et al., 2016) and in the lab (Soulsbury et al., 2020). Surprisingly, animal behavior science remains on the sidelines, despite producing critical evidence on which many animal ethics arguments are based (Webb et al., 2019a). In this way, Patter and Blattner (2020) advance core principles to follow with animals: non-maleficence, beneficence and voluntary participation (Webb et al., 2019b). Economic or convenience euthanasia of animals should be not an option (Hayashi et al., 2013; Matsuzawa, 2016). Animals are not objects, and many species display forms of consciousness and sentience (Low et al., 2012). If we hope to change the habits of humans around the world, researchers must use their knowledge to be the pioneers whose behavior with non-human animals is identical to that they would show with persons possessing such consciousness. Researchers should not carry out research *on* animals, but rather *with* animals, and this mindset must be applied at the different levels of research (researcher, institution, reviewers, editors, funders; Field et al., 2019).

CONCLUSIONS

A unanimous view that emerged several years ago is that we should no longer consider ourselves to be an element outside biodiversity, but rather a full component of it. We need to understand how we are interconnected to this world and its inhabitants. We must seek a new way of behaving toward domesticated species, find innovative means to replace our activities within ecosystems and live in symbiosis with other species (Criscuolo and Sueur). Instead of forcing animals to participate in certain work activities, we can use their remarkable socio-cognitive skills to interact with us and with other animal species (Bhattacharjee et al.). Indeed, ecological interactions between animal (and plant) species, whether it is symbiosis or competition, can be used for agriculture, farming or other services instead of using mechanical or chemical treatments that are harmful for human, animal or environmental health. However, animal behavior science is still insufficiently used. Evolutionary ethics thus proposes to cease differentiation between animal ethics and environmental ethics, and to replace human activities at the core of ecosystems. Non-human animals have always been important for human life due to the ecological, cultural and economic roles that they fulfill. However, one cannot work on animal welfare without involving human cultural aspects, making it difficult to impose universal standards of animal wellbeing, animal conservation and animal use (Kletty et al.; von Essen et al., 2020). Nevertheless, it is important to consider them as a part of our social and cultural capital rather than as material capital (Bourdieu, 1980; Throsby, 1999; Siisiainen, 2003). Parallels with previous human discriminations have been well documented (Kappeler, 1995; Dhont et al., 2020; Moffett, 2020) and non-human animals have to be considered as part of our societies (Donaldson and Kymlicka, 2011; Hoffman et al., 2018). This new animal consideration also involves us, the researchers. We should not continue to consider animals as simple inert objects for research but rather rethink our research and its scientific value in comparison with the number of animal lives we take (Costello et al., 2016; Webb et al., 2019a; Patter and Blattner, 2020; Soulsbury et al., 2020). Importantly, whatever the role of animals in our societies (pets, research, farm, etc.), their abuse is linked with psychopathological factors (Bègue, 2020), and respecting animals could lead us to see ourselves in a better light.

AUTHOR CONTRIBUTIONS

CS wrote a first draft. All authors contributed to the revision of the manuscript.

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Free-Ranging Dogs Are Capable of Utilizing Complex Human Pointing Cues

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Dogs are one of the most common species to be found as pets and have been subjects of human curiosity, leading to extensive research on their socialization with humans. One of the dominant themes in dog cognition pertains to their capacity for understanding and responding to human referential gestures. The remarkable sociocognitive skills of pet dogs, while interacting with humans, is quite well established. However, studies regarding the free-ranging subpopulations are greatly lacking. The interactions of these dogs with humans are quite complex and multidimensional. For the first time, we tested 160 adult free-ranging dogs to understand their ability to follow relatively complex human referential gestures using dynamic and momentary distal pointing cues. We found that these dogs are capable of following distal pointing cues from humans to locate hidden food rewards. However, approximately half of the population tested showed a lack of tendency to participate even after successful familiarization with the experimental setup. A closer inspection revealed that anxious behavioral states of the individuals were responsible for such an outcome. Finally, we compared the results using data from an earlier study with dynamic proximal cues. We found that free-ranging dogs follow distal cues more accurately compared to proximal cue. We assume that life experiences with humans probably shape personalities of free-ranging dogs, which in turn influence their responsiveness to human communicative gestures.

Keywords: interspecific communication, referential gestures, social cognition, distal cues, point following

INTRODUCTION

Interspecific communication (human–non-human animals), employing directional or referential gestures, has widely been studied in the last two decades. Several non-human animals like chimpanzees and bonobos (Tomasello and Camaioni, 1997; Mulcahy and Call, 2009), orangutans (Zimmermann et al., 2009), horses (Maros et al., 2008; Malavasi and Huber, 2016), seals (Shapiro et al., 2003), elephants (Smet and Byrne, 2013), cats (Miklósi et al., 2005), goats (Kaminski et al., 2005), dogs (Soproni et al., 2001, 2002; Miklósi and Soproni, 2006), and wolves (Udell et al., 2008; Virányi et al., 2008) have been shown to respond to such gestures from humans. Although an

initial surge was observed in the investigation of interspecific communication using non-human primates, scientists gradually shifted to testing canids which, in turn, facilitated the development and advancement of comparative research methods. As a result, a great deal of information on interspecific communication and the underlying evolutionary mechanisms were acquired.

Dogs (*Canis lupus familiaris*) are arguably the first species to have been domesticated, at least 10,000–15,000 years ago (Vilà et al., 1997; Savolainen et al., 2002; Frantz et al., 2016). Several studies have found distinct behavioral differences in dogs with regard to their closest living ancestors, the gray wolves (*Canis lupus lupus*) (Miklósi et al., 2003; Gácsi et al., 2005, 2009). Researchers have also highlighted the contribution of other key factors, such as ontogenic experiences and socialization (Wynne et al., 2008; Udell, 2015). Cognitive advancement in the communicative abilities has been observed in domesticated Bengalese finches (Okanoya, 2004). Similarly, complex social skills have evolved in dogs after domestication (Hare and Tomasello, 2005). Pet dogs are remarkably skilled at responding to various human social cues (Hare and Tomasello, 1999, 2005; Soproni et al., 2002; Miklósi and Soproni, 2006). A range of studies has elucidated their ability to comprehend human communicative intents such as pointing gestures (Miklósi and Soproni, 2006; Lakatos et al., 2009; Elgier et al., 2012). Pet dogs, in general, are capable of following human pointing cues, from the simplest (e.g., proximal cues) to the most complex types (e.g., distal cues) (Miklósi and Soproni, 2006; Lakatos et al., 2012). Wolves, on the other hand, have been shown to differ in utilizing human communicative signals, especially the momentary distal cues, because of less socialization and delayed emergence of such behavior (Gácsi et al., 2009). Nonetheless, both genetic predisposition (through domestication) and human socialization (or lifetime experiences) have impacted and shaped the point-following behavior of canids (Lampe et al., 2017). Unfortunately, most studies attempting to understand the abilities of dogs to comprehend human social cues have primarily focused on pet dogs who depend entirely on their owners for survival. Hence, their behavioral outcomes could just be a result of indirect conditioning. While the problem has been dealt with to some extent with studies examining shelter dogs' response to human pointing cues (Udell et al., 2010; Duranton and Gaunet, 2016), a larger picture can only emerge with quantifying responses of free-ranging dogs, which represent the largest population of dogs in the world (Hughes and Macdonald, 2013).

Free-ranging dogs are found in most of the developing countries and live without direct human supervision (Cafazzo et al., 2010). They are primarily scavengers depending on human leftover food but also display occasional begging from humans (Bhadra and Bhadra, 2014; Sen Majumder et al., 2014). Free-ranging dogs interact with humans regularly and receive both positive (food, social petting, etc.) and negative (beating, harassment, and even poisoning) stimuli. Therefore, these dogs are engaged in situations of conflict with humans in many dimensions (Vanak and Gompper, 2009; Gompper, 2015). Humans have been found to be responsible for causing 63% of early life mortality in free-ranging dogs (Paul et al., 2016). Earlier, we showed that at a population level, free-ranging dogs are aversive while making direct physical contact with unfamiliar humans (Bhattacharjee et al., 2017b). This could simply be a strategy to avoid any unprecedented conflict with humans. Therefore, lifetime experiences may vary and can have a significant impact on the social behavior of dogs. This can also lead to inter-individual differences in dogs in terms of responsiveness to unfamiliar humans. Situation-specific responsiveness toward varying human social cues is evident in free-ranging dogs (Bhattacharjee et al., 2018). They were found to comprehend friendly and varying levels of threatening signals from humans and react accordingly. However, communication using human pointing cues has not been studied extensively. In India, people typically feed free-ranging dogs using two distinct ways – (i) by bending down a bit in the front and (ii) throwing food items away and using pointing cues to help dogs locate the food (generally to avoid direct contact with dogs). Therefore, ecologically relevant studies pertaining to human cues ranging from simple to relatively complex (e.g., proximal cues to distal cues) need rigorous testing. Moreover, such an anthropogenic environment is likely to influence dogs' understanding of human social signals.

Spatial co-occurrence of local stimuli with the goal helps guide the behavior of animals in proximal or tapping cue conditions, making them easier to follow; however, in a distal cue condition, no cues co-occur with the goal object, requiring spatial learning skills (Morris, 1981). Earlier, we reported free-ranging dogs' ability to follow dynamic proximal pointing cues in all ontogenic phases – pup, juvenile, and adults (Bhattacharjee et al., 2017a). The study offered two key findings – an effect of ontogeny on the point-following behavior and its plasticity as a function of the reliability of the human experimenter (in adult dogs only). However, we did not quantify the behavioral states or the behavioral expression (e.g., friendly, anxious or fearful, shy, etc.) of the dogs toward the unfamiliar human experimenter, which might also have played an important role in their reactions. Thus, it is essential to examine free-ranging dogs with relatively complex human referential cues focusing on their behavioral states to better understand the nature of interspecific interactions with humans.

In this study, we aim to investigate free-ranging dogs' ability to understand two specific human pointing gestures – dynamic distal and momentary distal cues (Miklósi and Soproni, 2006). We used behavioral states of dogs as a proxy for their life experience with humans to further understand the responsiveness to such cues. Finally, we compared datasets from an earlier study testing free-ranging dogs with dynamic proximal pointing cues using identical experimental conditions (Bhattacharjee et al., 2017a). The comparative approach was used to draw a more complete picture of these dogs' point-following behavior. We hypothesize that free-ranging dogs would be able to comprehend distal cues from an unfamiliar human experimenter due to relevance in their day-to-day begging behavior. We also hypothesize that the behavioral states would play a key role in defining the repertoire of free-ranging dogs' responsiveness to such cues.

MATERIALS AND METHODS

Subjects and Study Sites

We tested a total of 160 adult free-ranging dogs in this study (test: dynamic distal cues = 60, momentary distal cues = 60; control: 40 dogs). All the dogs were randomly located on the streets of Kanchrapara (22°94′41″N, 88°43′35″E), Kalyani (22°58′30″N, 88°26′04″E), and Mohanpur (22°96′05″N, 88°56′74″E), West Bengal, India. Experimenters randomly walked on the streets to locate solitary individuals. All possible urban habitats where dogs can be found such as market places, railway stations, bus stations, and residential areas were sampled. Adult dogs that seemed physically fit (in appearance, without any sign of injuries and wounds) were considered for testing. We took photographs of the dogs, recorded coat color, specific color patches, scar marks, and approximate body size to avoid retesting. We confirmed the sexes of the dogs by observing their genitals (male - 91; female - 69).

Experimental Procedure

We used a two-way object-choice task, where two experimenters, namely, E1 and E2, were involved and played specific roles. E2 was consistent, while four other people played the role of E1. We used opaque plastic bowls (volume = 500 ml) and cardboard pieces as their covers. Small pieces of raw chicken (roughly 10–12 g) were used as hidden food rewards. Here, we provided adult free-ranging dogs with two types (momentary and dynamic) of distal pointing cues (Miklósi and Soproni, 2006) to locate hidden food rewards. We used a double-blind experimental approach where E2 and the subjects had no prior information regarding the location of the hidden food reward. E2 extended one of his arms only for 1 s toward one of the bowls and provided the momentary cue (**Supplementary Movie S1**) after which the arm rests at the side or back of the body. In dynamic cue condition (**Supplementary Movie S2**), the pointing cue was provided throughout the trial. Pointing cues using the left and right arms were counterbalanced. Separate sets of dogs were tested using momentary and dynamic distal cues.

Experimenters walked on randomly selected streets of the study sites to locate solitary free-ranging dogs. Once sighted, E1 lured the individual and carried out an initial familiarization phase. Further experimentation was done only after a successful familiarization phase. The detailed experimental procedure is described below:

Familiarization

Free-ranging dogs in India are not habituated to getting food from covered plastic bowls. Thus, this phase was carried out to familiarize them with the bowls used in the experimental setup. E1 carried out this phase for all the individuals without involving E2 (the person providing cues) in the process. E1 showed a raw chicken piece to an individual dog and allowed to sniff it closely, then placed it inside an opaque plastic bowl and covered it with cardboard. E1 placed the covered bowl on the ground at an approximate distance of 1.5 m from the dog and stood 0.5 m behind the bowl. Video recording of the process was done starting from the placement of the bowl and continued for a maximum period of 30 s or until an individual retrieved the food reward, whichever was earlier (Bhattacharjee et al., 2017a). We recorded the videos using a wide-angle Sony HDR PJ410 camera mounted on a tripod. Only the dogs that were successful in retrieving the food were included in the subsequent phases (either test or control phase) of study. We discarded a total of 37 dogs that failed to succeed in the familiarization phase. Selection of subsequent test or control phase was random.

Test (Using Dynamic and Momentary Distal Cues)

Following a successful familiarization phase, individuals were tested either with momentary or dynamic distal pointing cues in the test phase. Assignment of the type of cue was performed randomly, and we ensured that no dogs were retested with a different cue.

At first, E1 placed a food reward randomly in one of the bowls, false baited the other one by rubbing the raw chicken piece, and covered both using cardboard pieces. The baiting process was not shown to E2 and the focal dog, thereby maintaining the double-blind experimental setup (also see Bhattacharjee et al., 2017a). Therefore, E2 and the dogs had no prior information on the location of the hidden food reward. Immediately after that, E1 handed over the covered bowls to E2, who placed the bowls on the ground. The bowls were placed (1 m away from each other) in such a way that they remain equidistant from the focal dog. The approximate distance between the midpoint of the two bowls placed and the focal dog was 1.5 m. E2 moved 0.5 m back from the mid-point of the bowls after placing them on the ground. Since the dogs were not on leash, E2 sometimes had to reposition (by moving) himself before providing the cue to maintain the distances. E2 tried to catch the attention of the focal dog by clapping once. As soon as eye contact was established, E2 pointed randomly at one of the bowls (1–2 s for momentary or 30 s for dynamic, randomly decided). If the focal dog looked away or turned away during pointing, E2 clapped again to attract its attention. Since distal cues were used, the distance between the tip of the pointing finger and the covered bowl was roughly 0.5 m. E2 gazed at the focal dog throughout the trial for both the types of cues. Approach was defined when the dog moved toward any of the bowls (irrespective of the pointing signal) and uncovered it to inspect. Inspecting a bowl within 30 s ended a trial. The other bowl was immediately removed by E2 to avoid further inspection by the dog. If the dog found food reward upon uncovering a bowl, it was allowed to obtain it. E2 revealed the contents of both the bowls to the dog after an approach within 30 s or after completion of the trial, whichever was earlier. However, E2 never allowed a dog to eat the food reward if the dog chose a false-baited bowl. We carried out three consecutive trials with 5- to 10-s intervals in between. E2, sometimes changed his starting position of a trial to maintain the abovementioned distances as the dogs were not on leash. We tested separate sets of 60 dogs with the two types of pointing cues.

Control

The control condition was carried out with a different set of individuals (individuals not used for test condition) immediately after the familiarization phase. Here, E2 did not provide any pointing cue, stood in a neutral posture, and made eye contact

with the focal dog. The procedure was otherwise the same as explained in the test condition. Control trials were run to rule out further possibilities of olfactory cues and the effect of motion or orientation response hypothesis (Appelle, 1972). The control condition consisted of only a single trial without any repetitions as the reliability of dogs on E2 could only be calculated using test trials. We tested 40 dogs in the control condition.

Data Analysis

Videos were coded by a single coder, and a naive person also coded some of the videos (22%) to check for coder reliability. We coded the following parameters from the videos – approach to experimental setup, point following, latency of approach to the experimental setup, behavioral states of the individuals, frequency of gaze alternations between the bowls and E2, and the duration of gazing at E2 using only trial 1 data. This step enabled us to remove a bias of learning of the dogs and its potential impact on the later trials. In addition, single-trial-based controls allowed us to do our comparisons with trial 1 data of test conditions more consistently. However, we used data from all three trials to calculate the reliability of E2 on dogs (see later). All the parameters used are described below:

Approach

Approach was defined when a focal dog removed the cover of any of the bowls by moving toward it from his/her initial location. A focal dog could approach a bowl with or without following the pointing cue. When a focal dog stayed back in his/her initial position or left the place without inspecting (uncovering) a bowl, it was considered as no approach. Approach was coded as a binary variable.

Ability to Approach the Pointed Bowls

Only dogs that approached the experimental setup were considered for analyzing. Point following was defined by the approach of a focal dog toward the pointed bowl. Point-following behavior was coded as a binary variable.

Latency of Approach

It was defined as the time elapsed between the moment when the experimenter extended his arm (pointing cue) and a focal dog removed the cover of any of the bowls. Thus, individuals that did not approach the experimental setup had no latencies by default.

Frequency of Gaze Alternation

Gaze alternation has been considered as an intentional and referential communicative act in dogs (Merola et al., 2012; Marshall-Pescini et al., 2013). In this study, the frequency of alternation of gaze between the bowls and E2 was counted. We used a three-way gaze alternation method for coding. Therefore, an event of gaze alternation was counted when a focal dog looked at E2 and the bowls or vice versa within 3 s. We did not consider an event as gaze alternation when a focal dog looked away either from the bowls or E2 within the 3-s duration.

Duration of Gazing

Gazing is found to be a critical behavior in communication, which can provide valuable context-specific information on animal intentions (Miklósi et al., 2000; Maglieri et al., 2019). Gazing at the upper body (above the waist) of E2 has been assessed. Emphasis was given on the direction of the focal dog's nose. Eye contact between the focal dog and E2 was not necessary while calculating the duration of gazing. It was cumulative in nature, and hence, total duration was measured.

Behavioral States

Dogs were grouped under the following behavioral states:

- *Affiliative*: Proximity-seeking, fast or rapid tail wagging with the tail perpendicular to or below the body plane, ears pointed upward, maintaining eye contact with E2;
- *Anxious*: Ducking posture with tail between hind legs, excessive panting, lip-licking, corners of the mouth retracted down and back;
- *Neutral*: Resting without gazing at E2, lying down, or general disinterest. Approaching E2 without displaying affiliative or anxious responses were also considered within the neutral behavioral state.

Reliability

We hypothesize that a dog would rely more on human cues when he/she gets rewarded in a preceding trial by following a pointing cue; similarly, the reliability or the level of trust would reduce if the dog did not receive food after following a human pointing cue. It was measured using the method described by Bhattacharjee et al. (2017a). We used the following parameters to calculate the reliability of E2 – "positive reinforcement" (PR) and "lack of reinforcement" (LR). PR was considered when a dog followed human pointing cue and obtained a reward. LR, on the other hand, depicted the situation when a dog followed a human pointing cue but did not obtain a reward.

We measured the proportion of individuals that followed pointing in a consecutive trial after PR and those that did not follow pointing after LR as measures of behavioral adjustments of dogs. Here, we used data from all three trials of the test conditions in two sets (set 1 – trials 1 and 2; set 2 – trials 2 and 3).

A second person, naive to the purpose of the study, coded 22% of the trials to check reliability. It was perfect for point-following behavior and behavioral states (Cohen's kappa = 1.00), and almost perfect for latency (weighted Cohen's kappa = 0.90), frequency of gaze alternations (Cohen's kappa = 0.94), and gazing duration (weighted Cohen's kappa = 0.89). Shapiro–Wilk tests were run to check for normality of the data. We found them not normally distributed and performed non-parametric tests throughout. We used the goodness-of-fit chi-square tests to analyze the parameters of approach, point following, behavioral states, and reliability. Latency, frequency of gaze alternation and duration of gazing were analyzed using Kruskal–Wallis tests. *Post hoc* Mann–Whitney *U* tests were carried out using Bonferroni correction. We used a generalized linear model (GLM) analysis using a binomial distribution to investigate the effects of types of pointing cues, behavioral states, and sexes of the individuals on the approach response. We considered approach as the response variable, and types of cues, behavioral states, and sexes as predictors (fixed effects). Akaike information criterion values were considered for selecting the best-fitting

model. GLM analysis was performed using "lme4" package of R (version 3.0.2). All other analyses were carried out using StatistiXL (version 1.11.0.0).

RESULTS

Approach

50% (30 out of 60), 48% (29 out of 60), and 50% (20 out of 40) of the individuals approached in the dynamic distal cue (test), momentary distal cue (test), and control conditions, respectively. There was no significant difference in the approach responses (goodness-of-fit χ^2 test: $\chi^2 = 0.041$, $N = 160$, $df = 2$, $p = 0.97$) between the three conditions.

Ability to Approach the Pointed Bowl

Out of the individuals that approached, 80% (24 out of 30) and 79% (23 out of 29) of them approached the pointed bowl with dynamic and momentary distal cues, respectively. There was no significant difference between dogs' point-following behavior using the above two cues (goodness-of-fit χ^2 test: $\chi^2 = 0.000$, $N = 59$, $df = 1$, $p = 1$, **Figure 1**). A significantly higher proportion of individuals followed the two cues, as compared to the proportions who did not (dynamic cue – goodness-of-fit χ^2 test: $\chi^2 = 10.800$, $N = 30$, $df = 1$, $p = 0.001$; momentary cue – goodness-of-fit χ^2 test: $\chi^2 = 9.966$, $N = 29$, $df = 1$, $p = 0.002$).

Of the dogs that approached (20 dogs) in the control condition, 14 went to the false-baited bowl and 6 to the baited bowl. We did not find the difference to be significant (goodness-of-fit χ^2 test: $\chi^2 = 3.200$, $df = 1$, $p = 0.07$). However, when we compared the number of dogs that followed pointing cues and obtained food rewards in the two types of test cues (pooled data), it differed from the number of dogs that obtained food in the control condition (goodness-of-fit χ^2 test: $\chi^2 = 6.857$, $df = 1$, $p = 0.009$).

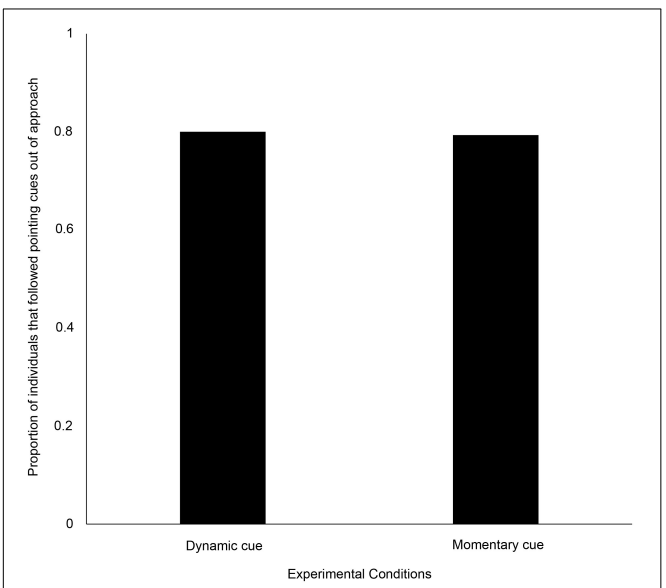

FIGURE 1 | Bar graph showing the proportion of individuals that followed the dynamic and momentary pointing cues.

Latency

Latencies of the individuals that approached did not vary between the test (dynamic and momentary cues) and control conditions (Kruskal–Wallis test: $\chi^2 = 3.559$, $N = 79$, $df = 2$, $p = 0.169$). In addition, there was no difference in latencies between individuals that followed the dynamic and momentary distal cues (Mann–Whitney U test: $U = 321.000$, $N = 47$, $df_1 = 24$, $df_2 = 23$, $p = 0.347$).

Frequency of Gaze Alternation

We found a difference in the frequency of gaze alternations between individuals in the test (dynamic and momentary) and control conditions (Kruskal–Wallis test: $\chi^2 = 11.354$, $N = 160$, $df = 2$, $p = 0.003$, **Figure 2**). *Post hoc* pairwise comparisons with Bonferroni correction revealed a significantly lower frequency of gaze alternations in the momentary cue condition compared to dynamic cue one (Mann–Whitney U test: $U = 2{,}395.000$, $N = 120$, $df_1 = 60$, $df_2 = 60$, $p = 0.002$). There was no variation between momentary cue–control condition (Mann–Whitney U test: $U = 1{,}323.000$, $N = 100$, $df_1 = 60$, $df_2 = 40$, $p = 0.390$) and dynamic cue–control conditions (Mann–Whitney U test: $U = 1{,}466.000$, $N = 100$, $df_1 = 60$, $df_2 = 40$, $p = 0.06$). However, note that the p value was just above the significance level (0.05) between the comparison of dynamic cue–control conditions.

Duration of Gazing

Individuals showed comparable durations of gazing behavior between the test and control conditions (Kruskal–Wallis test: $\chi^2 = 0.538$, $N = 160$, $df = 2$, $p = 0.764$).

Behavioral States

In the dynamic distal cue condition, 35, 23, and 47% of the dogs showed affiliative, neutral, and anxious behavioral states (goodness-of-fit χ^2 test: $\chi^2 = 3.100$, $N = 60$, $df = 2$, $p = 0.212$), whereas the percentages were 38, 32, and 30%, respectively, for the momentary distal cue condition (goodness-of-fit χ^2 test: $\chi^2 = 7.000$, $N = 60$, $df = 2$, $p = 0.705$). We found 17.5, 27.5, and 55% of the dogs to be affiliative, neutral, and anxious in the control conditions (goodness-of-fit χ^2 test: $\chi^2 = 9.050$, $N = 40$, $df = 2$, $p = 0.01$). Overall, behavioral states were comparable within the test conditions. Dogs showed higher anxious behavioral states compared to affiliative behaviors in the control condition (goodness-of-fit χ^2 test: $\chi^2 = 7.759$, $N = 40$, $df = 1$, $p = 0.005$). Other behavioral states were comparable (neutral–anxious – goodness-of-fit χ^2 test: $\chi^2 = 0.667$, $N = 40$, $df = 1$, $p = 0.05$; affiliative–neutral – goodness-of-fit χ^2 test: $\chi^2 = 0.889$, $N = 40$, $df = 1$, $p = 0.34$). We further emphasized the anxious behavioral responses and compared test and control dogs. We found that dogs in the control condition were significantly more anxious than in the test conditions pooled (goodness-of-fit χ^2 test: $\chi^2 = 3.967$, $N = 160$, $df = 1$, $p = 0.04$).

We emphasized on the test conditions further, pooled the data, and found a significant effect of behavioral states on the

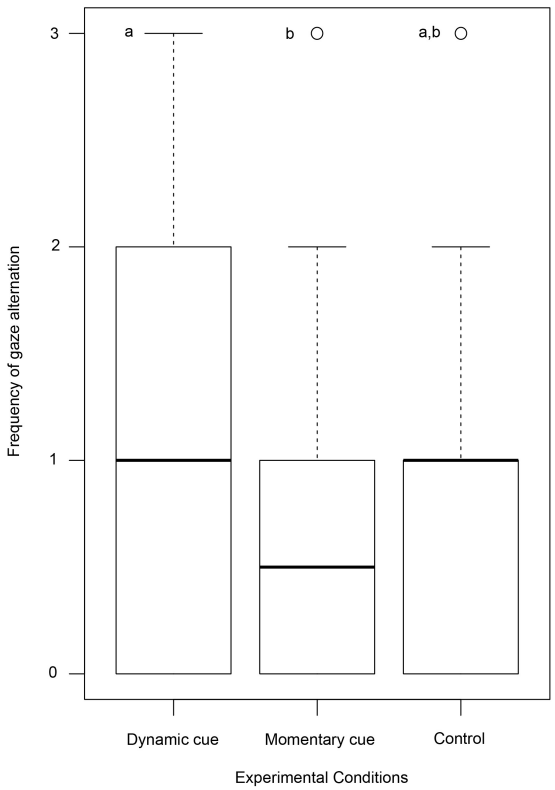

FIGURE 2 | Box and Whisker plot showing the frequency of gaze alternation by dogs. Boxes represent the interquartile range, horizontal bars within boxes indicate median values, and whiskers represent the upper range of the data. Different letters indicate significant differences between the experimental conditions.

approach responses. Approximately 23, 16, and 61% of the individuals that did not approach showed affiliative, neutral, and anxious behavioral states, respectively, with the response levels being significantly different (goodness-of-fit χ^2 test: $\chi^2 = 41.333$, $N = 81$, $df = 2$, $p < 0.001$). Fearful or anxious individuals showed higher "no approach" compared to the affiliative (goodness-of-fit χ^2 test: $\chi^2 = 21.314$, $df = 1$, $p < 0.001$) and neutral (goodness-of-fit χ^2 test: $\chi^2 = 32.008$, $df = 1$, $p < 0.001$) ones. Affiliative and neutral responses were comparable (goodness-of-fit χ^2 test: $\chi^2 = 0.973$, $df = 1$, $p = 0.323$).

In addition, out of the 25 individuals that displayed affiliative state, 22 of them (88%) followed pointing cues. Similarly, out of 20 dogs that displayed neutral behavioral state, 16 (80%) individuals followed pointing cues. Finally, out of the 14 dogs that showed anxious behavior, 9 (64%) of them followed pointing cues. We found the responses to be comparable (goodness-of-fit χ^2 test: $\chi^2 = 3.117$, $N = 59$, $df = 2$, $p = 0.21$).

Effect of Sex, Behavioral States, and Type of Pointing Cues on the Approach Response

GLM analysis revealed only a significant effect of anxious behavioral state on the approach response (**Table 1**). "No approach" was strongly predicted by anxious behavioral states of individuals. We found no effect of sex (GLM: $p = 0.64$) and types of pointing cues.

TABLE 1 | Generalized linear model (GLM) showing the effects of sex, behavioral states, and types of pointing cues on the approach response (binomial distribution).

	Estimate	Standard error	*z* value	Pr(>|*z*|)
Coefficients				
Intercept	0.8101	0.5163	1.569	0.117
Sex male	0.1630	0.3567	0.457	0.648
Anxious behavioral state	−1.7787	0.4286	−4.150	3.33e−05***
Neutral behavioral state	0.2967	0.4466	0.664	0.506
Dynamic distal cue	−0.2409	0.4674	−0.515	0.606
Momentary distal cue	−0.5891	0.4743	−1.242	0.214

*The analysis revealed only a significant effect of anxious behavioral state on the approach response. "No approach" was strongly predicted by anxious behavioral states of individuals. ***$p < 0.001$.*

Reliability

We found that individuals adjusted their point-following behavior based on the reliability of E2. However, the effect was only restricted to PR (goodness-of-fit χ^2 test: $\chi^2 = 16.030$, $N = 33$, $df = 1$, $p < 0.001$). This was suggestive of dogs' tendency to follow human pointing cues in a trial significantly more if the individuals followed cues and rewarded in a preceding trial. No effect of the LR was found (goodness-of-fit χ^2 test: $\chi^2 = 2.333$, $N = 21$, $df = 1$, $p = 0.127$), suggesting the inability of dogs to adjust their point following behavior when received "misleading cues" (i.e., pointing toward empty bowl).

Comparison Between Dynamic Distal, Momentary Distal, and Dynamic Proximal Cues

We compared the proportion of individuals that followed pointing in dynamic proximal, dynamic distal, and momentary distal cue conditions. The comparative analysis revealed a significant difference of the proportion of individuals following pointing cues in the dynamic proximal, dynamic distal, and momentary distal cue conditions (goodness-of-fit χ^2 test: $\chi^2 = 7.2933$, $df = 2$, $p = 0.026$, **Figure 3**). Dogs followed dynamic momentary cues significantly higher compared to dynamic proximal cues (goodness-of-fit χ^2 test: $\chi^2 = 4.075$, $df = 1$, $p = 0.04$). However, the responses for dynamic proximal and momentary distal cues were marginally insignificant (goodness-of-fit χ^2 test: $\chi^2 = 3.739$, $df = 1$, $p = 0.05$).

DISCUSSION

Our study showed that free-ranging dogs are capable of following complex pointing cues from humans. Dogs that approached the experimental setup followed both the pointing cues at significantly higher rates, suggesting their ability to rely on complex human referential gestures. Only half of the

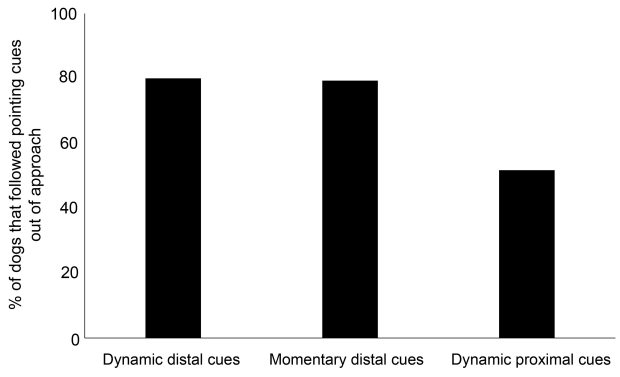

FIGURE 3 | Bar graph showing the percentage of adult dogs that followed the dynamic and momentary distal and dynamic proximal pointing cues.

tested population approached the experimenter, which could be indicative of free-ranging dogs' population-level perception of humans. Anxious dogs were mostly reluctant to approach the unfamiliar human experimenter even after succeeding in the familiarization phase, whereas their neutral and affiliative counterparts showed significantly higher approach. The varying responses in approach can be explained by dogs' lifetime experience (with unfamiliar humans), differences in motivation to participate, and the inability to use the referential property of human pointing. We nullify the second possibility as dogs that did not approach in the test or control trials participated in the familiarization phase earlier, so a lack of motivation cannot be the reason for this response. In addition, free-ranging dogs are scavengers and are generally expected not to be well fed (personal observation). We also discard the last possibility as our findings clearly suggest that these dogs can indeed follow distal pointing cues. It is also important to note that the approach rate was also 50% in the control condition where no cue was provided. Thus, the most plausible explanation would be that the behavioral states of the individuals modulated their responsiveness. The initial approach in the familiarization phase was possibly observed because the dogs were allowed to sniff the food reward and watch the baiting process, thus being certain of the reward before approaching. However, in the later phases (either test or control), the uncertainty of getting a reward along with a longer duration of encountering an unfamiliar human could have deterred the anxious individuals from approaching the setup.

The comparative approach (using dynamic proximal, dynamic distal, and momentary distal cues) highlighted a lower tendency of dogs to follow dynamic proximal cues. Since the experimental design was comparable for all the cues, we believe that the type of cue itself (dynamic proximal cue) had affected dogs' responses. In "Introduction" section, we have mentioned two different ways by which free-ranging dogs in India typically obtain food from humans. While this has not been extensively tested, it is likely that dogs are more accustomed to humans throwing a piece of food away from themselves as a response to begging, or to a human putting/dropping food on the ground and moving away. The complex pointing gestures used in the current experiments simulate these situations quite closely. However, though the proximal pointing cue is considered to be a simpler cue to follow from a completely anthropomorphic perspective to an untrained dog, this might be a more "difficult" situation, with an unfamiliar human constantly pointing at the container, and thereby being in very close proximity to the food source. Adult free-ranging dogs are known to maintain a certain distance from unfamiliar humans and avoid making contact with them (Bhattacharjee et al., 2017b, 2018). It is thus likely that a reduced perception of threat elicited a higher response by the dogs to the distal cues, although the proximal cue is likely to be more definitive and less ambiguous as a signal.

Gaze alternation has been suggested as an intentional and referential act in dog–human communication (Virányi et al., 2006; Marshall-Pescini et al., 2009; Gaunet and Deputte, 2011). Free-ranging dogs displayed comparatively lower frequency of gaze alternations in the distal momentary cue condition as compared to the distal dynamic one. This can be explained by the involvement of higher movements in the dynamic distal cue conditions, which might have influenced the dogs to alter their gaze accordingly. Interestingly, free-ranging dogs have recently been found to discriminate between active and inactive human attentional states and at the same time differ in responses compared to pet and shelter dogs (Brubaker et al., 2019). It seems that the dogs in the streets have been well adapted to using human-directed gazing and gaze alternations. Pet dogs have been found to be deceived by incorrect or wrong cues (Szetei et al., 2003; Prato-Previde et al., 2008; Marshall-Pescini et al., 2011), but they also have some understanding of human reliability (Szetei et al., 2003; Scheider et al., 2013; Takaoka et al., 2015). In an earlier study, we reported free-ranging dogs' ability to adjust their point-following behavior based on the reliability of the human experimenter (Bhattacharjee et al., 2017a). Here, we found similar outcomes for the complex cues, in spite of the cues being more subtle than the proximal one, further supporting and strengthening the earlier claim.

This study confirms our earlier reports on free-ranging dogs' ability to follow human gestures, in spite of having no training. They show a high degree of behavioral plasticity in their response to unknown humans, and this suggests a critical role of learning during ontogeny in the dogs. It is possible that largely negative experiences with humans during their early development make dogs more wary of humans, while those dogs that experience positive human interactions early in life are more friendly and approachable. We suggest that humans play a role, albeit inadvertently, in shaping the personalities of free-ranging dogs. This conjecture is supported by a recent study in which we observed that dogs respond differently to unfamiliar humans calling out to them in areas that differ in human flux – dogs in areas of intermediate human flux are more friendly and approachable than those in low and high human flux zones (Bhattacharjee et al., 2019, under review). In India, dog–human conflict is a major problem in many urban areas, and very little is understood about how humans influence the behavior of dogs on streets.

The free-ranging dogs have existed on Indian streets for centuries and are excellent urban adaptors (Debroy, 2008). Understanding the dynamics of the dog–human relationship in the urban environment can help in better management of conflict as well as provide insights into urban adaptation in general.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by IISER Kolkata Animal Ethics Committee (approval no. 1385/ac/10/CPCSEA). Written informed consent was obtained from the individual(s) for the publication of any potentially identifiable images or data included in this article.

AUTHOR CONTRIBUTIONS

DB and AB designed and conceived the study. SM, PS, MV, and AV carried out the field experiments. SM played the role of consistent experimenter (E2). DB analyzed the data and wrote the first draft of the manuscript. AB edited the manuscript and supervised the entire work.

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Implicit Measures Help Demonstrate the Value of Conservation Education in the Democratic Republic of the Congo

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Biodiversity is being lost at unprecedented rates. Limited conservation resources must be prioritized strategically to maximize impact. Here we introduce novel methods to assess a small-scale conservation education program in the Democratic Republic of Congo. Lola ya Bonobo is the world's only sanctuary for one of humans' two closest living relatives, bonobos, orphaned by the illegal trade in bushmeat and exotic pets. The sanctuary is situated on the edge of the country's capital, Kinshasa, its most densely populated region and a hub for the illegal wildlife trade that is imperiling bonobos and other endangered species. Lola ya Bonobo implements an education program specifically designed to combat this trade. Previous evaluation demonstrated the program's efficacy in transmitting conservation knowledge to children. In Study 1, we use novel implicit tests to measure conservation *attitudes* before and after an educational visit and document a significant increase in children's pro-conservation attitudes following direct exposure to bonobos and the education program. In Study 2, we show that adults exhibit high levels of conservation knowledge even before visiting the sanctuary, likely due to the sanctuary's longstanding education efforts in Kinshasa. In Study 3, we explored adults' empathetic attitudes toward bonobos before and after the sanctuary tour. Our results support the conservation education hypothesis that conservation education has improved relevant knowledge and attitudes in Kinshasa. Crucially, the present study validates new methods for implicitly assessing attitudes about environmental and social issues. These methods overcome typical biases in survey sampling and can be employed in diverse populations, including those with low literacy rates.

Keywords: conservation, education, bonobo, Congo, great apes, Central Africa

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INTRODUCTION

Overwhelming scientific evidence points to severe threats against our planet's ability to sustain high levels of biodiversity. Human population growth, climate change, industrialization and many other forces are all working in concert to drive an exponential increase in species extinction (Ceballos et al., 2017). One of the main tools utilized to combat extinction is environmental education

(Bickford et al., 2012). Many international non-profit organizations have invested tremendous time and effort into providing educational resources to encourage conservation efforts among their target populations (Stern et al., 2014; Thomas et al., 2019). The *conservation education hypothesis* (CEH) suggests that people are more likely to defend conservation if they have been exposed to knowledge about endangered species and ecosystems (Bickford et al., 2012; Ardoin et al., 2018). This hypothesis would predict that a change in knowledge about a given species, or familiarity with facts about the ecology, biology, conservation threats, and conservation status of a given species or its ecosystem, also leads to positive changes in attitudes toward them. Pro-conservation attitudes are ways of thinking or feeling that support the welfare and survival of a given species or ecosystem. The null hypothesis in this case suggests that most environmental education programs do little to change attitudes at a scale that can have a significant impact (Struhsaker et al., 2005). In this case, priority investments should be made in policies and actions that directly protect habitat or threatened environments over education programs (Ferraro and Pattanayak, 2006). Testing the predictions of the CEH is increasingly important as communities, governments and non-profits try to determine how best to allocate finite resources.

A key test of the CEH involves evaluating existing education programs. Many conservation education programs survey individuals before and after their educational experience (Monroe et al., 2017). The prediction in these pre-experience/post-experience surveys is that the participants will show higher levels of knowledge and more positive attitudes toward conservation afterward. The advantage of this assessment approach is that it is easy to implement in a variety of settings and is relatively inexpensive. Survey evaluations have been able to identify programs that effectively communicate their message, optimize existing programs, and detect programs that are not effective (Kruse and Card, 2004; Cutter-Mackenzie and Smith, 2010). Various non-profit organizations are increasing their use of such survey assessments to demonstrate the impact of their education programs. However, even with more assessments, there is skepticism regarding the value of small-scale education programs – particularly those implemented across cultures (Carleton-Hug and Hug, 2010; Cutter-Mackenzie and Smith, 2010; Braun et al., 2018; Briggs et al., 2019). There is concern that effective education programs cannot realistically reach the increasing population sizes in areas surrounding vulnerable wildlife populations (Struhsaker et al., 2005). Reviews of these programs have suggested that given the costs of these conservation education programs, a net positive impact of conservation education may not exist at a more macro-level (Struhsaker et al., 2005; Ardoin et al., 2018).

The uncertainty of the impact of education programs underscores the importance of assessment and refinement. It also raises the question of which techniques are best for evaluating conservation education. Traditionally education program surveys *explicitly* ask questions about attitude toward conservation. However, decades of research on human cognition suggest that explicit questions of attitude are likely to be influenced by experimenter demand effects and answers may not be related to the actual internal preferences of the individual assessment-taker (Kintz et al., 1965; Cunningham et al., 2004; Nosek, 2005). If a tour is led by a conservationist at a conservation site, participants may be inclined to answer "yes" if asked "do you think more effort should be invested in this species' conservation" even if it's not how the participant truly feels. The results of explicit questions of attitude may therefore overestimate the pro-conservation attitudes of participants in conservation education programs.

Another methodological impediment for conventional pre–post experience evaluations is that they often rely on written surveys that can only be used with literate population. This precludes surveying large portions of the adult and child populations in many biodiversity hotspots around the world like Central Africa, Southeast Asia and the Amazon where childhood education is not universal (Jha and Bawa, 2006). It is with these populations, however, that NGOs are increasing their focus on sustainable development and conservation initiatives (Jha and Bawa, 2006; Bradshaw et al., 2015). Effective biodiversity conservation also often relies on changes in knowledge, attitudes and behaviors of multiple populations across several linguistic, ethnic and national lines (Briggs et al., 2019). Language translation often makes comparing the effectiveness of conservation programs across different cultures difficult (Evans et al., 2007; Briggs et al., 2019). Developing evaluation techniques that do not rely heavily on reading or writing will facilitate comparative evaluations since they can be implemented across cultures, therein helping organizations to develop programs that have the greatest impact on larger scales.

To test the CEH, we designed a pair of surveys for use at the Lola ya Bonobo sanctuary. Located in Kinshasa, a city of over 10-million citizens and the capital of the Democratic Republic of Congo, Lola ya Bonobo is the world's only sanctuary for orphaned bonobos (*Pan paniscus*). Lola ya Bonobo functions as the only venue in the capital for adults, children, and governmental decision makers to observe and learn about great apes in person. This function is particularly vital because the Democratic Republic of Congo is home to the largest remaining populations of wild apes in Africa, including the world's only bonobos as well as populations of chimpanzees and gorillas. Both bonobos and chimpanzees (*Pan troglodytes*) are humans' closest living genetic relatives (Prüfer et al., 2012). The sanctuary provides high quality life-time care to wild-born bonobos that have been rescued from the illegal hunting and pet trades. The bonobos arrive in variable states, sometimes physically distressed—malnourished and riddled with parasites—as a result of the improper captive living conditions from which they have been rescued. They are also sometimes psychologically traumatized, having been separated from their mothers and their natural habitat (Wobber and Hare, 2011). Once they have arrived at the sanctuary, young infant orphans are provided with specialized care to help them overcome the acute trauma of their capture from the wild (Wobber and Hare, 2011). They are first cared for by substitute human mothers who help provide the first steps of rehabilitation. After 1–2 years with the substitute mothers, they are gradually integrated into peer groups where they enjoy rich social lives in large forested enclosures similar to what they would experience

TABLE 1 | Rationale for the series of surveys in Studies 1-3 examining conservation attitudes and knowledge in children and adults.

	Child	Adult
Knowledge	André et al., 2008 Does the tour of the sanctuary increase children's knowledge and understanding of bonobos and their conservation status?	*Study 2: Knowledge Assessment* Does the tour of the sanctuary increase adults' knowledge and understanding of bonobos and their conservation status?
Attitude	*Study 1: Attitude Assessment* Does the tour of the sanctuary impact children's attitudes toward bonobos and their conservation?	*Study 3: Empathy Assessment* Does the tour of the sanctuary affect adults' empathic attitude toward bonobos?

Previous research found that the education program at Lola Ya Bonobo had a significant impact on children's knowledge relevant to bonobo conservation (André et al., 2008). The current research extends this work by assessing how the same program impacts children's attitudes toward bonobos, as well as how the program impacts knowledge and attitudes of adults.

in the wild. Ultimately, the vast majority of bonobos experience a full recovery, living species-typical lives, exhibiting species-typical behavior and cognition (Wobber and Hare, 2011), and sometimes even being released back into the wild.

Six days a week, the sanctuary's education team provides guided tours around the sanctuary for national and international visitors. Tens of thousands of children, adults and civil servants are exposed to the natural behavior of the highly charismatic bonobos while learning about their natural history and the threats to their survival in the wild. This includes information about the importance of the Congo Basin for the health and wellbeing of the people who live there as well (André et al., 2008).

In 2009, Lola ya Bonobo conducted a survey with 400 Congolese children to assess the education program's success in transmitting conservation knowledge (André et al., 2008). All children took a knowledge assessment before and after participating in the education program. Half of the participants had never visited the sanctuary before, and half had done so 1 year earlier. In the pre-test, first-time visitors scored at or below chance on all questions whereas return children scored above chance on the majority of questions. In the post-test, children of both groups scored at ceiling on all questions (**Figure 1A**). This study shows that the sanctuary's education program not only successfully teaches children key facts about conservation but also that the majority of what they learn is retained for at least a year.

This previous study also briefly assessed children's explicit attitude toward bonobos. Participants were also asked if they found bonobos amusing, scary, dangerous, or beautiful. Less than 10% of participants described bonobos as amusing before their first tour whereas nearly 90% did so after observing bonobos at the sanctuary. While this explicit attitude assessment was limited to a single question it appears a similar pattern may also apply to the positive feeling children attribute to bonobos after their visit.

Building on this work, in the current study we test the CEH with two additional assessments of the education program at Lola ya Bonobo (**Figure 1** and **Table 1**). In Study 1, we use novel implicit methods to measure changes in children's conservation attitudes in response to the education program. These picture-based methods minimize experimenter-demand effects and do not require that participants can read or write. In Study 2, we investigate the education program's ability to improve conservation knowledge of adult visitors, as adults are the primary decision-makers involved in conservation policy. In Study 3, we explore whether the education program has an effect on adult visitors' empathy toward bonobos. For all of these studies, we predicted that in accordance with the CEH, participants in our experiments will show higher levels of knowledge and more positive attitudes toward bonobo conservation after participating in an educational visit to the sanctuary. Though the ultimate goal of conservation education is to encourage long-term behavior change that benefits the welfare of wildlife species, assessing the impact of programs on behavior change is notoriously difficult. Given the lack of studies of any type on conservation education in *in situ* programs in the Democratic Republic of the Congo, this study provides ample assessment of programs impact on knowledge and attitude changes in a population, which will help pave the way to study long-term behavior changes in the future.

TABLE 2 | Descriptive information for participants for all studies.

	Sample size	Mean ± Std. err	Std dev	Mean age ± Std err	*M/F* ratio
Study 1: Attitude					
Pre-Test	101	0.68 ± 0.02	0.15	12.05 ± 0.23	1.12
Post-Test	102	0.73 ± 0.02	0.15	12.73 ± 0.28	0.92
Study 2: Knowledge					
Pre-Test	81	0.59 ± 0.0	0.17	23.5 ± 1.24	1
Post-Test	100	0.59 ± 0.02	0.16	20.58 ± 1.03	1.57
Study 3: Empathy					
Pre-Test	34	0.48 ± 0.0	0.19	30.57 ± 1.82	0.81
Post-Test	29	0.40 ± 0.03	0.18	34.71 ± 1.67	0.36

STUDY 1: ATTITUDE ASSESSMENT

In this study we extend the André et al. (2008) assessment of Lola ya Bonobo's conservation education program by again surveying children before and after they visit the sanctuary. However, to do so, we introduce novel implicit measures to assess participants' conservation attitudes. The assessment was designed to appear to participants as if we were requesting their input for new designs for publicity for the sanctuary. Because participants are not made explicitly aware that they are being asked about their attitudes toward bonobos and their habitat, these measures are able to overcome experimenter demand effects and, therefore, should more honestly reflect participants' conscious or unconscious beliefs about conservation issues. Consistent with the conservation education hypothesis, we predict that educational visits to the sanctuary will improve conservation attitudes.

Attitude Assessment Methods

Participants were grade school students of Congolese origin attending one of four schools in Kinshasa (N = 203, mean

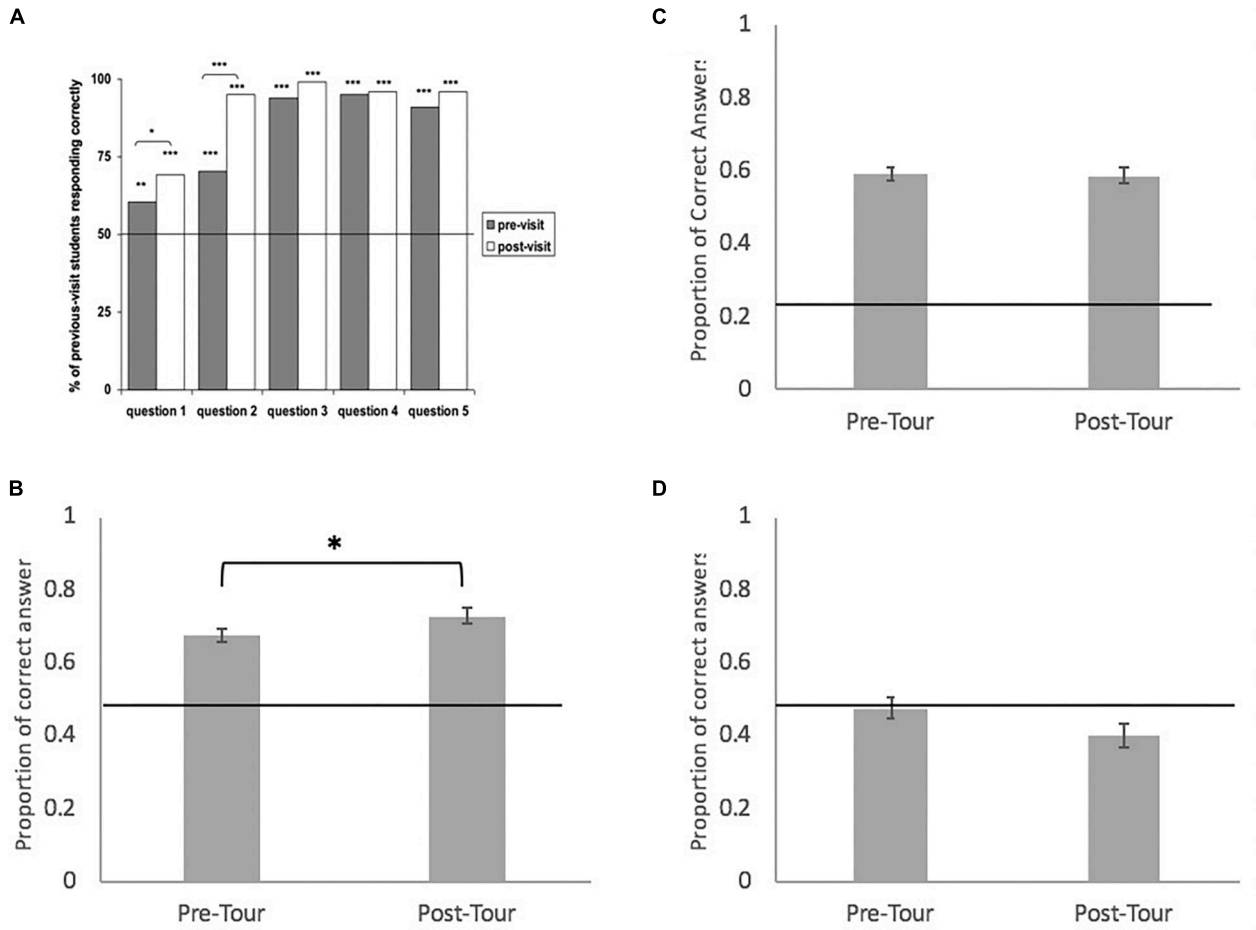

FIGURE 1 | Results for conservation knowledge and attitude assessments among children and adults in the DRC. **(A)** (Reprinted with permission from Springer/Nature) results from André et al. (2008)'s knowledge assessment with percentage of correct responses to the following T/F questions: (1) Bonobos do not make good pets; (2) Bonobos are not an endangered species; (3) Hunting and snares are dangerous for bonobos; (4) Planting trees is something you can do to help bonobos; and (5) The bushmeat trade threatens bonobos with extinction. All participants were children visiting the sanctuary for the first time, and participants did significantly better on all five questions after the tour compared to before the tour. **(B)** Displays the mean proportion of correct answers in the pre-tour and post-tour Attitude Assessment. Overall, the mean proportion of correct answers were significantly higher in the post-tour condition than in the pre-tour condition (estimate = 0.27, $p = 0.006$). **(C)** Displays the proportion of correct answers for the pre-tour and post-tour Knowledge assessment. There was no difference between means on the two assessments, and the mean overall proportion of correct answers for both conditions were above chance. **(D)** Displays results for the Empathy assessment. There was no difference between overall scores and means for both assessments were below chance. **(B–D)** All display standard error.

age = 12.39, range = 7–19 years, M/F = 97/96). Two of the schools (Kimbala and Mamfufu) were in relatively rural regions outside the city and the other two schools (Nova Eligio and Ngolu) were in urban areas in the city center. None of the participants had previously visited the sanctuary. Experimental instructions were explained to the students by a familiar teacher.

The Attitude Assessment contained twelve questions that implicitly examined whether participants held pro-conservation or non-conservation attitudes (see **Supplementary Material**). Photos, instead of text, were used to control for literacy levels among participants. Each participant was given an assessment sheet that contained 12 blocks of photos, each block containing two photo options. Each of the twelve questions had two photo options that the participants could circle: relative to the question, one option corresponded to a positive attitude toward bonobo conservation (pro-conservation option) and the other option corresponded to either a neutral or negative attitude toward bonobo conservation (non-conservation option). We determined which option was pro-conservation or non-conversation based on the messaging and lessons emphasized by the education team during the tour. The questions addressed participants' attitudes toward the following categories: (1) bonobos as pets, (2) the value of Congolese forest, (3) perceptions of bonobo social behavior, and (4) tendency to objectify or humanize bonobos. This study used a between subject's design. To control for differences between schools, half of the children in each school were assigned to the *pre-tour* condition and half to the *post-tour* condition. Students in the *pre-tour* condition ($N = 101$) completed the Attitude Assessment at their schools before an in-school information session conducted by the sanctuary's

education staff. In the *post-tour* (N = 102) condition, a separate group of students took the Attitude Assessment at Lola ya Bonobo immediately following the guided tour. The order of the photo blocks was determined randomly, and there were two versions of the assessment that counterbalanced the order of the photos within each of the photo blocks. All assessments were anonymous in order to avoid potential experimenter effects.

At the beginning of each week, the education team went to schools to conduct the in-school information session. Before the lesson began, a member of the education team who acted as the experimenter split the classroom into the pre and post-tour groups. The groups were determined by splitting the group in half alphabetically by first name, with the first half being in the pre-tour condition, and the second half in the post-tour condition. Those in the post-tour group were asked to temporarily leave the room while the students took the assessment. Each of the students in the pre-tour group was then given a copy of the survey and a pen. The experimenter stood at the front of the room and first explained the instructions, emphasized that the survey should be taken individually and silently, and emphasized that there were no right or wrong answers. The survey was framed not as an evaluation of conservation attitudes, but as a request for information needed to design advertisements to help Lola ya Bonobo attract more visitors like themselves. Each question corresponded to one of the blocks of photos. While asking the question, the experimenter held enlarged versions of the two photo options to ensure all participants were on the right set of photo options. After asking the question, the experimenter instructed the participants to circle the photo that they thought best answered the posed question. At the end of the 12 questions, the experimenter instructed students to fill out the demographic questions and provided assistance for those who needed it. The assessment was written and conducted in French and approved by Congolese members of the Lola Ya Bonobo Education team for clarity and cultural appropriateness.

The photo options were predetermined as either "pro-conservation" or "non-conservation." Participants' responses for each question were scored as "pro-conservation" or "non-conservation" based on which option they marked, circled, dashed, fully underlined or partially underlined. The vast majority of responses unambiguously marked a single answer that could reliably be scored. In the few cases where responses were ambiguous (multiple responses circled), the question was scored as unanswered.

All analyses were conducted in R version 1.0.136 using the glm function. Two analyses were conducted for this study: the first compared the means of the pre-tour and post-tour conditions' total number of pro-conservation answers. For this overall analysis, we used a generalized linear model (GLM) to analyze whether there was a difference between the mean number of correct responses in the pre-tour and post-tour conditions. Age, gender, and school were included as covariates in this model. For the categorical variables, gender and school, a reference group was pre-determined against which the other groups within the category would be compared. Female was set as the reference group for gender, and Kimbala school was set as the reference group for school.

The second GLM examined the difference between the mean number of correct answers for the pre-tour and post-tour conditions for each individual question. Age, gender, and school were included as predictor variables in the same way they were for the previous analysis. Binomial tests were also conducted to assess whether the mean scores for individual questions were above or below the 50% chance value.

Attitude Assessment Results

Results from the GLM show that participants chose more pro-conservation options in the post-tour (0.73 ± 0.02) than pre-tour condition (0.68 ± 0.02) (estimate = 0.27, p = 0.006) (**Figure 1B** and **Table 2**). Participants attending the reference group school (Kimbala) overall answered with significantly more pro conservation responses than participants from the Ngolu school (estimate = −0.432, p = 0.001). There was no effect of age or gender.

Participants responded above chance levels with pro-conservation responses in 7 out of 12 questions in the pre-tour condition and 10 out of 12 in the post-tour condition (see **Supplementary Table S1**). Subjects scored particularly high (79–99% correct) in at least one condition for five questions (3, 6, 8, 10, and 12) and low (<30% correct) in the pre-tour condition for question 9 (i.e., which group do you think bonobos belong to? Monkeys or humans?).

Examining descriptive statistics (**Supplementary Table S1**), mean pro-conservation responses increased post-tour in five questions (range: 7–24%), did not change for six and decreased in one (27%). These differences were significant for 8, 9, and 10 in which post-tour correct responses were higher (Question 8: Which photo better shows the value of the forest? Lumber or the standing uncut forest?: estimate = 2.296, p = 0.001; Question 9: Which group do you think bonobos belong to? Monkeys or humans?: estimate = 1.211, p = 0.017; Question 10: which photo do you think is best for an advertisement about LyB? A photo of Africa or a photo of the DRC?: estimate = 2.496, p = 0.029) and for question 2 where correct responses significantly decreased post-tour (Which group do you think bonobos belong to? Wild Animals or Domesticated Animals: estimate = −1.356, p = 0.007).

Comparing questions individually across schools again shows that participants in Kimbala School, the reference school, chose more pro-conservation responses than participants from the Mamfufu School (estimate = −1.601, p = 0.003) and the Ngolu School (estimate = −1.932, $p < 0.001$).

Attitude Assessment Discussion

In support of the conservation education hypothesis, our attitude assessment using implicit measures suggests that interactions with bonobos on guided tours at the sanctuary increase pro-conservation attitudes among grade school age children. Overall participants in the post-tour condition selected more of the pro-conservation responses than those in the pre-tour condition, with significant increases in pro-conservation responses in three questions and a decrease in only one.

Four questions asked participants to choose images to use in an advertisement for Lola Ya Bonobo. All showed increases in pro-conservation responses with two being significant increases

post-tour. Participants were significantly more likely in the post-tour condition to prefer bonobos being depicted in the wild than in human contact as a pet (Question 10) and were more likely to choose to represent the value of a forest in its natural state rather than as lumber (Question 8).

A subset of questions examined whether participants were likely to humanize or objectify bonobos. In these questions, participants had the option of grouping bonobos with (1) humans or monkeys, (2) humans or vermin, and (3) humans or inanimate objects. The results for these questions are mixed since children were more likely to group bonobos with humans as opposed to with objects or pests, but they were less likely to group bonobos with humans as opposed to with monkeys. Children did shift their preferences to grouping bonobos with humans after the tour, but the mean was still below 50%. This suggests that the tour's discussion of the genetic, physical, emotional and behavioral similarities shift attitudes in a positive direction, but within limits.

The use of implicit measures designed to reduce experimenter effects was a novel feature of the assessment. Results provide validation for this form of assessment since it largely replicates previous findings using explicit knowledge assessment (André et al., 2008). The use of pictures as choice options also increases the feasibility of assessing attitudes in populations where there are tremendous disparities in literacy levels.

Children at the Kimbala school outperformed children at the Ngolu school and outperformed participants from the Mamfufu school in certain questions. This is perhaps due to proximity—Kimbala is the closest of the four schools to the Sanctuary. Lola Ya Bonobo employs individuals and sources food and supplies from nearby communities. Though none of the participants at Kimbala had previously visited Lola Ya Bonobo before, they perhaps had more awareness of the sanctuary because of friends or families who were employed by the sanctuary.

Overall Lola ya Bonobo's educational tours have a positive impact on conservation knowledge (André et al., 2008) and attitudes in children (the present study). What is needed next is to understand if similar effects occur in adult visitors, whose choices about whether to engage in the illegal wildlife trade directly impact bonobo conservation.

STUDY 2: KNOWLEDGE ASSESSMENT

The majority of the efforts at Lola Ya Bonobo focus on the education of children and young adults, as they are assumed to be the populations most receptive to conservation messaging. Older individuals also visit the sanctuary but adults may be less open to changes in their beliefs about or attitude toward conservation of endangered species. However, they are responsible for policy changes that influence the future of biodiversity in the DRC. Thus, in study 2, we examined whether adults also learn the core conservation messages that the sanctuary aims to communicate. Study 2 was therefore designed to test how the education program affects knowledge among visitors who are more representative of the general population of Kinshasa in age, economic and educational background.

Knowledge Assessment Methods

Participants in the Knowledge Assessment were day visitors to Lola Ya Bonobo Sanctuary (N = 181, mean age 21.88, age range 8–59; M/F ratio: 93/73). The majority of participants were of Congolese origin (146/181), with the remaining participants of Western European or American origin. Most participants reported being first time visitors to the sanctuary (117/181).

The Knowledge Assessment examined whether visitors to the sanctuary absorbed the main information points emphasized by the sanctuary education program. These points were identified based on observation of the education program in action, and through consultation with the education team. The knowledge assessment was designed to measure what visitors knew about bonobos and facts relating to their conservation. It included twelve true/false and multiple-choice questions, addressing bonobos' (1) habitat, (2) social organization, (3) similarities to other great apes including humans, and (4) the rehabilitation process for bonobos at the sanctuary. In addition to conservation knowledge questions, we collected demographic information about participants' age, gender, country of origin, country of residence, and whether or not they had previously visited the sanctuary (see **Supplementary Material**).

In a between-subjects design, participants completed the questionnaire at the sanctuary either immediately before (pre-tour condition, N = 81) or after a guided tour (post-tour condition, N = 100). The sanctuary offers four scheduled guided tours each day, 6 days a week. While visitors were waiting for the tour to begin at the Education Center, the guide introduced the optional survey, told visitors that they would receive candy for completing the survey. Each arriving party would randomly be assigned to either the pre-tour condition or the post-tour condition. At the beginning of the tour, the guide handed the surveys, clipboards and pens to participants in the pre-tour group and instructed them to complete the survey individually and silently. He would instruct those in the pre-tour condition to not share anything about the survey with those in the post-tour condition. The pre-tour condition participants had 10–15 min to complete the survey and then the hour-long tour began. Right before the end of the tour, when all participants were back in the Education Center, those in the post-tour condition were given the survey with the same instructions. The assessment was written and conducted in French and approved by Congolese members of the Lola Ya Bonobo Education team for clarity and cultural appropriateness.

Scoring was the same as in Study 1. Like study 1, two analyses were conducted; a GLM that compared the overall number of correct answers between the pre-tour and post-tour conditions which included age group, gender, and number of visits to the sanctuary as covariates. Another GLM was also used to compare the pre-tour and post-tour responses for each individual question, with age group and gender as covariates. Question 3 was used as the reference group for this analysis

because there was no difference in mean responses between the two conditions for question 3. All analyses were conducted in R version 1.0.136.

Knowledge Assessment Results

Overall participants were above chance in their responses in both the pre and post-tour conditions, resulting in no significant difference between these conditions (**Figure 1C** and **Table 2**). Participants responded above chance levels with correct responses in 10 out of 12 questions in the pre-tour condition and 9 out of 12 in the post-tour condition (see **Supplementary Table S2**). Subjects scored particularly high (79–99% correct) in both conditions for five questions (1, 3, 5, 8, and 11) and low (<30% correct) in at least one condition for three questions where chance was 25% (6, 9, and 12).

Mean pro-conservation responses increased post-tour in five questions (range: 6–18%), did not change for six, and decreased in six (1–24%). These differences were significant for question 1 and 4 in which subjects increased correct responses in the post-tour condition. (Question 1: In which country do bonobos live?: estimate = 1.344, $p = 0.018$; Question 4: which of the following is not illegal in the DRC?: estimate = 2.453, $p = 0.005$).

We found no differences between the responses of first-time visitors and returning visitors within or between the two tour groups. Examining age as a variable we did find that those in the post-tour condition in age group 2 (ages 16–18) made more correct responses than other participants across conditions (estimate = 1.414, $p = 0.011$).

Knowledge Assessment Discussion

Unlike the prediction of the Conservation Education Hypothesis, composite scores did not increase from the pre-tour assessment to the post-tour assessment. However, in line with this prediction, we did find significant increases in correct answers on two questions. Moreover, the lack of overall difference between conditions likely comes from the high number of correct answers on the assessment in both the pre-test and post-test conditions.

Adult visitors came to the sanctuary with a high baseline level of knowledge about bonobos as reflected in their pre-tour assessment scores. It is important to highlight that given that this population is choosing to visit the sanctuary and paying the entrance fee, they are likely of a higher socio-economic status and education level than the average Congolese citizen. There was no increase or decrease in mean scores in the post-tour condition. The high baseline scores perhaps stem from widescale efforts of programs like Lola Ya Bonobo to disseminate information about bonobos in schools and communities over the past 20 years.

Questions on this knowledge assessment fell into one of two categories: natural history of bonobos and conservation of bonobos. Participants scored well above chance in both conditions for all except three questions (6, 9, and 12). Question 6 (What is the social organization of bonobos?) and Question 9 (Which of the following is least related to a bonobo?) were natural history questions. Both of these questions may have been too detailed for visitors to have known before visiting the sanctuary. Incongruity between the tour guides conveying the answers to these questions and visitors' observations of the bonobos may have led to confusion of the right answer. Question 12 (Why should we save bonobos) was a conservation related question and may have been perceived as subjective to visitors (the correct answer was *d*: all of the above).

Question 1 (Where are bonobos found?), a natural history question, and Question 4 (Which of the following are not a threat to bonobos), a conservation question had significantly more correct answers in the post-tour compared to the pre-tour condition. Despite having high baseline scores, the results from these two questions support the Conservation Education Hypothesis.

Given the high level of knowledge about bonobos among this population, we next explored whether high levels of pro conservation attitudes existed among a similar subset of adults.

STUDY 3: EMPATHY ASSESSMENT

Finding little evidence that the guided tour has little effect on the visitor's knowledge about bonobos and their conservation, we next examined if the tour impacted visitors' empathy toward the species. We again wanted to assess the effect of the tour on empathy in the general population of Kinshasa who are representative of the current policy decision makers in the DRC. It is commonly thought that to increase support and interest in species' conservation, we must increase empathy for the species (Schultz, 2000; Sheeder and Lynne, 2011); however, whether or not conservation programs actually engender empathy in their visitors has not been thoroughly examined (Berenguer, 2007; Sevillano et al., 2007; Tam, 2013). This final study examined whether the guided tour at Lola Ya Bonobo increased visitors' empathy toward bonobos. We used a novel paradigm using implicit measures to assess empathy in the general population that visited the sanctuary. Our implicit measure for this study was the use of *mentalistic language*, as opposed to *descriptive language*, as a measure of empathy. Mentalistic language describes the internal thought processes of an individual, whereas descriptive language describes the apparent actions of the individual. Bonobos have been shown to have complex social cognitive capacities previously only ascribed to humans (Krupenye et al., 2016, 2017, 2018; Krupenye and Hare, 2018; Krupenye and Call, 2019). Evidence from developmental and social psychology suggest that using mentalistic language to attribute such an inner life to others (e.g., she *feels* happy as opposed to she *looks* happy) is an indication of an individual's ability to understands the internal thoughts of others, and consequently is a trait commonly thought to underlie the ability to empathize with others (Ruffman et al., 2002; Symons, 2004). The use of mentalistic language as a measure of empathy has been examined among groups of humans, both adult and children (Ruffman et al., 2002). This study is the first to examine attribution of mentalistic language between humans and an endangered species.

Empathy Assessment Methods

Like the Knowledge Assessment, participants for the Empathy Assessment were adult day visitors to Lola Ya Bonobo ($N = 63$). Among those who recorded their age and gender, the mean

age was 31.95 years and the male/female ratio was 27/17. Only 39 participants responded to the question about whether or not they had previously visited the sanctuary. Of those 39 participants, 28 participants indicated it was their first visit. The procedure for this study was identical to the procedure for the Knowledge Assessment.

This assessment examined whether the experience of seeing and interacting with the bonobos at the sanctuary increased visitors' empathy for the bonobos. We examined the use of *mentalistic language* as a measure of empathy. All survey materials were in French. The survey consisted of six photos of bonobos doing various actions like eating, playing, pointing, or sitting. Underneath each photo were two options that described what was happening in the photos—one option used mentalistic language and the other option used descriptive language. The survey instructed participants to choose which of the two options best described what was happening in the photo. In addition to the six questions, we also collected information about participants' age, gender, country of origin, country of residence, and whether or not they have previously visited the sanctuary (see **Supplementary Material**). There were two versions of the survey that counterbalanced whether the mentalistic or descriptive option was displayed first. The two different versions were randomly distributed among participants.

For this between-subject design, participants in the *Pre-Tour* condition (N = 34) completed the Empathy Assessment at Lola Ya Bonobo before the start of the guided tour and those in the participants in the *Post-Tour* condition (N = 29) took the assessment immediately following the guided tour. The assessment was written and conducted in French and approved by Congolese members of the Lola Ya Bonobo Education team for clarity and cultural appropriateness.

Scoring for this study used the same criteria as those in previous studies. One challenge we encountered in this study was that not enough participants filled out the demographic information to use any of the demographics as covariates.

For the overall analysis, the same GLM was used as in the attitude assessment. Binomial tests were also conducted to assess whether the mean scores for individual questions were above or below the 50% chance value. We used the available but incomplete demographic data to test the effect of age and gender.

Empathy Assessment Results

There was not an overall significant difference between the pre- and post-tour groups (**Figure 1D** and **Table 2**). Participants responded above chance levels with empathy responses in two out of six questions in the pre-tour condition and one out of six in the post-tour condition (see **Supplementary Table S3**). Subjects did not score particularly high in any of the six questions but scored low (<30% pro-empathy) in at least one condition for three questions out of six (3, 5, and 6). There was no apparent effect of age or gender. Like the Knowledge Assessment, the sample population for this study is not representative of all of Kinshasa. Because they are choosing to visit the sanctuary and pay the entrance fee, this study population is likely wealthier and more educated than the average Congolese citizen.

Mean pro-empathy responses increased post-tour in one question (8%) and decreased in five (1–29%). None of these differences were significant for individual questions. Although not significant, the post-tour group showed a 26 and 29% drop, respectively, in empathic responses after the tour in question two and six.

Empathy Assessment Discussion

Results from the Empathy Assessment do not provide further support the Conservation Education Hypothesis. Question 4 was the only question where participants in the post-tour condition chose the mentalistic language above chance. However, this study may not have been sufficiently sensitive to capture positive changes in empathy. Further research should investigate other potential implicit attitude assessments among adults, especially those that explore changes in empathy toward animals, and should attempt to calibrate assessments to prevent such ceiling effects in pretest results. Using mentalistic language as an implicit measure of attitude toward species is still novel. Further exploration of mentalistic language and other implicit measures is needed to best assess changes in adults' attitudes toward bonobo conservation in this population.

GENERAL DISCUSSION

Building upon the previous knowledge assessments conducted at Lola Ya Bonobo in 2008, our results in children support the Conservation Education Hypothesis. There is less support for the hypothesis among adult visitors.

An assessment conducted in 2008 supported the prediction that the education tour at Lola Ya Bonobo sanctuary positively impacted children's conservation knowledge of bonobos. The Attitude Assessment described in study 1 further demonstrates that children are likely to have stronger pro-conservation attitudes toward bonobos after the sanctuary tour compared to before the tour. Specifically, results suggest that the tour reinforces children's belief that bonobos are not appropriate pets and that the forest habitat of bonobos has inherent value. This advance is important because it suggests, while controlling for experimenter demand effects, that children may internalize and update their own personal views as a result of the pro-conservation teaching offered by the sanctuary. Moreover, this paradigm offers a new tool for assessing implicit changes in attitudes in a wide range of populations with varying degrees of literacy.

The Knowledge Assessment (Study 2) and Empathy Assessment (Study 3) did not provide strong support for the CEH. However, they contributed important insights by examining the tour's influence on pro-conservation knowledge and attitudes in adults, a critical population that had not been previously studied at this sanctuary. Study 2 found that adults came into the tour with a high level of knowledge about bonobos and their conservation. There was no significant overall change in level of knowledge after the tour, although adults showed significant improvements on question 1 (In which countries do bonobos live?) and question 4 (which of the following is

not illegal in the DRC?). Although these results may suggest that the tour itself did not dramatically impact adult visitors' knowledge about bonobos and their conservation, it may be that the education outreach the sanctuary has conducted over the past 20 years has raised baseline levels of knowledge among the general population of Kinshasa in the Democratic Republic of the Congo. The null results for the Empathy Assessment (Study 3) suggest that further research is needed on how to best assess conservation attitude change among this population of adults. A future study that includes a larger sample size of Congolese participants would also further illuminate what best influences attitude changes.

In addition to the support for the Conservation Education Hypothesis, the novel methods used in the Attitude Assessment highlight the importance of developing implicit attitude assessments that can be implemented with a wide variety of populations. Using implicit studies that do not heavily rely on language will allow for more objective quantitative comparison of different populations that play a role in the future of great apes.

Even though the analyses of the composite results for the Knowledge Assessment and Empathy Assessment do not strongly support the conservation education hypothesis, certain questions from across all three studies provide important feedback on how the sanctuary can refine its tour to best encourage pro-conservation attitudes. Well-intended messages conveyed by the program could have unintended effects on the audience. For instance, the tour heavily emphasizes the evolutionary relationships between bonobos and humans. Results from Question 9 (Which of the following are bonobos least related to?) in the Knowledge Assessment reveals that participants perform at or below chance on a question related to this topic both before and after the tour. This might be due to religious and cultural beliefs conflicting with the sanctuary's emphasis on scientific-based messages. Given this result, the education team can experiment on whether or not decreasing the focus on bonobos' genetic and behavioral similarity to humans will lead to increased pro-conservation attitudes among adult visitors. This example highlights how results from individual questions should be scrutinized under both cultural and educational frameworks to improve the outcomes of a conservation-minded program. Conservation education program evaluations should be adapted to the cultural norms and cultural practices of the program's target populations.

Our research here is limited in several ways. We used a between-subject design as opposed to a within-subject design. These studies were designed to be between subject primarily to reduce demand on participants. Additionally, instructing participants that they will take an assessment both before and after the tour ay encourage participants to attend to information in a way that is not representative of the average visitor experience.

In the Attitude Assessment, implicit attitude measures conducted with children are not concurrently compared to the results of a more conventional explicit assessment of attitude. To account for this, we relied on qualitative comparisons to the limited attitude assessment conducted among children in André et al. (2008).

The Knowledge Assessment was limited to adults who voluntarily visited the sanctuary. Voluntarily coming to the sanctuary suggests pre-existing interest in learning about bonobos and their conservation. Additionally, the entrance fee ($5 USD) is higher than the average wage/day in Kinshasa ($2 USD/day), which suggests that the population visiting the sanctuary is considerably more middle-class than the average individual in the DRC. This middle-class population of Kinshasa though not fully representative of the DRC, mirrors sanctuary and zoo-going visitors in other countries that have been more thoroughly studied. The knowledge assessment was indeed the only study in this series that did not involve implicit measures. It was targeted toward the more educated, middle class population visiting the sanctuary among whom literary levels and experience with surveys was higher than the average population in Kinshasa. Although participants generally performed well on the Knowledge Assessment, future work could simplify questions that proved difficult and adapt the questionnaire for a more diverse sample.

The Empathy Assessment is limited because it may not have assessed attitudes pertinent to this Congolese population. The emphasis on empathy toward animals may be culturally dependent (Paul, 2000). In more industrialized and Western countries, animals are more likely to co-habitate with humans and are seen as part of a family (Negra and Manning, 1997; Daly and Suggs, 2010). This proximity breeds stronger feelings of empathy toward animal more generally. This attitude may contrast with conventional attitudes toward animals in Central Africa, where animals are viewed in more utilitarian ways and as belonging to a domain distinctly separate from humans. For this Congolese population, viewing bonobos in a semi-wild habitat may highlight exactly how different they are from humans. The experience of the tour may in some ways counteract the sanctuary's desire to increase empathy for bonobos among adult visitors. Further cross-cultural research is needed to understand the different role empathy plays in cultivating pro-conservation attitudes toward species like bonobos.

As it relates to all three studies, assessments were only conducted directly after the tour. Future studies will need to develop innovative and implicit methods of assessing how educational interventions, such as guided sanctuary tours, affects both children's and adults' changes in knowledge, attitude, and behavior in the days, weeks, and months that follow.

Despite limitations, the Conservation Education Hypothesis provides a useful framework for exploring the effectiveness of environmental education programs. Activities like poaching as well as climate change resulting from human behavior have caused mass species extinction. Some species, like the three species of African Great Apes, are currently being pushed toward extinction because of human behavior. It is crucial that conservation organizations allocate their finite resources toward programs that demonstrate effective change for wildlife conservation. These organizations can improve their

outcomes by employing recommendations from evidence-based research. Testing the Conservation Education Hypothesis is one way organizations can explore whether their education programs are effectively changing conservation attitudes and behaviors.

The results from these three studies underscore the important role wildlife sanctuaries play in changing the knowledge and attitudes of their visitors. In particular, this study highlights the importance of focusing on communities that have major influence on the future of endangered species. The population of the DRC drives the greatest demand for bushmeat in the Congo Basin (Wilkie and Carpenter, 1999), but Congolese populations have not been extensively studied regarding the drivers that influence attitudes toward wildlife. Future studies with this population should consider the local cultural histories and beliefs in order to design new communication strategies that can most effectively lead to pro-conservation attitudes. A reliance on empathy, while proposed to be an effective strategy for generating attitude and behavior change in more Westernized cultures, may not be an effective communication strategy or measure of change in this community. Alternatively, future studies with this population could explore additional ways to test changes in empathy toward bonobos that were not explored in the present set of studies.

Children play an important role in influencing their peers and family members to pursue more pro-conservation behaviors. Since Lola Ya Bonobo's inception, a significant number of phone calls about bonobos as pets in need of rescue have come from children who have previously visited the sanctuary (André et al., 2008). Children play an important role in wildlife conservation, but adults have the agency to stall imminent threats of species extinction and climate change. Therefore, in addition to further work on children, future studies should focus on behavior change in adult populations. Though the results can only be qualitatively compared due to differences in method, these set of studies found significant changes in attitudes in children but not in adults. Future studies should focus on social, economic, and political reasons why conservation education experiences are less likely to shift pro-conservation attitudes in adults, while incorporating more direct comparisons between children and adults. Determining ways to encourage pro-conservation attitudes and behaviors from childhood through adulthood is ultimately how conservation education programs can help reverse the threats of wildlife extinction.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

ETHICS STATEMENT

Ethics approval for all studies was granted by the Duke University Campus IRB protocol #D0939. Approval was granted as a secondary analysis of data originally collected by the Lola Education team for program improvement purposes.

AUTHOR CONTRIBUTIONS

AB, CK, and BH designed the studies. AB analyzed the data and wrote the manuscript. AB and CK conducted the studies. PM and FM supported study implementation at Lola ya Bonobo.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2020.00386/full#supplementary-material

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OPINION
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An Evolutionary Point of View of Animal Ethics

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INTRODUCTION

The observation that animals may respond to the emotional states of conspecific or even heterospecific individuals is not new. Darwin broached the question by underlying the ability of animals to express sympathy, i.e., the response to non-self-emotional status, even across species barriers. More importantly, he tried to find the evolutionary origin of this animal trait, suggesting that it evolved from the selective advantages of kinship behavior in the struggle for life (Darwin, 1872). Such a behavior corresponds, for instance, to alloparental care, which is relatively common in mammals and birds and is now also characterized in fishes and insects (Josi et al., 2019; Wu et al., 2020). After more than one century, the need to define what exactly non-human animals are able to feel and—from this starting point—rethink the legal status and place of animals in human societies is becoming increasingly necessary. This can mainly be considered as an indirect consequence of people's increasing awareness of the consequences of dramatic human-driven impacts on the global climate and biodiversity, but this also holds true for the daily issues concerning animal life and welfare. However, because assessable currencies are required to establish laws, animals were classified into categories based on ecological (e.g., invasive species, pest, wild, and domestic), biological (e.g., vertebrates and invertebrates), or cognitive (e.g., primates and cephalopods) traits. This should help lawyers to define ethical rules of animal use by humans and, from that, determine the rights of animals (Rollin, 2006; Donaldson and Kymlicka, 2011). A major issue of such an approach to animal ethics is, however, that it remains human-centered (i.e., anthropocentrism) and focused on human thought (i.e., anthropomorphism). Indeed, the human empathy tree appears to be different to the phylogenetic tree, meaning that human empathy toward other organisms is not equally distributed within the tree of life (Miralles et al., 2019). Why, for instance, are cognitive capacities considered to be highly important in defining which animals can be used for human benefit? Why are individual lifespans or animal culling considered to be the most important parameters in the ethical equation? This is all because these criteria are what define us, citizens of modern human societies, as the superiors. We project our wishes and expectations regarding longevity, issues of euthanasia, and the death penalty onto animals.

Due to the varied cultural differences in human society, there exists a large panel of moral intuitions, and social activism for animal rights has increased for multiple reasons (Herzog and Golden, 2009); however, most of these keep in mind common currencies of human morality. While, in Biology, an animal is defined as a heterotrophic multicellular organism, its legislative definition is more restricted to vertebrates or domestic animals. However, if we want to legislate animal rights in an unbiased way, a non-anthropocentric definition of animal beings—and, more generally, all living beings—should be established, and in biology nothing has sense out of evolution (Dobzhansky, 1973). In this article, we aimed to raise the incongruity of defining animals from a human point of view. Indeed this point of view, while being understandable due to anthropomorphism, does not take into account what evolution could to tell us about ethics. We have proposed an alternative non-anthropocentric view of how thinking of animal beings from an evolutionary perspective may

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help us to redefine animal ethics. Evolutionary ethics defines how we should behave with relation to human heterospecific living beings by freeing us from human-based cultural or emotional considerations. We have proposed that animal ethics (principally based on individuals) cannot be distinguished from environmental ethics, and evolutionary ethics may therefore also help us to solve the paradoxical position of humankind concerning biodiversity; we know that we are doing wrong, but, by doing wrong, we have promoted, thus far, the survival and propagation of our own species. Exactly what evolution actually focuses about? Evolutionary ethics is thus also concerned with human evolution and promotes the exit of humanity from the evolution paradigm.

ANIMAL ETHICS FROM A HUMAN PERSPECTIVE

Ethical Considerations

Animal ethics (animalism) usually differs from environmental ethics (environmentalism). The first one is supposed to be concerned with defending animals as individuals and caring about their use and welfare. The second one defends animals as species and their related environments. For instance, the environmentalist school of thought would consider the eradication of cats as an invasive species killing endemic ones in Australia, but the animalist school of thought would not. The two ethics are, however, becoming increasingly connected due to the complex consequences of human activities. For instance, recent Australian mega-fires have raised both environmental and animal ethical issues (Nolan et al., 2020). Indeed, it is likely that there are two main reasons that have led to the increased demand from citizens, at least in more economically developed countries, to change the policy defining our relationship with the animal world. The first one is related to the fact that animals and their ecosystems actually form a whole functional entity, human species included. The accelerated sixth mass extinction of the Earth's history (Ceballos et al., 2017), related to the domination of humans over most ecosystems, directly threatens human civilization *via* its impact on ecosystems' viability. For scientists, the fact that biodiversity is the cornerstone of the stability and productivity of ecosystems has been recognized for a long time, and has become an important discipline within the field of ecological research (Tilman, 2000). This is not a scientific claim based on theoretical considerations or modeling, but it results from the accumulation of experimental and observational evidence (Bolund and Hunhammar, 1999; Worm et al., 2006; Zhang et al., 2007). Decision making regarding protection laws have necessitated a demonstration of the decreased biodiversity that has endangered numerous ecosystem services, including food production, fresh water filtering, or waste recycling, all of which are of tremendous importance for human survival. However, because human activities are harmful toward biodiversity but are also largely beneficial in the short term for human society (e.g., politics supporting rapid economic growth), there has had to be a trade-off between economics and ecology (e.g., Varijakshapanicker et al., 2019). Thereby, the rights of wild animals, but also those of farmed animals, have been taken into account so far in the human-biased point of view, and this has largely been based on the valuable societal benefits they provide. However, animals belong to ecosystems, and they cannot therefore be considered separately from issues of ethics. They consequently stand at the collision point between our own survival considerations (the most profitable and productive ways to exploit animals) and purely ethical considerations (the limits of our exploitation of animal resources), leading to a split between animalism, abolitionism, and welfarism.

Fundamentals of Morality

The second reason for changing our behavior toward animals is based on the special position humans have granted themselves in the tree of life (which is actually an assemblage of bushes of life and a non-directional evolutionary process) (Rokas and Carroll, 2006) as being the only species with enough cognitive capacities to think for others. The rules established so far to decide what can and cannot be done with animals have inevitably followed the subjective feelings of humans, though only, of course, to a certain extent. Bentham's question of "can they suffer[?]" is not human-related but "suffering-related" (Nussbaum, 2004), even if humans also experience pain and suffering. If it is indeed "a non-sense situation if we want to establish [all] rules of animal ethics based on human morality concepts," the question of "can they suffer[?]" is *not* a human morality rule but a broad biological one. This should be recognized, but the fact that it is human-centered to give less importance to arthropods, such as manta, spiders, ants, or bees, should also be recognized; they sacrifice their own lives and are eaten alive for the sake of the group and species. Such (mainly moral) concerns, for instance regarding cruelty toward animals, were first presented in ancestral religious texts, but the underlying reasons remain that cruel behaviors toward animals may be extended if not punished toward human conspecifics (Rollin, 2006). This human-centered questioning regarding animals—including the issue of the definition of an animal, e.g., vertebrates vs. insects and others (see House, 2018)—has prevailed, even with the recognition of animal rights in society. For instance, the codification of animal use in the mid-twentieth century was first restricted to non-human primates, excluding mice and rats (despite representing >90% of the animal models for scientific research) and farmed animals (for obvious economic reasons, which could also be interpreted as evolution-derived decisions to maximize human fitness). More recently, legislation was extended to vertebrates in general (birds, anurans, fishes, etc.) and cephalopods (Hartung, 2010). Still, what are the bases for this discrimination between animals with rights and others? Because being requires thinking as well as just feeling, animals that retain some cognitive abilities can be classified as "human-like" and can then benefit from rules protecting them. Such animal awareness or consciousness (i.e., sentience, the ability of animals to be conscious of suffering) was established by cognitive ethologists from comparative studies of behavioral and neuroanatomy homologies between animals and humans (Allen and Bekoff, 2007). An additional drawback to applying human morality to animals is that animals are amoral beings. For instance, predation, infanticide, and forced

copulation have all coevolved with numerous animal life-history strategies because they may promote individual fitness, which is the driving force of species evolution. We are facing a non-sense situation if we want to establish rules of animal ethics based on human morality concepts. One may ask "what is the meaning of morality from a human frame of reference"? Humans are certainly in an unbalanced system conducting to issues for all living beings, humans included. Even without morality, species live in stable ecosystems through the use of evolutionary stable strategies [ESS, (Taylor and Jonker, 1978)]. This principle of ESS is now applied to human activities without referring to morality but with more focus on balanced systems (He et al., 2019).

Extending Ethics to Non-animal Beings

One clear dichotomy in humans is the distinction we make between animals and non-animals, such as plants or mushrooms. This distinction is based on clear morphological, physiological, and ecological traits as well as evolutionary origin but also, for the purposes of ethics, on the capacity for suffering or of sentience. To our knowledge, no study showed that plants are sentient. Plants or mushrooms have no organs with which to centralize information and create or process mental states (e.g., feelings) (Calvo et al., 2017; but see Pelizzon and Gagliano, 2015). However, this conceptualization of sentience as something needing centralization of information is quite human-centered. Even if plants and mushrooms are not capable of sentience, they are at least capable of reception and integration of different information sources [e.g., chemical, visual, and tactile (Trewavas, 2016; Calvo et al., 2017)]. Some recent studies have shown that they are able to learn, react to mechanical stress, and even communicate (Poelman et al., 2012) about this stress (Khait et al., 2019). Of course, we do not say that a plant is akin to a vertebrate or even an insect, but the ethical dichotomy we make between animals and plants appears so far to be too simplistic. Again, the evolution of the perception of humans (anthropocentrism and anthropomorphism) may have favored this ethical dichotomy.

Human Interests in Ethics

This is certainly a very rough picture of the present debate on animal ethics, but it appears to be in line with an issue strictly related to humans and to human fitness (i.e., the growth rate of the human population). In fact, by following this way of thinking, we are trapped in an equation that has been simply resolved so far by natural selection, which sees human fitness as paramount. This has worked very well since the human population has never been so large, and the quality of living conditions has also improved exponentially over the last century. Humans care about animal ethics once their own ethical issues are resolved. The evolution of civilizations shows different steps in human morality; first came the abolition of slavery, and this was followed by gender equality, children rights, and then animal ethics. This means that only once human populations have reached an upward threshold level of life quality may they care about the well-being of other species. This process might be thought of in terms of fitness too, and we may wonder whether reviving human interests in animal ethics is not fitness-oriented due to the challenges imposed by the global changes. For instance, when the use of biodiversity endangers human health, animals may be better protected, such as through the wildlife trade and animal protection policies in China, which will likely be more regulated in light of the recent SARS or Covid-19 spread (Bell et al., 2004; Bonilla-Aldana et al., 2020; Hemida and Abduallah, 2020). The only limit to human fitness is imposed by the environment, and the forthcoming consequences of global warming will largely be deleterious for human populations (Burke et al., 2017). Because of that, we need to get out of the evolutionary trap of animal ethics as it is currently imposed by its anthropocentric definition.

ANIMAL ETHICS FROM AN EVOLUTIONARY PERSPECTIVE

Interconnected Species

We are living in a world that hosts an incredible diversity of life forms, from invisible unicellular organisms to plants and to huge marine vertebrates. Earth biodiversity even transports us to old ages *via* the continuous discovery of incredible fossils of all forms. Life on Earth, then, first refers to the past, and the functioning of the current ecosystem is the result of a rich history of co-evolution that is 3 billion years old. This is the very first and most important fact to recognize when trying to escape the human perspective of animal ethics. One first consequence is that the ethics of animals is not different from the ethics of ecosystems because all species have evolved as interconnected entities (Thébault and Fontaine, 2010; Ulanowicz et al., 2014), and if one is granted rights, the second automatically obtains the same rights. This might happen directly, with animals and plants being parts of the ecosystems, or indirectly, such as protecting a flag or umbrella species, e.g., the giant panda, for the protection of the all ecosystems (Shen et al., 2020). Granting legal identity to rivers protects more than just the rivers themselves; it also protects biodiversity, cultures, and ethnicities (Wilson and Lee, 2019). Respect is universal; it is not limited to our needs or feelings. Distinguishing between animals and their environments is merely driving down the road of domestication and will transform animals into non-evolutionary objects.

Domestication and Ethics

From our point of view, pets are the most common representation of non-evolutionary animal objects, being entirely integrated into the human ecosystem and our morality rules, and it is not surprising that they are the first animals to be granted animal rights. Domestication is not totally aberrant in the context of evolution because it has been beneficial both to humans (i.e., mainly in the production of food) and to animal species, which has succeeded in terms of diversification (to a point, see Destoumieux-Garzón et al., 2020), survival, reproduction, and population dynamics. One can see farming as a human–animal symbiosis: it is good for all at the species level. The application of evolutionary questioning to production science actually opens up for interesting avenues of applied research to improve the living conditions of farming animals and better define their ability to adapt to the current environmental

changes (Destoumieux-Garzón et al., 2020). The latter is exactly what the current laws of animal ethics want to rule out. Reducing animals to objects ("good" like pets or "bad" like potential human predators or competitors) has at least two drawbacks: it favors anthropomorphism and annihilates the reality of non-human living beings, thereby justifying human overexploitation of ecosystems. In addition, it intuitively places humans as the drivers of the future evolution of animal species and strengthens the idea that humans do not actually belong to the animal kingdom, and all this for insufficient reasons, such as specific evolutionary history (i.e., granting us with an exceptional cognitive capacity).

Replacing Human Activities With Ecosystems

In fact, trying to define and categorize animals using the consciousness or the animal sentience argument (even through the precautionary principle, Birch, 2017) could largely be attributed to the self-proclamation of humans as superior organisms. By accepting this, however, we forget that evolution is a random process with no directionality or final objective (of which the final objective is certainly not the creation of *Homo sapiens*). Moreover, humans often try to distance themselves from what they call *nature*—creating a binary between nature and culture, urban environments and natural ones. They do not feel belonging anymore to where they come from. Nature is a concept, an abstraction invented by humans that allows us to establish a distance between ourselves and non-humans so as to better dominate them (Descola, 2019). Replacing the human–animals/ecosystems relationship in the context of symbiosis (i.e., equality of species in relation to benefits) and applying it to wild species will naturally help us to redefine but also accept the rights of animals and all livings beings (the main right being to live freely) merely by recognizing their role in the global functioning of the environment we are living in. For instance, humans have always accelerated the extinction of large animals because they represent a threat to humans and our livestock (Haynes, 2018), thereby favoring human and livestock population growth. The current issue represented by the population dynamics of large predators in modern countries is mainly discussed within the context of the economics of livestock management. However, we could also consider livestock as potential prey interacting with predators and try to select for appropriate anti-predator behaviors (Frid, 1997; Moreira-Arce et al., 2018) that may reduce the economic costs (and, perhaps more importantly, the bitterness of farmers) within acceptable limits. These limits should not apply only to parts of the society that are the more exposed to animal interactions (farmers), and ethical efforts should concern public research, the food-processing industry, and citizens in general.

Symbiosis Over Exploitation

Nevertheless, humans may consider themselves as a superior species for good reason; it may help us to reassess human fitness through the regulation of human population dynamics. This remains the only way to reallocate environmental space to animals and to reduce global warming, i.e., to define evolutionary animal ethics. Adopting rules that will lead to a decrease in the human population is a painful renunciation of our selected inclination toward increased individual fitness. While being a crucial step for the planet, this Malthusian theory (Chu and Tai, 2001) remains the most difficult concept to explain to the population because it contradicts the optimal (and so far very successful) fitness trade-off of the human species that has been selected over thousands of generations. As such, it is written in our genes and holds a central place in our animal subconsciousness. Moreover, it also politically challenges the individual liberty of the life-history decisions of citizens. Still, such an evolutionary puzzle, like the reproduction/longevity trade-off (i.e., that which prevents simultaneous maximization of both traits), has previously been resolved by our species, as human are the only long-lived primate with high fertility (Walker et al., 2007). Moving away from a successful life-history strategy is a natural non-sense as well as a radical paradigm change for the entirety of society, and for these reasons it is likely to be a long-term objective that is incompatible with the environmental urgency of the twenty-first century. Nevertheless, it is up to our public authorities to launch the beginnings of such a political message and to find short-term alternatives, such as helping countries to define wildlife animal ethics, and linking it with immediate economic benefits could be one possible solution. It will be necessary to create a national index of animal biodiversity that corresponds to an internationally recognized economic value, each species being granted with a specific value based on its rarity, role in the ecosystem (including criteria for the attractiveness of ecosystems for the sake of tourism), as well as importance for scientific research and education. This would help to drive international policies for environmental protection and animal rights in relation to their economic payoffs.

CONCLUSION

Animal ethics is a fundamental question for human beings, not because it promptly refers to animals but because it returns humans to their original roots. Because all life on Earth is the product of natural selection, humans are first defined by evolutionary trade-offs related to fitness. To maximize our survival, the environment has been anthropized, including animal species selection and control of population dynamics. To do this, we have also defined what animals should be. Rather than doing this, however, and by using evolutionary theory, we have suggested that we should make the ultimate human step to remove ourselves from the process of natural selection and escape the human focus on evolutionary trade-off optimization when helping to define what animals really are. This new evolutionary ethics thus proposes to halt the differentiation between animal ethics and environmental ethics and to replace human activities at the core of ecosystems. It is also a true ethical issue that belongs to economically developed countries in which human welfare has reached a sufficient level so as to make room for caring about animals and the

environment on a global scale. These are the bases of evolutionary animal ethics.

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The idea for this opinion paper occurred during an animal ethics training session for scientists given by CS at the University of Strasbourg.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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CONCEPTUAL ANALYSIS
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Compassionate Conservation Clashes With Conservation Biology: Should Empathy, Compassion, and Deontological Moral Principles Drive Conservation Practice?

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"Compassionate Conservation" is an emerging movement within conservation science that is gaining attention through its promotion of "ethical" conservation practices that place empathy and compassion and the moral principles of "first, do no harm" and "individuals matter" at the forefront of conservation practice. We have articulated elsewhere how Compassionate Conservation, if adopted, could be more harmful for native biodiversity than any other conservation action implemented thus far, while also causing more net harm to individuals than it aims to stop. Here, we examine whether empathy, compassion and inflexible adherence to moral principles form a solid basis upon which to meet the goals of conservation biology as specified by pioneers in the discipline. Specifically, we examine a large empirical literature demonstrating that empathy is subject to significant biases and that inflexible adherence to moral rules can result in a "do nothing" approach. In light of this literature, we argue that our emotional systems have not evolved to provide a reliable basis for making decisions as to how best to ensure the long-term persistence of our planet. Consequently, in its most radical form, the Compassionate Conservation philosophy should not be enshrined as a legalized guiding principle for conservation action.

Keywords: compassionate conservation, empathy, compassion, ethical bias, conservation decision making

INTRODUCTION

Conservation science is concerned with phenomena that affect the maintenance, loss, and restoration of biodiversity and the science of sustaining evolutionary processes that engender genetic, population, species and ecosystem diversity (Groom et al., 2006; Hunter and Gibbs, 2006; Van Dyke, 2008; Sahney et al., 2010). The need for conservation science stems from estimates suggesting that up to 50% of all species on the planet will disappear within the next 50 years (Koh et al., 2004), which will contribute to poverty, starvation, and will reset the course of evolution on this planet (Jackson, 2008; Millenium Ecosystem Assessment, 2009). One of the founders of conservation science, Michael Soulé (1985) described five guiding principles for the

field: (1) diversity should be preserved, (2) untimely extinctions should be prevented, (3) ecological complexity should be maintained, (4) evolutionary processes should continue, and (5) biological diversity has intrinsic value (Lacy, 1993; Possingham and Davies, 1995; Christensen et al., 2009; Kareiva and Marvier, 2012; De Leenheer, 2014). Hence, preserving the diversity of life is a core tenet of conservation.

One can ask why conservation biology places so much emphasis on maintaining biodiversity. Soulé's first four principles can be justified on the basis of utilitarian arguments. First, biodiversity provides humans with numerous health, social, spiritual and economic returns, as well as potential unpredictable opportunities for future innovations in all these domains (WHO, 2016). Second, due to the interdependent nature of all living beings, biodiversity sustains ecosystem function, which in turn sustains life. It is important to point out that, under these utilitarian arguments, the conservation of species is not really a goal in itself, but an instrument for achieving a goal. Soulé's last principle is the only one to allude to the intrinsic value of biodiversity and its right to be conserved over and above its utilitarian benefit to humans.

To meet the goal of maintaining biodiversity, conservation practice requires on-the-ground actions. Decisions of what conservation management actions to implement were originally based on the gut feel of conservation practitioners. Scientific evidence has begun to take precedence, however. To this effect, practitioners have developed a suite of optimal decision-making tools that minimize subjective human influences, such as project prioritization protocols (Joseph et al., 2009), protected area placement (Christensen et al., 2009; De Leenheer, 2014) and species management (Lacy, 1993; Possingham and Davies, 1995). The over-arching aim of these frameworks is to ensure that best practice is evidence-based, where evidence pertains to the effectiveness with which a conservation action is in line with the stated goals of conservation biology.

These decision-making structures are being challenged by the recent emergence of a compassionate conservation movement, which argues that conservation actions should be founded first and foremost on empathy and compassion (Bekoff, 2013; Ramp and Bekoff, 2015; Wallach et al., 2018). By founding conservation practice on moral rules including "first, do no harm" and "individuals matter" (Wallach et al., 2018), compassionate conservation suggests shifting decision making in conservation biology from a utility-based practice to a moral-based practice. While utilitarian considerations determine whether an action is appropriate based on whether it maximizes a given utility for all, moral considerations examine whether an action is right based on whether stated moral principles are respected (McConnell, 2018). Endorsing such a paradigm shift requires a closer examination of whether using morality as a foundation for conservation actions is compatible with the over-arching goals of conservation biology, that is, to restore the perturbed and dysfunctional ecosystems that currently support a fraction of biodiversity that existed even just a few centuries ago (Ceballos et al., 2015).

In this article, we address two questions. Drawing upon a large body of empirical work on empathy and compassion by psychologists, we ask whether these capacities form a solid foundation on which to build conservation practice. Then, we examine closely the particularly controversial issue of species lethal control, which we re-frame in the light of an extensive body of psychological research on moral reasoning. Similar to our exploration of empathy, we address the question of whether principles such as "first do no harm" and "individuals matter" form solid foundations for sound decision making in conservation practice. We conclude by highlighting what we see as an important distinction between energizing public engagement and enshrining compassionate conservation moral principles into environmental law.

EMPATHY AND COMPASSION AND THEIR POTENTIAL ROLE IN CONSERVATION DECISION MAKING

A central tenet of compassionate conservation is that empathy should form the founding principle for conservation action (Vucetich and Nelson, 2013). Although the motivations for making empathy a cornerstone of conservation practice are possibly diverse, one identifiable origin is in a proposed return to virtue ethics to address the "depraved morality that Utilitarianism offers" (Cafaro, 2001; Vucetich and Nelson, 2013). Virtue ethics are a very ancient approach to defining how humans ought to act. In virtue ethics, morality stems from the character of an individual, rather than being a reflection of the actions of that individual (Hursthouse and Pettigrove, 2018). For example, in the time of ancient Greece, Aristotle defined the purpose of human life as living well, which is, living according to reason. Bravery, generosity, temperance, and magnanimity were considered manifestations of that purpose (Kraut, 2018). Honesty, courage, compassion, generosity, tolerance, love, fidelity, integrity, fairness, self-control, and prudence are all examples of virtues. Vucetich and Nelson (2013) have proposed that in the context of conservation, "the purpose of a person living a sustainable life would have to be "*to treat others as one would be treated, if one were in their position*." It is here that empathy plays a crucial role. Indeed, empathy is taken to provide the "objective, empirical knowledge . . .about the conditions and capacities of others (to flourish and suffer)" (Vucetich and Nelson, 2013).

Empathy has a long and strong study tradition amongst psychologists. One use of the term refers to the capacity to feel what you infer others are feeling (de Vignemont and Singer, 2006; Singer and Klimecki, 2014; Bloom, 2017a). Within this view, *empathy*, also referred to as *affective empathy*, *emotional empathy*, *experience sharing*, or *personal distress* (Zaki and Ochsner, 2011; Bloom, 2017b; Zaki, 2017), is a form of shared affective arousal (e.g., sadness), which is triggered automatically and involuntarily, although people can retain agency in how closely they subsequently align their empathic reactions to their goals (Zaki, 2018). Empathy thus defined is distinguished conceptually and empirically from other aspects of social cognition, including, for example, people's interest in taking, and understanding of, the perspectives of others (referred to as "cognitive empathy") and *fantasy*, specifically, the tendency to identify with fictional characters (Davis, 1983; Decety and Jackson, 2004;

Eisenberg and Eggum, 2009; Jordan et al., 2016). Other researchers view empathy as a multi-dimensional construct encompassing affective, cognitive and emotion regulation dimensions (Decety, 2011; Eres and Molenberghs, 2013; Baldner and McGinley, 2014). Taking an evolutionary perspective with the aim of emphasizing phylogenetic continuity and adaptive significance, Preston and de Waal (2002) argue that their Perception-Action model of empathy recoheres discrepant views into a unified whole. The model refers to the object as the primary individual who experiences an emotion or state and to the subject as the individual who secondarily experiences or understands the emotion/state of the object. Empathy is then defined as "*any* < italics added by the present authors > process where the attended perception of the object's state generates a state in the subject that is more applicable to the object's state than to the subject's prior state or situation." Yet, what should and should not be included under the term empathy remains a matter of debate (Bloom, 2017a; Zaki, 2017).

Over and above the debate on how exactly to define and measure empathy, there is significant support for the hypothesis that empathy predicts prosocial behavior (Batson et al., 1981; Batson, 1998, 2016). As a result, there are many advocates of the idea that empathy can be used as a moral compass. The issue of significant concern here is that an extensive body of work has now demonstrated that our empathic responses are fraught with biases (Fetherstonhaugh et al., 1997; Kogut and Ritov, 2005; Slovic, 2007; Cikara et al., 2011). The biased nature of our empathetic responses has caused scholars of empathy to urge for the creation and commitment to institutional, legal, and political systems that draw upon reasoned analysis and not empathy (Slovic, 2007; Bloom, 2011, 2017a; Slovic et al., 2011; Västfjäll et al., 2017; Zaki, 2017). These calls cast serious doubt on whether our empathetic responses are the best tool to replace the utilitarian based principles that currently underpin conservation actions on the ground. We discuss these biases below.

The first bias of empathy that may interfere with sound conservation decisions is that empathy favors the familiar and the in-group (reviewed by Cikara et al., 2011), and new research is beginning to show that these preferential responses have distinct neural signatures (Xu et al., 2009; Eres and Molenberghs, 2013). For example, work examining the relationship between the willingness to help and the number of humans in need of help has revealed that an identified single victim elicits considerably more assistance than a non−identified single victim (Kogut and Ritov, 2005; Västfjäll et al., 2014). Willingness to help varies with the type of identifying information, however, people contribute more toward individuals identified with a picture than individuals identified only by age (Kogut and Ritov, 2005). These findings are in line with the more general finding that people are more generous toward an identifiable victim than toward a statistical victim (Slovic, 2007; Small et al., 2007a). With regards to in-group biases, research has shown, for example, that people are more likely to help individuals to whom they are genetically related (Burnstein et al., 1994) and with whom they share a nationality (Levine and Thompson, 2004). Applied to conservation practice, these familiarity and in-group biases mean that species we are familiar with and species that resemble us are likely to elicit more empathy than those we are unfamiliar with and dissimilar to. As a result, conservation actions involving these species are likely to seem more morally justified independent of whether that action serves to restore/maintain biodiversity. Compassionate conservationists who advocate for empathy to become a guiding principle of conservation practice restrict their compassion almost entirely to large, charismatic mammals (Hayward et al., 2019).

The second bias of empathy that raises concerns over its use as a foundational moral principle in conservation science is that empathy does not scale. That is, people are deeply moved by one person's suffering but remain affectively untouched by large-scale losses of human life (Fetherstonhaugh et al., 1997; Slovic, 2007; Slovic et al., 2011; Västfjäll et al., 2014). Humans can experience both psychic numbing, which is a reduced emotional sensitivity to shocking and emotionally overwhelming experiences (Lifton, 1967; Slovic, 2007; Slovic et al., 2011; Dickert et al., 2012) and psychological numbing that consists of a cognitive and perceptual form of insensitivity that reduces our ability to evaluate the consequences of our actions (Fetherstonhaugh et al., 1997). Kogut and Ritov (2005) found that people tend to report feeling more distress and compassion when considering a single identified victim than when considering a group of victims, even if identified. We also know that people put more weight on the proportion of lives saved than on the number of lives saved even when the number of lives saved is the same or even less (Slovic, 2007). Fetherstonhaugh et al. (1997) showed that people are less willing to send help that would save 4,500 lives in Rwandan refugee camps as the size of the camps' at-risk population increased. This is because saving 80% of 100 lives elicits a greater affective response than saving 20% of 1,000. The failure of our emotional systems to track the suffering of large-scale atrocities is invoked to explain the indifference with which many of the 20th century mass murders were treated (Slovic et al., 2011; Västfjäll et al., 2014). By the same token, psychological and psychic numbing are likely to be adaptive. Research has shown that individuals scoring high on empathy are more prone to depression and anxiety, that is, excessive empathy leads to burn-out (Schreiter et al., 2013).

Biases in empathy that favor small numbers of identifiable individuals might potentially arise because we process information related to individuals in fundamentally different ways to which we process information on groups of individuals. As Bloom (2017a) puts it "Empathy resonates to the suffering of identifiable victims but is largely silent when it comes to both future costs and statistical benefits." Our empathic responses likely served us well to protect individuals and their small family and community groups from present, visible, immediate dangers, but they did not evolve to help us respond to distant calamities. As a result, researchers have argued that "deliberate mechanisms are needed to counteract the innumeracy and parochialism of empathy" (Västfjäll et al., 2017), and over and above any discrepancy in the definition of empathy, scholars mostly agree that affective empathetical responses should not be used as a guide to social policy, legal systems (Bloom, 2017a,b) and large-scale collective actions of organizations and nations (Västfjäll et al., 2017; Zaki, 2017). These calls for caution are

equally applicable to conservation actions, which should involve careful consideration of statistical and predictive information to guide evidence-based decision making (Urban et al., 2016).

In addition to empathy, compassionate conservation, as the name indicates, asserts that compassion should also become a moral foundation of conservation practice. One problem is that the study of compassion is fraught with even greater terminological debate than empathy – so much so that some consider compassion to be an equally poor guide when assessing what is right and wrong (Västfjäll et al., 2017). For example, some define compassion as "feeling sorrow or concern for the suffering of another person, coupled with the desire to alleviate that suffering" (Keltner et al., 2014), which seems to give compassion the same affective component as empathy. Other scholars of empathy and compassion distinguish between the two by referring to feeling *for* (compassion) vs. feeling *with* (empathy) the other (Singer and Klimecki, 2014). In this framework, empathy – the capacity to feel what one infers others are feeling – is separate from compassion, which involves feelings of warmth, concern and care for others with a strong motivation to help (Singer and Klimecki, 2014). In line with this framework, qualitative research in palliative care suggests that empathy and compassion are distinguishable and are experienced differently by terminally ill patients (Sinclair et al., 2017). Gilbert (2016) has defined compassion as "a sensitivity to suffering in self and in others with a commitment to try to alleviate and prevent it," a definition that brings to the fore the motivation to prevent suffering in the self and others. In a recent review of definitions and controversies, however, Gilbert (2017) reports that compassion has many textures and definitions and it would be unwise to settle on certain definitions without a better understanding of the processes that underpin compassion. Some have argued that the definition of compassion remains too vague to be sure compassion is not biased in the very same way as empathy (Västfjäll et al., 2017). For example, it has been argued that studies investigating biases in empathy are actually biases in compassion. Self-report and psychophysiological data indicate that people's bias toward an identifiable victim (Small et al., 2007b) and single individuals (Västfjäll et al., 2014) are not driven by empathy but rather a loss of compassion (Västfjäll et al., 2014, 2017).

There is an increasing interest in training humans to experience compassion (Klimecki et al., 2013; Weng et al., 2013; Chierchia and Singer, 2017) and a recent systematic review has found small to medium effects on self-reported emotions and observed behavioral outcomes (Luberto et al., 2018). Whether compassion training generates enduring states of being that are free from the biases of empathy and have a smaller risk of apathy is not yet known. Skilled Buddhist monks trained in love and compassion meditation practices for decades hardly seem like a reasonable working model for compassion training in the broader population. Further, if compassion is distinct from empathy but requires large-scale training in the general population, then the breadth and the time lag hardly seem suited to addressing the urgency of the biodiversity crisis.

As Slovic and Västfjäll (2010) put it: "Left to its own devices, moral intuition will likely favor individual victims and sensational stories that are close to home and easy to imagine. Our sizable capacity to care for others may be demotivated by negative feelings resulting from thinking about those we cannot help, or it may be overridden by pressing personal and local interests. Compassion for others has been characterized by social psychologist Daniel Batson as "a fragile flower, easily crushed by self-concern" (Batson, 1983, 1990). Faced with genocide and other mass tragedies, we cannot rely on our moral intuitions to guide us to act properly. All too often, these intuitions seduce us into calmly turning away from massive losses of human lives, when we should be driven by outrage to act. This is no small weakness in our moral compass."

Outpourings of support for individually identified animals, coupled with the frequent indifference of humans toward the destruction of natural habitats suggest that our empathy toward non-humans is fraught with the same biases as our empathy toward humans (Macdonald et al., 2016; Levin et al., 2017; Buhrmester et al., 2018). Gross errors of our empathic responses can be found in our obsession with saving injured wildlife, even if it condemns them to a life in a cage or is ultimately ineffectual (Augee et al., 1996; Sharp, 1996), and feeding wildlife in ways that cause disease and suffering (Bryant, 1994; Orams, 2002). The narrow-minded and innumerate quality of our empathetic responses make them fundamentally ill-tuned to determining whether a conservation action that seeks to safeguard biodiversity is justified or not. Compassion toward non-humans, just like our compassion toward humans, in so far that we even know what compassion is, might well be fraught with the same biases as our empathetical responses and provides no better avenue. To replace reason-based principles with principles that draw upon our empathic responses to living creatures is to formalize, legalize, and solidify our evolutionary biases into decision-making structures. It is likely that evidence of these biases can already be found in conservation practice (Heeren et al., 2017) but based on what we know about our empathic systems, we should be seeking to reduce the influence of empathy, not enhance it.

THE ROLE OF MORAL JUDGEMENTS AND MORAL DILEMMAS IN SPECIES LETHAL CONTROL

Of central concern to those who adhere to the ideas of compassionate conservation is the killing of introduced species as a means to restore and manage ecosystems. For example, rabbits (*Oryctolagus cuniculus*), red foxes (*Vulpes vulpes*), feral cats (*Felis catus*) and common mynas (*Acridotheres tristis*), a songbird, are species introduced to Australia by European colonialists within the last 200 years that are lethally managed across large areas of the country (Mahon, 2009). Lethal control is not limited to introduced species, however, as is evident in management of native songbirds (e.g., noisy miners *Manorina melanocephala*), flying foxes *Pteropus spp.*, and kangaroos *Macropus spp.* (Descovich et al., 2016; Florens, 2016; Beggs et al., 2019). Compassionate conservationists have repeatedly reiterated their opposition to such practices based on the moral principles

"individuals matter" and "first, do no harm" (Bekoff, 2007; Wallach et al., 2018). The conservation practice of killing non-human animals violates legitimate values of life that place the emphasis on individual-level animal welfare.

The problem of killing invasive animals can be viewed through the lens of a moral dilemma. Moral dilemmas arise when two moral rules come into conflict, for example, the moral duty to help vs. the moral duty not to harm. Viewed through the lens of a moral dilemma, lethal control of introduced species creates conflict between adhering to the moral duty to save those animals at risk of extinction, and a moral aversion to inflicting harm on living creatures.

How people resolve moral dilemmas is heavily researched in the fields of moral psychology and moral cognition, and increasingly in the neurosciences (Greene et al., 2001; Christensen and Gomila, 2012; Conway and Gawronski, 2013). The most common experimental paradigm is the "trolley dilemma," which involves a runaway trolley that is heading for five railway workers who will be killed if the trolley continues its course. Participants are asked to take the perspective of a character in the scenario who can choose to leap in and to pull a switch to redirect the trolley onto a different track and save the five railway workers. However, redirecting the trolley on to an alternative track will kill one railway worker who would otherwise not have been killed. The "action" that the character in the scenario can choose to carry out, or to not carry out, is referred to as a moral transgression whereas the choice between the act of committing or omitting to carry out the moral transgression is termed a moral judgment. Other experimental paradigms involve global epidemics, terrorist attacks, desperate survivors on lifeboats, and speeding trains.

Sacrificial dilemmas are used with the view that they provide a useful contrast between utilitarian and deontological principles (Singer, 2005; Greene et al., 2008; Christensen and Gomila, 2012; Conway and Gawronski, 2013; but see Kahane, 2015). Deontology is an ethical theory that advocates the use of rules to distinguish right from wrong actions, whereas utilitarianism is a form of consequentialism, an ethical theory that judges the right or wrongness of actions by their results. The principle of deontology posits that the morality of an action is determined by the inherent nature of the action, while the principle of utilitarianism posits that the morality of an action is determined by its consequences. For example, while inflexible adherence to deontological principles asserts that lying is wrong, consequentialism results in the view that lying is right if it saves someone's life (Schermer, 2007). In a sacrificial dilemma, the decision to commit the harm is referred to as a utilitarian moral judgment, because it weighs costs and benefits (sacrifice one to save a greater number), while the decision to refrain from doing harm, and in the context of such dilemmas "do nothing," is a deontological moral judgment (it is wrong to do so), because it gives more weight to the "do not kill" principle. In the former, aggregate welfare is maximized, while in the latter, adherence to moral rules takes precedence.

Considerable research has examined the psychological mechanisms that underpin dilemma responses (Christensen and Gomila, 2012). Although there is now evidence that affect and deliberative processing play some role in both utilitarian and deontological inclinations, evidence overwhelmingly supports the claim that deontological responses involve relatively more affective processing about harmful actions (Bartels, 2008; Conway and Gawronski, 2013; Conway et al., 2018), mediated by the sensorimotor representations of performing harm (Miller et al., 2014) and in generating harm in others (Christov-Moore et al., 2017). By contrast, utilitarian responses tend to involve relatively more deliberative reasoning about outcomes. For example, requiring participants to undertake another cognitive task while simultaneously making moral judgements makes them slower or less likely to select a utilitarian outcome, but does not affect deontological choices (Greene et al., 2008; Trémolière et al., 2012; Conway and Gawronski, 2013; Jeurissen et al., 2014), while increasing empathy enhances deontological inclinations without impacting utilitarian ones (Conway and Gawronski, 2013). Higher emotional arousal predicts deontological judgment (Szekely and Miu, 2015; Zhang et al., 2017) while lower self-regulation as indexed by resting heart rate variability is associated with utilitarian judgements (Park et al., 2016).

Deontological concerns are positively associated with empathic concerns, perspective taking and religiosity, while utilitarian concerns relate to the need for cognition and the ambition to reason extensively – a component of active, open-minded thinking (Conway and Gawronski, 2013; Szekely et al., 2015). People who make utilitarian judgments tend to score high on measures of reflective thinking vs. intuitive thinking (Bartels, 2008), working memory (Moore et al., 2008), and performance on the Cognitive Reflection Test, a measure of general reflective ability and open-minded thinking to some extent influenced by numeracy (Byrd and Conway, 2019). Positive reappraisal in which thoughts of attaching a positive meaning to negative events reduces deontological choices via its reducing effect on emotional arousal (Szekely and Miu, 2015).

Compassionate conservation's strong stance against lethal control (Wallach et al., 2018) presents the hallmarks of a deontological resolution of the moral dilemma that lethal control creates. That is, faced with the moral dilemma of sacrificing a few to save the many, compassionate conservationists defer from harming anything and in so doing ultimately harm many more (Hayward et al., 2019; Callen et al., 2020). Compassionate conservationists do not want to kill because it is morally wrong to harm, that is, adherence to the moral rule takes precedence over the utilitarian benefit of saving many. This view is consistent with the emphasis of compassionate conservation on individual level welfare, potentially driven by a strong experience of single individual-oriented empathy (Gleichgerrcht and Young, 2013), which in turn acts as a strong motivator to avoid harm. As a result of the deontological moral choice, a "do nothing" approach is favored by compassionate conservationists over intervention. Indeed, compassionate conservationists have been vocal in expressing the view that humans should step back from managing the natural world, and "let nature take over" (Vucetich and Nelson, 2013; Marris, 2018; Wallach et al., 2018).

The deontological resolution of the moral dilemma also explains why compassionate conservation is immune to arguments that killing some animals improves animal welfare

because ultimately it saves more animal lives. For example, when one fox is killed, there can be no doubt that the prey that fox would have eaten during its lifetime will be spared from predation by that fox (Callen et al., 2020). When one rabbit is killed, there can be no doubt that the vegetation it would have eaten remains available to less effective foragers who run less risk of starvation (Dawson and Ellis, 1994). Compassionate conservation is not open to such utilitarian reasoning because for compassionate conservationists, adherence to the moral rule "do not harm" always trumps any kind of utilitarian reasoning, even when it comes to individual-level animal welfare considerations. This inflexible stance is a constant source of frustration in heated exchanges amongst proponents and opponents of compassionate conservation because it results in inherent contradictions amongst compassionate conservations' own principles. For example, if predation by foxes reaches levels where its prey species are reduced to the extent that they can no longer find a mate, or even cease to exist, or if rabbits consume so much vegetation that other animals starve, then the compassionate conservation principle of "first, do no harm" violates the principle of "individuals matter." That violation cannot be resolved without some degree of utilitarian reasoning at the level of individual animal welfare.

CONCLUSION

Much of the driving motivation behind advocates of compassionate conservation seems to originate in an experience of frustration with so-called numerous failures of conservation (Bekoff, 2013). Clearly, despite 40 years of work in the field of conservation science, natural habitats continue to be destroyed at rates never seen before and human activity remains the prevailing force behind the sixth mass extinction. Proponents of compassionate conservation seem convinced that this disastrous state of affairs provides evidence that the utilitarian, evidence-based decision-making frameworks that underpin conservation science have failed and should therefore be overhauled and replaced with empathy and the moral principles of "first, do no harm" and "individuals matter," despite reviews finding conservation actions work (Hoffmann et al., 2010).

We argue that many of these failures are not failures of conservation science *per se*. Scientific principles remain the most powerful means of understanding and predicting the responses of natural systems (Urban et al., 2016). Most of the "failures" result not from the scientific method and the utilitarian principles that aim to restore and maintain biodiversity, but from the way in which conservation-related information is politically manipulated to precisely tap our emotional systems and drive scant resources toward causes toward which we feel more empathy and therefore greater moral duty to act. While some species can serve as a cause to indirectly protect habitat (Poiani et al., 2001; Roberge et al., 2008), many cases receive more attention than they deserve based on utilitarian principles (e.g., whales) precisely because they tap the evolutionary biases of our empathic systems (Small, 2011; Wallmo and Lew, 2012; Colléony et al., 2017). To attack conservation science on moral grounds using the argument that conservation failures prove that the scientific method is not working is to overlook the social and political complexities that lie at the heart of the current biodiversity crisis.

Empathy has its place in fostering pro-environmental attitudes amongst the general public in that it can act as a strong motivator of individual-level action (Eisenberg and Miller, 1987). The person who sees koalas burning in bushfires is suddenly sufficiently motivated to write to their local politician to demand action on climate change. This is good thing in our view and an appropriate application of empathy. Affect is a key component of decision making and without it, people are impaired in their capacity to make decisions (Damasio, 1994; Gupta et al., 2011; Jamil, 2014). But acknowledging and allowing space for affect to drive individual-level pro-environmental actions is a very distinct agenda from advocating that empathy and the deontological moral judgements empathy energizes should be formalized and legitimized into the political and legal structures that underpin conservation action and determine whether or not invasive animals can be controlled. For that agenda, we need to heed the concerns of the scholars of human behavior and avoid being attracted to intuitively appealing but elusive concepts like empathy and compassion, and their associated inflexible adherence to two moral rules.

AUTHOR CONTRIBUTIONS

AG wrote the manuscript with the assistance of KK-T. All authors contributed to the conception, design of the manuscript, literature overview, edited, and improved the manuscript.

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REVIEW
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The Importance of Human Emotions for Wildlife Conservation

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Animals have always been important for human life due to the ecological, cultural, and economic functions that they represent. This has allowed building several kinds of relationships that have promoted different emotions in human societies. The objective of this review was to identify the main emotions that humans show toward wildlife species and the impact of such emotions on animal population management. We reviewed academic databases to identify previous studies on this topic worldwide. An analysis of the emotions on wildlife and factors causing them is described in this study. We identified a controversy about these emotions. Large predators such as wolves, coyotes, bears, big felids, and reptiles, such as snakes and geckos, promote mainly anger, fear, and disgust. This is likely due to the perceptions, beliefs, and experiences that societies have historically built around them. However, in some social groups these animals have promoted emotions such as happiness due to their values for people. Likewise, sadness is an emotion expressed for the threatening situations that animals are currently facing. Furthermore, we associated the conservation status of wildlife species identified in the study with human emotions to discuss their relevance for emerging conservation strategies, particularly focused on endangered species promoting ambiguous emotions in different social groups.

Keywords: anger, disgust, fear, happiness, mammals, reptiles

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INTRODUCTION

Since our origins, wildlife has always had a very important role in human life. The very diverse and continuous human–wildlife interactions can be seen from three main perspectives: (1) Utilitarian, in which wild species provide goods for human well-being, such as food, clothing, transport, tools, raw materials, and companionship, among others; (2) Affective, where human beings feel sympathy, admiration, and respect for animals because of religious, mystical, or philosophical reasons (Kellert et al., 1996), which has greatly contributed to cultural development worldwide (Herzog and Galvin, 1992; Alves, 2012); and (3) Conflictive, because of the real or potential damage that wild species may inflict on people and their interests (e.g., attacks on humans, livestock predation, damage on crops, and infrastructure, among others; Lescureux and Linnell, 2010). Human–wildlife conflicts have motivated animal killings for centuries, which in many cases continue nowadays (Woodroffe, 2001).

Human–wildlife relationships have relied on the uses, values, and meanings that animals represent for people through time and space in different cultures (Driscoll, 1995;

Prokop et al., 2010). Societies have developed a cultural predisposition for emotional reactions toward wild animals (Kellert and Wilson, 1993), causing either positive or negative effects depending on the species (York and Longo, 2017). Fear, anger, and disgust are emotions generating attitudes and behaviors against the presence of some species (Fritts et al., 2003; Jacobs, 2012). In contrast, emotions, such as happiness, which comes out when cherished species are seen in a given place, or sadness before the vulnerability of others, may generate positive attitudes for their conservation (Prinz, 2004). This relationship between human emotions and attitudes has an effect on the presence, absence, and recovery of wildlife populations (Herzog and Burghardt, 1988). Understanding the transcendence of the emotional factors triggered by animals on human beings would improve our knowledge on the human dimensions of wildlife conservation. In this paper, we offer an overview of the influence that emotions have had on the relationships between wildlife and people through time. A substantial amount of the literature reviewed consists of studies conducted on large carnivores in Europe, such as the brown bear (*Ursus arctos*) and the wolf (*Canis lupus*), as well as on snakes around the world. We analyze and discuss relevant aspects that could be considered in further studies on threatened and culturally relevant animal species across Latin American countries.

ORIGINS OF EMOTIONS TOWARD WILDLIFE

Darwin (1897) recognized that emotions are manifested by all persons throughout their lifetime, but they vary in an individual between different moments of its life span. Frijda and Mesquita (1998) mentioned the main points characterizing the emotions in their theoretical perspective: (1) emotions are considered individual responses to relevant events producing feelings of pleasure or pain; (2) they help to find solutions to concerns that cannot be treated routinely; (3) they are always about something, they are used to accept or decline the interaction with a real or imagined object, person, or wild animal in this case; (4) they tend to control behaviors and thoughts (e.g., angry impulses, behaviors, and thoughts); and (5) emotions are correlated with psychological, physiological, and social components establishing, changing, or maintaining a particular relationship with a specific object in a concrete situation.

There is a wide array of studies analyzing human emotions, their origins, functions, and presence in human life (Ekman, 1999; Plutchik, 2001a; Nummenmaa et al., 2014, among many others). Six basic emotions have been proposed: happiness, surprise, disgust, anger, fear, and sadness (Ekman et al., 1969). Izard (2009) suggested classifying emotions into two groups: "positive," representing interest and joy (happiness and surprise), and "negative," including anger, disgust, fear, and sadness. This classification is an artifact of traditional psychology not informed about an evolutionary approach. Here, we have focused on basic emotions to explain human–wildlife relationships because secondary emotions (the combination of basic emotions) are more useful for assessing social relationships among human beings (Harelli and Parkinson, 2008).

In this review, we consider two different approaches to explain the origins of basic emotions aiming to understand human–wildlife relationships through time. The first is the evolutionary approach, which suggests that emotions have evolved to solve adaptive problems in different environments (Plutchik, 2001b), such as social communication, reproduction processes, and mechanisms for information processing leading to behavioral responses to specific events or objects (Al-Shawaf et al., 2016). Predator presence could have been one of such events contributing to the evolution of human emotions and the development of physiological, psychological, and morphological responses for survival (Öhman and Mineka, 2001; Prokop and Randler, 2018). In particular, fear and disgust are adaptive emotions helping to react toward something representing a risk for human life (Ekman and Cordaro, 2011). Fear and disgust, for instance, have been the most studied emotions due to their implications for human survival since the origin of our species (Polák et al., 2019). Fear probably was a defense mechanism against dangerous animals, particularly large predators (Öhman, 1986; Dalgleish, 2004). It is believed that potential alert signals emitted by human groups facing predators, with whom they coexisted and sometimes competed for space, water, prey, and other resources, triggered physiological reactions such as heart rate increase, profuse sweating, and pupil dilation, allowing the generation of alert responses. In that way, human beings have historically developed greater awareness toward potentially perilous animals, such as snakes and spiders (Öhman et al., 2001; Öhman and Mineka, 2003; LoBue and DeLoache, 2008). This adaptation mediated by fear has probably been genetically fixed throughout generations, provoking the innate physiological responses mentioned above when dangerous species are or could be present (Öhman, 1986). The amygdala is the brain region where fear-generating stimuli are processed into a strong reaction that in some cases may affect human vision (Phelps et al., 2006). On the other side, disgust can help protect the individual against infections and disease (Curtis et al., 2011). Disgust is saved in memory to avoid future exposure to the subject, in this case with potentially threatening animals (Al-Shawaf et al., 2016).

The second approach explaining the origins of basic emotions is the cultural context, where people integrate their physical environment with individual and collective experiences, perceptions, meanings, attitudes, and animal-related traditions to construct emotional diversification (Prinz, 2004; Johansson et al., 2012). In this view, it can be said that human emotions associated with wildlife have evolved over time and continue to be gradually built and rooted in our societies all over the world. Under the cultural context approach, emotions can be understood on two levels: (1) the individual level, involving meanings, beliefs, attitudes, and behaviors based on personal experiences, knowledge, and perceptions, and (2) the social level, where emotions are determined by collective factors such as experiences, meanings, beliefs, and myths typical of a certain region or culture, which are transmitted among individuals throughout generations (Ekman, 1999; Prinz, 2004).

SPECIES-SPECIFIC EMOTIONS

Physical characteristics of wildlife species and their "personalities" created by humans have generated a variety of emotions (Kellert et al., 1996; Kruuk, 2002; Prokop and Randler, 2018). Emotions such as fear and anger may be induced by predators that are bigger and heavier than persons, as in the case of large carnivores (e.g., bears, wolves, and big cats) (Røskaft et al., 2003) or by those species unattractive for most people, like worms, small carnivores, bats, and reptiles, which are often perceived as harmful (Knight, 2008; Prokop and Tunnicliffe, 2008; Prokop et al., 2009). In contrast, beloved animals such as colorful birds or small herbivore mammals (e.g., rabbits) may cause happiness providing they are not noxious for people or their livelihoods (Prokop and Kubiatko, 2008). However, these animals are sometimes perceived in different ways. For some social groups (e.g., farmers), small mammals such as rabbits as rodents may represent a threat due the damage they can inflict on crops, cattle, properties, and human health (Morzillo and Merting, 2011; Breed and Moore, 2016). Actual or potential damage can promote negative attitudes motivated by emotions of anger, disgust, and fear.

Animal body shape is another physical feature that has been found to be important for the expression of emotions such as fear and disgust. In the case of class Reptilia, two groups could be recognized by people according with their similar morphotype (with legs and legless). Reptiles with legs (lizard, turtle, and crocodile) tend to cause fear in many people; crocodiles, specially generate intense fear in many people, in part because of the number of attacks occurring worldwide (CrocBITE, 2020). In contrast, legless reptiles (e.g., amphisbaenia and *Larutia*) that have thin bodies, smooth textures, small eyes, and dull colorations generate disgust (Janovcová et al., 2019; Rádlová et al., 2019). Specifically, snakes have long bodies, scales with contrasting patterns, bright coloration, and silent, rolling movements that immediately calls up human attention (LoBue and DeLoache, 2008, 2011; Rádlová et al., 2019). It is likely that both fear and disgust can be simultaneously felt by a person observing a particular species (Rádlová et al., 2019). The ample diversity of snakes around the world makes it difficult to generalize emotions across cultures toward different taxa.

Species coloration has been an attribute to help identify dangerous animals (Prokop and Fančovičová, 2013), allowing emotional responses in human beings (Öhman, 1986). Striking color ("aposematic") combinations such as bright red and black in some snakes and spiders intensify fearful reactions (Öhman and Mineka, 2003; LoBue and DeLoache, 2011; Prokop et al., 2018). On the other hand, it has been reported that striking coloration allowed perceiving snakes as beautiful animals (Marešová et al., 2009) in spite they are fearsome (Janovcová et al., 2019). It is noteworthy that aposematic species are simultaneously fearsome and attractive particularly for young persons between 10 and 20 years of age, promoting their interest in those animals (Prokop and Fančovičová, 2013). On the other hand, animals' coloration could be attractive for humans and motivate "positive" feelings. In this sense, Lišková et al. (2015) discovered that hues of blue and green in birds of the Pittidae family promote human preference. Psychologists have found that green is usually associated with happiness, relaxation, and comfort because it is related to nature, while blue elicit happiness, relaxation, and peacefulness, among other feelings (Kaya and Epps, 2004). However, human affection for birds also represents a pressure for wild populations, especially for those charismatic species used as pets, promoting illegal trade (Alves et al., 2013).

Feeding habits of species may also influence emotions: large predators are usually regarded as hazardous and fearsome, while their prey provoke sadness (Prokop and Kubiatko, 2008). Large herbivores and omnivores in some places are often seen as less fearsome than strict carnivores. This is the case of the mainly vegetarian brown bear (*Ursus arctos*) in some regions of Europe (Lescureux and Linnell, 2010). However, in other areas and cultures, large herbivores such as elephants (*Loxodonta africana*) cause intense emotions of anger and fear because of the damage they inflict on crops and rural villages (Lamarque et al., 2009). Although "dangerous" animals promote the attention of people (Prokop and Randler, 2018), it is interesting to note that human emotions may vary depending on the life stage of the animal. For example, jaguar (*Panthera onca*) cubs and lion (*Panthera leo*) cubs are perceived as lovely and safe animals given their physical features, causing minor concern in societies, while adult jaguars and lions are generally considered less attractive and very dangerous, promoting fear (Knight, 2008). This trend is also reported for amphibians, for which people show more disgust toward the adult stage than for tadpoles (Prokop and Fančovičová, 2012).

Venom in animal species is one of the most remarkable features triggering fear across cultural groups. As a consequence, snakes constitute an interesting case study in which most species produce fear all over the world, although particular species are in fact perceived as beneficial due to their role as controllers of agricultural pests, producing positive feelings in local farmers (Ballouard et al., 2013). In this regard, Ballouard et al. (2013) observed different intensities of fear toward selected snake groups (cobras, vipers, and boas) depending on the nationality and cultural background of their interviewees.

Animal activity patterns constitute one more physical factor influencing human emotions toward wildlife. Humans are not adapted for living in the darkness; they have a poor vision to act in this kind of environment, hence they may associate nocturnal species such as felines, some snakes, rodents, and bats with danger (Buss, 2016). In addition, these animals historically have been linked to "evil forces" damaging human beings worldwide (Prokop et al., 2009). Contrastingly, many diurnal species (e.g., most of the birds and ungulates) are usually related to positive values such as peacefulness and wisdom that have inspired leaders and rulers to make better decisions (Cano-Contreras, 2009).

Physical characteristics have been useful to classify animals depending on the emotions they produce on people. In this sense, tarantulas, snakes, sharks, and mosquitoes have been categorized as perilous, generating agonistic emotions. Contrastingly, large, charismatic species that have traditionally been regarded as dangerous but intelligent at the same time motivate emotions that may result in actions for their protection, as it has occurred for lions (*Panthera leo*), tigers (*Panthera tigris*), leopards (*Panthera*

pardus), and polar bears (*Ursus maritimus*) (Driscoll, 1995; Landová et al., 2018). These categories have emerged after the anthropomorphization of animals, a process in which cultural groups attribute human features and "personalities" to wildlife species (Kruuk, 2002). For instance, the panda bear (*Ailuropoda melanoleuca*) inspires tenderness and happiness when it is observed, but those emotions are overcome by sadness after considering its high vulnerability to extinction. In this case, positive attributes facilitate particular species to become flagships for wildlife conservation (Root-Bernstein et al., 2013).

In rural communities where people frequently interact with wildlife, knowledge about the behavior of culturally relevant species develops better than in other areas. This facilitates the anthropomorphization of certain animals calling them "shy," "noxious," and "monstrous," among other adjectives, which intensifies fear and rejection toward them (Lescureux and Linnell, 2010). Furthermore, if the presence of an animal implies economic losses for residents of a community, their predominant perception will be negative and will produce anger that may end in lethal management (Naughton-Treves, 1997). Contrastingly, animals inspiring greatness and qualified as "kings" of the wilderness will likely motivate local people to feel happiness and pride because of their presence in the region (Lescureux and Linnell, 2010). These examples help identifying the relevance of animal physical features in emotions, which transform throughout history according to the natural, social, and economic context of each human generation. In some cases, emotions produce attitudes against the conservation of unpopular species (Knight, 2008). Therefore, we propose to highlight the ecological role of dangerous or disgusting species as a potential way to mitigate negative emotions toward them.

EMOTIONS AND SOCIODEMOGRAPHY

Emotions induced by wildlife differ among individuals according to variables such as their sex, age, cultural and natural environment, and perceived vulnerability to each species (Johansson et al., 2012). It has been shown that young children (under 3 years of age) of both sexes take more time to detect a snake and react toward it than their parents (LoBue and DeLoache, 2011). That behavior was explained by DeLoache and LoBue (2009), proposing that fear and alert signals in front of this kind of animals develop later, when individuals start to explore their environment and link adult behaviors with animal species.

Fear and disgust have been the most studied emotions between genders. In general, women tend to express stronger negative emotions (fear and disgust) toward invertebrates, amphibians, predatory mammals like bears, wolves, lynx (*Lynx lynx*), and wolverine (*Gulo gulo*) and toward snakes compared to men (Öhman and Mineka, 2003; Røskaft et al., 2003; Ballouard et al., 2013; Bajwa et al., 2014; Prokop and Fančovičová, 2016; Prokop et al., 2016). This difference seems to be related to the female gender role taken since the start of human evolutionary history, where men developed skills for both hunting and escaping from predators (Prokop and Fančovičová, 2010). Likewise, men gradually reduced their fear of large animals, while women kept distance from those species in part because of their household activities and their care for children in safer places (Røskaft et al., 2003; Prokop et al., 2011). However, differences within genders are usually present in different cultural and geographic contexts (Kellert and Berry, 1987; Bjerke et al., 2001; de Pinho et al., 2014). In some societies, women, particularly adolescents, have a greater disposition to spend more time in wildlife related activities as compared to men (e.g., volunteer programs; Kidd and Kidd, 1997). This information could be useful to direct conservation programs in spaces as zoos where experiences with uncharismatic and endanger animals could help to promote positive emotions and attitudes.

Age is a significant variable determining the presence and intensity of agonistic emotions toward animals, which may be related to personal experiences. Childhood is the critical life stage when fear of predators starts and when attitudes and behaviors to avoid encounters with them develop (Öhman, 1986). It is likely that fear of predators intensifies with learning from parents, given that as the child gets older, his/her reactions become faster when facing species such as snakes (LoBue and DeLoache, 2008). In this regard, fear of animals may either decrease (Kaltenborn et al., 2006) or increase (Røskaft et al., 2003) with age.

Besides age, the natural and cultural environments in which an individual grows determine the knowledge, perceptions, and emotions related to animals (Frynta et al., 2011). For a person raised in close contact with nature, an encounter with a wild animal can induce happiness, while the same species may produce fear in an individual that has always lived far away from natural spaces (Kellert, 1993; Manfredo, 2008; Almarcha, 2019). The presence or absence of different species in human territories has a role in the generation of emotions. Residents of rural areas who frequently interact with wildlife are usually less fearful of animals than city dwellers. This is because closeness with native animals promotes knowledge about their ecology and behavior, allowing for building better management strategies and reactions toward them (Røskaft et al., 2003).

Likewise, recreational activities involving contact with wildlife such as hiking, bird watching, fishing, and hunting have direct influence in emotions, facilitating the overcoming of fears and phobias by promoting learning through first-hand experiences, although in some cases, these activities decrease with age (Bjerke et al., 2001; Røskaft et al., 2003; Prokop et al., 2011). In particular, emotions produced by hunting deserve further discussion. Subsistence hunting as a traditional practice in many rural areas of the world usually involves local regulations to avoid overexploitation and feelings of respect by the hunters toward their prey (e.g., Santos-Fita et al., 2015). In contrast, sport hunting is more focused on the pleasure of the hunter for finding and killing his target species, which has been a motive social dispute in different contexts, generating anger in broad sectors of society considering this an unacceptable practice (Nelson et al., 2016). Some of these recreational activities involve parents and their children, who get used to those practices at an early age (Amiot and Bastian, 2015). This can be an important inter-generational strategy to avoid negative attitudes toward fearsome and disgusting animals and promote positive emotions

(i.e., happiness and surprise), especially in areas where human–wildlife conflicts may arise.

Significant differences have been found among people with different levels of study with respect to fear of wildlife species: individuals with higher levels of education are generally less fearful of wild animals than those with lower degrees of studies (Røskaft et al., 2003). It is likely that individuals with higher education had more opportunities to receive information on the environment and wild animals in particular, which may have reduced their negative prejudices and perceptions about non-charismatic species, maximizing their perspectives on the ecological benefits provided by those animals.

EMOTIONS THROUGH TIME AND SPACE

The geographic space where an event occurs triggers distinct emotions, which have varied according to the lifestyles of societies (Mesquita and Frijda, 1992). This argument could be used to understand emotions historically induced by wildlife, considering the different worldviews of each culture. For example, snakes were regarded as deities in Mesoamerican cultures, including *Quetzalcoatl* or *Kukulkan* (the feathered serpent), which was the most important deity for the Aztecs and the Maya, respectively (Díaz, 2007). Snakes were also given high rankings among the deities of the ancient Greek, Egyptian, Hindu, and Roman civilizations, where some of these reptiles were associated with values of wisdom, justice, and power (Stanley, 2008; Al-Rawi, 2012). These reptiles have also starred countless stories and myths around the world (Ménez, 2003), but for Christians, Muslims, and Jews, snakes have traditionally represented evil and death (González, 2003; Al-Rawi, 2012). Nowadays, myths about the damage caused by snakes are important elements to promote and intensify fear in rural communities (Fita et al., 2010). The social fear could be learned, inherited, and used by societies across generations, driving particular attitudes toward wild species (Öhman, 1986). In this case, the relevant ecological role of snakes as predators and pest controllers has been largely neglected.

Another interesting example is that of wolves, which have been protagonists of many stories and myths worldwide. These carnivores have traditionally been portrayed as fearsome and dangerous animals, producing social rejection in most areas where they are present, nonetheless, in particular cases such as that of ancient Rome (whose founders were suckled by a she-wolf) and that of native North American cultures, for whom wolves were spiritual symbols related to power and intelligence (Fritts et al., 2003; Prokop et al., 2011).

Beyond mythology, other elements that have facilitated the development of cultures (e.g., art, literature, symbolism, religion) have had their foundations in the relationships between humans and wildlife, involving emotions promoting respect and admiration (Fritts et al., 2003; Alves, 2012; Almarcha, 2019). These emotions frequently lead to attitudes favorable for animal care and conservation.

Other events that have always happened, but which have received special attention in recent decades because of the human population growth and expansion, are the attacks of large carnivores on people and livestock, and crop damage by large herbivores (Inskip and Zimmermann, 2009). These events make jaguars, tigers, lions, leopards (*Panthera pardus*), hyenas (*Crocuta crocuta*), African wild dogs (*Lycaon pictus*), and African elephants (*Loxodonta africana*), among others, be considered problems in rural communities, giving place to misunderstandings and false beliefs about their behavior (Marchini and Macdonald, 2012; Dickman et al., 2014). This situation has contributed to magnification of the actual damages of those species, stimulating even more fear, disgust, and rejection toward them (Lescureux and Linnell, 2010).

In this sense, the individual background and experiences of humans contribute to their emotions and behaviors. For example, the presence of large predators may produce fear and thoughts of escape in most people, while some others may feel encouraged to confront the danger (Al-Shawaf et al., 2016). The context of the encounter with an animal may also be relevant for the emotions manifested. For a given person, the sighting of a carnivore such as a female puma with their offspring while hiking on a forest trail may produce fear and desire to escape. In contrast, the same person may feel surprised and delighted to have the same sighting from the safety of a car (narratives collected by the first author in Chiapas, Mexico). Furthermore, local knowledge and the emotional links between people and wildlife could be useful to identify flagship species to foster interest in nature (Bowen-Jones and Entwistle, 2002). Flagship species [e.g., giraffe (*Giraffa camelopardalis*), elephants, and lions, among others] are usually charismatic and popular and may be relevant for promoting positive emotions in a public that has been distant from wild animals. Differently, more complex sets of emotions (both positive and negative) are usually present where people are in constant interaction with these animal species (Bowen-Jones and Entwistle, 2002; de Pinho et al., 2014).

Zoos represent spaces where emotional confrontations take place. For instance, Marseille et al. (2012) observed visitors watching imposing and charismatic polar bears. The authors found that visitors felt happy in front of the bears, but at the same time they felt sad after recognizing the small size of the enclosures and the stereotyped behavior of the captive animals. Interestingly, visitors' emotions transformed into fear and even greater sadness when they were told about observing polar bears in their natural habitat, which was associated with concerns about human safety and habitat vulnerability. Another element that has an effect in the affection of children for wild animals is the presence of pets (Bjerke et al., 2001). Pets can boost appreciation emotions, such as happiness, while naturalistic, ecological, humanistic, and moralistic attitudes may also be encouraged (Prokop and Tunnicliffe, 2010).

MISINFORMATION CAUSES A MIX OF EMOTIONS

Although knowledge about animals usually differs between urban and rural communities, the lack of accurate information about the species and their contribution to ecosystem services is persistent in both environments (Gomes et al., 2017). It

promotes the intensification of emotions such as danger and disgust, especially for species that are unattractive to people. Disgust has also been identified as one of the emotions inducing human rejection. It may arise when people perceive nasty odors in animals, or when unpleasant feelings emerge while touching (or thinking about) the fur of certain mammals (Johansson et al., 2012) or the skins of amphibians such as frogs (LoBue and DeLoache, 2011). In other cases, disgust may be brought after linking animals such as spiders and rats with dirtiness, pollution, disease spreading, and potential crop damage (Kellert, 1993; Davey, 1994; Prokop and Tunnicliffe, 2010). Furthermore, animals that cause disgust are often perceived as ugly (Janovcová et al., 2019).

Contempt of human societies for amphibians and reptiles intensifies misinformation about them and favors negative attitudes toward them (Manzano-García and Martínez, 2017). For example, it has been documented that non-venomous snakes are killed just because of their resemblance to poisonous species (Breed and Moore, 2016). Moreover, misinformation is an intensifier of disgust, for instance, when considering geckos (*Hemidactylus turcicus*) as venomous animals or vectors of skin diseases (Ceríaco et al., 2011), or bats as a threat for fruit crops and responsible to infect people with parasites and viruses (Musila et al., 2018). In this sense, the case of bats and pangolins (Pholidota) could be cited, which are considered the main transmitting agents of the novel coronavirus (COVID-19; van Staden, 2020). The respiratory illness has become a pandemic infecting million and killing many thousands of people around the world (Nature, 2020). It is likely that the disease has a zoonotic origin as a result to the food and medicinal uses of animals (van Staden, 2020). Therefore, in some places there has been motivation to eliminate these animals (Zhao, 2020). This event might increase the negative perception and emotions of anger, disgust, and fear for this kind of animals and will encourage the eradication of populations without considering their importance in ecosystems. In this regard, it has been found that women and residents living near caves tend to believe in myths about bats more than men and people living far from caves (Musila et al., 2018).

BIOPHILIA VERSUS BIOPHOBIA

Fearsome and disgusting species frequently induce rejection attitudes in social groups (Öhman and Mineka, 2001), a phenomenon known as "biophobia" that is used to express the feeling of panic, fear, and disgust in front of a particular non-human living being. Phobia for animals (agrizoophobia) is one of the most frequently reported biophobias in the general population (Antony and McCabe, 2005), but there are actually around twenty-five documented phobias to particular animal groups, such as that for snakes (ophidiophobia), spiders (arachnophobia), insects (entomophobia or insectophobia), ants (myrmecophobia), bees (apiphobia or melissophobia), and birds (ornithophobia), among others (Fredrikson et al., 1996; Antony and McCabe, 2005; Prokop and Fančovičová, 2013). However, there are no specific phobias for carnivores, probably because the coevolution between humans and these animals has been too short in comparison with other groups such as snakes (Prokop and Randler, 2018).

Biophobia may promote persecution and extermination attitudes (Zhang et al., 2014). Avoiding contact with animals or killing them are the most frequent reactions without considering their long-term impacts on ecosystems (Antony and McCabe, 2005; Al-Shawaf et al., 2016). Orr (1993) mentioned that one of the causes of biophobia is social distancing from nature. In a parallel way, biophilia has a genetic basis and consists of the interest and empathy of humans for other living beings (Wilson, 1993). As industrialization and urbanization increase around the world, lifestyles change in human societies, sometimes in radical ways (Steffen et al., 2008). These processes have contributed to the distancing of people from their natural environment even in rural communities (Louv, 2008; Lescureux and Linnell, 2010). However, there are still spaces such as zoos and natural parks facilitating social approach and understanding of wildlife in most of the cities and large towns all over the world. In those spaces, visitors are generally safe in front of animals that otherwise would be considered dangerous or harmful, and they may feel sadness and even culpability after recognizing the impact of the human population on those species. In this sense, Vining (2003) suggested that visiting zoos and natural parks may represent opportunities for reconnecting people and wildlife to enhance social cooperation in conserving biodiversity.

EMOTIONS AND WILDLIFE CONSERVATION

Human emotions transcend over time. A specific emotion is saved by the individual as an experience that may be used in future behavior and decision-making (Izard, 2009). Protection attitudes toward spiders, insects, amphibians, and reptiles are milder than those shown for other groups, such as birds and mammals due the sentiments of danger or disgust that these animal groups provoke in humans (Prokop and Fančovičová, 2013; Prokop et al., 2016). In addition, emotional experiences may have an effect on wildlife management techniques (Larson et al., 2015). This has occurred during experiences of invasive species management. One example is that of the house sparrow (*Passer domesticus*), which competes for food and space with native birds and generates anger or disgust when managed through nest and egg removal, repellents, and traps. In contrast, bluebirds (*Sialia sialis*) stimulate happiness in people watching them and listening to their songs, who at the same time feel sadness for these birds due to the negative impact of human activity on their populations. These feelings motivate protection attitudes favoring the persistence of the liking bird species (Larson et al., 2015).

It is important to recognize that fear impacts human attitudes and behaviors toward keystone species, particularly those regarded as dangerous or harmful (e.g., wolves, bears, and big cats). Fear may limit the involvement of local communities in managing predator populations because of the high costs implied or because the social acceptance of certain techniques,

such as reintroduction, may be difficult (Johansson et al., 2012). Examples of this include reintroducing wolves in Mexico and the United States, where emotions have played fundamental roles in the acceptance of new wolf populations (Straka et al., 2019). Mexican wolves (*Canis lupus baileyi*) were eradicated from the Mexican territory in the 1960s because of conflicts with farmers and negative perceptions due to livestock predation (Leopold, 1959; Moctezuma et al., 2004). Wolf reintroduction projects have been started recently in Northwestern Mexico, where it has been clear that social acceptance is the primary limiting factor for their success (Araiza et al., 2012; García, 2014; Lara-Díaz et al., 2015).

Society's emotions toward wildlife may be key elements for decision-making on conservation issues. Anger is one of the primary collective emotions that can lead to positive changes for natural resource management when social pressure is put on government leaders to improve and enforce environmental legislation. However, anger may have other implications and cause social fragmentation (Buijs and Lawrence, 2013). In these cases, participation of wildlife management agencies is crucial given their social confidence. If the capacity of these agencies is not appropriate, collective distrust and fear of dangerous and disgusting animals may stimulate hostile environments for their proper management (Johansson et al., 2012). Community confidence in environmental agencies is especially relevant where threatened species are under recovery, as is the case with wolves in different countries (Swenson and Andrén, 2005), or where people take action by themselves, such as in the case of the killings of Andean bears (*Tremarctos ornatus*; Figueroa, 2015).

It seems clear that some wildlife species are far more significant to humans than others (Herzog and Burghardt, 1988), perhaps linked to their evolutionary closeness (e.g., primates, and particularly the great apes; Gunnthorsdottir, 2001; Miralles et al., 2019) or because of their cultural, aesthetic, or affective attributes favoring more interest and attention toward them. Interest and attention favor people's attitudes for conserving these species, differently from others without a transcendental meaning for social groups. This idea highlights the relevance of designing conservation strategies fomenting interest for wildlife through generating affective links between humans and animals both in rural and urban areas.

Beautiful and attractive animals causing "positive" emotions (e.g., happiness and surprise) receive special attention driving *in situ* and *ex situ* conservation actions (Gunnthorsdottir, 2001). This could be a limitation for conservation efforts focused on species considered unattractive particularly in zoos. The preferences of human societies to watch specific animals have promoted that zoos keep attractive species more than those needing protection due to their conservation status (Frynta et al., 2010, 2013). Mammals constitute the preferred group among zoo visitors around the world (Moss and Esson, 2010). However, these spaces keep only 179,868 individuals belonging to 1,048 species (Frynta et al., 2013), which represent just 16.4% of known living species (Burgin et al., 2018). This preference is strongly biased toward large, attractive, and active mammals belonging to the families Ailuridae, Felidae, Phascolarctidae, Ursidae, Giraffidae, Elephantidae, Equidae, Macropodidae, Mephitidae, and Cervidae, among others (Frynta et al., 2013). The same correlation between human preference and species kept in zoos was found for large, colorful, and long-tailed parrot species (Frynta et al., 2010). In contrast, small and unpopular species do not motivate the same appreciation, even if they are endangered. As a consequence, zoos generally keep a few of those local species (Frynta et al., 2013). In this sense, zoos and other places keeping wildlife need to implement exhibition strategies to promote human interest on less attractive but highly relevant animal species of threatened ecosystems (Bitgood and Patterson, 1987; Frynta et al., 2009).

Considering this distinction in preference, it is relevant to spread information about the ecological importance of animals in ecosystems, especially regarding native and endangered species (Conde et al., 2011), Messages to promote "positive" emotions in people could be a way to support the appropriation of endangered species by societies and improve their attitudes toward them in the long term. Massive media communication may be of utmost importance for these purposes, especially if the appropriate images of and messages about target species are transmitted to the general public (Gunnthorsdottir, 2001). Following Breed and Moore (2016), successful conservation projects require focusing on promoting wide social empathy for wildlife species, particularly those that generate fear and disgust (e.g., large predators, venomous species, and many amphibians) motivating their killing or removal (Bishop et al., 2012; Prokop and Fančovičová, 2012; Prokop et al., 2016).

FINAL REMARKS

Individual and collective idiosyncrasies have promoted a diversity of attitudes toward wildlife species (Herzog and Burghardt, 1988) motivated in part by a diversification of emotions built with dynamic biological and cultural elements. Identifying and understanding diversified emotions and their local precursors (e.g., in areas where protected areas and human presence are relevant) would allow analyzing wildlife problems and their solutions through multidisciplinary strategies.

Considering that knowledge is a relevant element for the expression of emotions, we propose that regional strategies to integrate information on the biology, ecology, and management of culturally important animal species (particularly those regarded as fearsome, dangerous, harmful, and disgusting) should be included in national education systems and massive media campaigns throughout the Neotropics (Espinosa and Jacobson, 2012). These strategies must be carefully designed by taking into account the impact of mass media (e.g., news, television shows, documentaries, films, and public text books, among others) may have on the public about wildlife conservation (Røskaft et al., 2003; Knight, 2008; Ceríaco et al., 2011; Wieczorek, 2012). When an animal species is projected as aggressive, a negative emotional experience can be produced in the public. This negative experience may in turn lead the individual to believe the species is a dangerous agent or threat to human life, bringing about attitudes against its conservation (Prokop and Fančovičová, 2017). On the contrary, if wildlife species are positively seen by children through different media

outlets, where the real facts about unpopular animals are shown, it is more likely that fear and disgust decrease, while empathy may grow (Prokop et al., 2011). Ensuring the continuity of transmitting traditional ecological knowledge about animal species will be equally important to stimulate positive emotions and a long-term interest of the new generations in wildlife conservation (Jacques-Coper et al., 2019).

Another strategy that could have a positive impact on emotions toward fearsome and disgusting animals is promoting physical interactions with them (e.g., touching snails, rays, amphibians, mice; Randler et al., 2012; Prokop and Fančovičová, 2016); the new knowledge about the animals and physical contact with them could reduce the anxiety of danger. Recognizing that emotions are culturally influenced, we propose developing outreach strategies by retrieving traditional aspects that formerly favored empathy with animal species, including the non-charismatic or unpopular ones, even if they are threatened.

This review aimed to discuss the role of emotions in the conservation of species which a have been transcendent for the human species throughout history and that in many cases are currently threatened by extinction. In particular, we stress that the social component is of utmost importance in wildlife conservation across Latin America, especially in megadiverse countries where ethnozoological studies have documented the relevance of human–wildlife relationships (Jácome-Negrete et al., 2013; Sarukhán and Dirzo, 2013; Manzano-García and Martínez, 2017).

AUTHOR CONTRIBUTIONS

NC-H wrote and edited the manuscript. EN translated and edited the manuscript. DS-F and EE-L edited the manuscript. All authors read and approved the final manuscript.

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OPINION
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The Concept of Radical Responsibility for Non-human Animals

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Keywords: human-animal relations, animal ethics, radical responsibility, moral response, animal use ethics, animal usage

INTRODUCTION

As La Follette said, "we are [...] part of a culture which rather cavalierly uses animals for food, clothes, for research in the development of new drugs, and to determine the safety of household products or cosmetics. And many of these uses require inflicting a great deal of pain on animals" (La Folette, 1989, p. 80). From this point of view, I assume that we should look at non-human animals not from a human-related perspective but from a suffering-related one (Nussbaum, 2004), as suggested by (Bentham, 2000 – first edition 1781). Only then can cruel practices be limited. In this opinion piece, I claim that radical responsibility is conducive as a tool to direct our actions so that they minimize the suffering of non-human animals derived from those actions. Only radical responsibility covers all ranges of animal uses that are present in Western culture—those presented as *explicite* as well as those presented as *implicite* in our daily lives. Thus, I present the concept of responsibility present in previous animal/environmental ethics discussions[1].

MORAL RESPONSIBILITY IN ETHICS

Responsibility for one's actions is one of the most important concepts in ethics, and it is strictly connected to the issue of blameworthiness and praiseworthiness. Moral responsibility has the following formula: "subject S is morally responsible (i.e., blameworthy or praiseworthy) to degree *d* for object O" (Khoury, 2017, p. 2). It involves a three-place predicate that relates to certain subject and object. Historically, many philosophers have focused on individual responsibility. However, after the World War II, some philosophers raised the issue of responsibility as a constructive answer or explanation to what has happened (Jonas, 1987; Levinas, 1987). Others philosophers rather focused on its collective context (Lewis, 1948; Feinberg, 1970; Arendt, 1987). According to (French, 1976, p. 443–444), this situation is similar to the object of our responsibility—it can be an individual action or collective action, i.e., action that can be brought about collectively. In terms of animals, this distinction applies as well.

Apart from the two mentioned distinctions, Khoury (2017, p. 3) also introduced a temporal distinction in the concept of responsibility, namely, synchronic responsibility and diachronic responsibility: "More precisely, synchronic responsibility concerns the extent to which an agent at time t_1 is responsible for an action that occurs at t_1. Diachronic responsibility concerns the extent to which an agent at some later time t_2 is responsible for an action that occurred at t_1. Synchronic responsibility involves the responsibility of an agent at the time of action, while diachronic responsibility involves the responsibility of an agent at some time after the action occurs" (Khoury, 2017).

[1]The differences and connections between these two disciplines are explained by Criscuolo and Sueur (2020).

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MORAL RESPONSIBILITY AND ANIMALS

Throughout the history of Western normative ethics, moral responsibility has applied to relations between human beings. However, the idea of widening the moral circle has for some time been present in animal ethics and environmental ethics in the postulate of an expanding moral circle (Singer, 1981) or, to put it differently, an enlarging *moral consideranda* (Birch, 1993). Both concepts claim that our moral obligations are not limited to human beings only. Thus, whom should we consider? All ecosystems (Leopold, 1949)? All living beings (Taylor, 1986)? All sentient beings (Singer, 1975)? Even though I, in this opinion piece, adopt an ecocentric perspective, I focus only on our relationship with non-human animals from the perspective of our responsibility for them. I put forth the concept of responsibility to overcome the ambiguity—or, as it is called by Francione (2000), moral schizophrenia—that marks our relations with animals. The concept of radical responsibility is proposed to be included in our moral choices, as non-human animals can suffer. It is built on the double theoretical foundation—on Hans Jonas' concept of responsibility for the environment as well as on Nigel Dower's claim of radical responsibility.

Jonas' works (Jonas, 1979, 1982, 1984) outlined and elaborated on the concept of responsibility that appeared for the first time in Georg Picht's publications (Picht, 1969), namely, the idea of responsibility for the environment. Thus, claiming that not only human beings are the subjects of moral responsibility, "Hans Jonas considers all nature as an object of human responsibility" (Mantatov and Mantatova, 2015, p. 1,057). However, animal exploitation is so strongly rooted in western culture that simple responsibility for nature is not enough—we need a radical form of responsibility, much like that found in Dower's writings.

THE RADICAL RESPONSIBILITY

Radical responsibility is a form of moral responsibility that pushes our moral obligations further. It states that we are responsible "for the unintended (and often unnoticed) consequences of our actions and our failures to act" (Dower, 1989, p. 18). Radical responsibility is not only related to our actions, but Dower also introduces the concept of an indirect footprint on something that includes responsibility for what others have done for us.

This therefore raises a question of responsibility for when we do not perform a deed ourselves but we let the things being done for us or we do not act to prevent some actions even if they are morally wrong or dubious. Nigel Dower explore this issue; he asks a question about the so-called logic of omission and provides an explanation of it. According to him, "there is one difference between typical cases of killing and typical cases of letting die. Whereas, with killing the death of someone is what is intended, either as an end result or as a necessary means to an end; with "letting die" the death of someone is neither what one aims to achieve—one does not want them to die—nor is it a means to some other end. It is simply an unwanted and often unthought of consequence of pursuing one's other objectives" (Dower, 1983, p. 22). However, in terms of the concept of indirect footprint, we are still responsible for it; the unwanted or unthought consequences of our actions are still in the range of our moral responsibility, and we should act in a way that enables us to escape it. Dower claims that "if it is in our power to prevent something very bad happening without thereby sacrificing anything of moral importance, we ought to do it" (Dower, 2018). Peter Singer also makes a very clear point about not acting when one can do something to prevent the wrong things from happening: "passivity, when people are able to act to prevent evil, is morally wrong" (Singer, 1985, p. 834).

RADICAL RESPONSIBILITY AND NON-HUMAN ANIMALS

The human–animal relation is a complex one. It involves all abovementioned forms of moral responsibility, and this could be seen in many cases of animal uses, such as in analyzing animal experimentation. For example, a subject might be the individual and collective; the individual researcher holds a responsibility for his experiments, but he is also a part of bigger community that enabled him to conduct experiments on animals (for example, ethical committees that allow the use of animals, research funding institutions, the whole of the research community that agrees that *in vivo* experiments are an agreeable practice, and even administrative or technical workers that make experimentation possible or are part of it). The object of our responsibility might be individual or collective. To provide compelling evidence, the research must be carried out on a group of animals. Only this will provide profound data. This collective sacrifice of animal lives includes a significant amount of non-human animal suffering (see Singer, 1975). The temporal dimension is also included in animal use, as the researcher is responsible synchronically as well as diachronically for the pain inflicted during experimentation (for example, if a non-human animal is not provided with proper anaesthetization) as well as long-term consequences (for example, if animal is not cared for properly after experimentation or experimentation causes durable consequences that condemn an animal to euthanasia). These are some of the examples of responsibility for animals that have been discussed for quite a long while, at least since Singer's (1975) eye-opening publication.

However, the human–animal relation is far more complex; most of non-human animal uses or exploitation involve a lack of our direct engagement into actions. In most cases involving animal suffering, we are not doers—we might never perform an action that inflicts pain on a non-human animal, and yet we might use a cosmetic product or medical equipment or a drug that has been tested on some sentient being. We might never kill an animal, but eating meat, for example, supports an industry that derive benefits out of it. Thus, we may benefit from these actions indirectly by choosing a good that was produced in a way that involves animal use. Recognition of our moral obligation for indirect footprint and for cases of omission enables us to take a radical responsibility for animals. This is a step further

along in our moral approach to non-human animals. Thus, the radical form of moral responsibility for non-human animals invites us to consider every single choice involved in what we eat, buy, or support. It also necessitates active involvement in actions to alleviate animal suffering. It is necessary to avoid passivity and omission that might lead to causing pain to any sentient being. The idea of radical responsibility has been present *implicite* in previous discussions of animal ethics, and this paper is a contribution to conceptualize it and recognize it as a form of moral progress in our relations with non-human animals.

AUTHOR CONTRIBUTIONS

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

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Uncoupling Meat From Animal Slaughter and Its Impacts on Human-Animal Relationships

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Slaughter sets the debate about what is acceptable to do to animals at an extremely low bar. Recently, there has been considerable investment in developing cell-based meat, an alternative meat production process that does not require the raising and slaughtering of animals, instead using muscle cells cultivated in a bioreactor. We discuss the animal ethics impacts of cell-based and plant-based meat on human-animal interactions from animal welfare and rights perspectives, focusing on industrial meat production scenarios. Our hypothesis is that the insertion of cell-based meat in the global meat market may alleviate farm animal suffering and potentially restore resources for wild fauna. We employed a conservative estimation of the cell-based meat contribution to the global meat market in the year 2040 to analyze the consequences for human-animal relationships for both wild animals and farmed domesticated animals. We discuss possible effects of an animal cell domestication process, previously described as the second domestication, on human-animal relationships. We consider its potential to reduce the impact of human demographic changes and land use on animal life, in particular whether there would be increased biomass availability and free land for wild animals. We anticipate a major reduction in animal suffering due to the decrease in the number of individual animals involved in food production, which justifies the adoption of cell-based meat from a utilitarian perspective. For the conventional animal food production that remains, further consideration is needed to understand which systems, either high or low welfare, will be retained and the impact of the innovation on the average farm animal welfare. Additionally, it seems likely that there will be less acceptance of the necessity of animal suffering in farming systems when meat production is uncoupled from animal raising and slaughter, supported by a deontological perspective of animal ethics. Consequent to this is anticipated the mitigation of relevant barriers to animal protection and to the recognition of animals as subjects by legislation. Thus, the development of the alternative meats may be related to a significant change in our relationship with non-human animals, with greater benefits than the *prima facie* effects on farm animals.

Keywords: animal protection, animal suffering, cell-based meat, second domestication, human-animal relationship

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INTRODUCTION

Ever since humans first domesticated animals for the production of food, our manipulation of animals for the process has been expanding in scope. Darwin (1861) recognized our growing intervention in animal form and function in his Origin of Species: "Man selects only for his own good," living as he did in an era and a country in which selective breeding was becoming widely used in agriculture. The next major event in selective breeding came with artificial insemination, allowing the so-called superior males to fertilize millions of females; then, embryo transfer, allowing the so-called superior female genes to be propagated more widely than through natural births; and, finally, or so we thought, cloning, perfecting the opportunity to perpetuate or even immortalize the genes of just one superior individual. However, over the last few decades, a technique for bypassing the animal altogether to produce meat has been in development, by growing muscle cells *in vitro*, which brings a different set of ethical questions and stances.

The main prompt for the development of these more efficient ways of producing meat is that the human population is expected to grow to 9.1 billion by the year 2050, which coupled with increased affluence that supports greater expenditure on food, requires annual meat production to raise substantially to 470 million tones (FAO, 2012). The need to alleviate food shortages and poverty suggests further intensification of animal production systems (FAO, 2018a), which is often associated with poor animal welfare (Bessei, 2006; Stafford and Gregory, 2008; Grandin, 2018). However, even with the development of incremental technologies for the intensification of production, the necessary gain in future meat production from agriculture may not be achieved (FAO, 2012). In addition, 48 authors from relevant institutions at national and international levels have signed the statement that "future technologies and systemic innovation are critical for the profound transformation the food system needs" (Herrero et al., 2020). Therefore, disruption of the conventional meat systems seems fundamental. Responses to this situation are under full consideration, as recently there have been much effort and investment in developing animal cell-based and plant-based meat alternatives. Both may potentially uncouple meat from slaughter, although each one faces important challenges, as for example, the fact that plant-based alternatives are not exactly meat and that cell-based options are not yet fully free of animal-derived ingredients. However, technology advances may bring the attributes of plant-based substitutes closer to those of conventional meat, as well as solutions for animal-free cell growth media.

Beyond the animal ethics benefits, additional advantages of replacing conventional meat for slaughter-free alternatives are straightforward: gains in environmental aspects, food security, public health, and food safety stand as the most clear-cut benefits, out of a long list of possible advantages (Gasteratos, 2019). Both plant-based and cell-based meat substitutes require less resource input per kilogram of product, as can be inferred from the impressive gains in carrying capacity, i.e., the number of people that could be fed from an agricultural land base, with changes from omnivorous diets to vegetarian or vegan diets (Peters et al., 2016), and from comparative estimates on cell-based meat production for environmental resource use (Tuomisto and Teixeira de Mattos, 2011; Röös et al., 2017). The overall environmental gains of diminishing conventional meat are also evident as the negative effects of the lowest-impact animal products typically exceed those of vegetable substitutes (Poore and Nemecek, 2018). In addition, the production of cell-based meat in closed bioreactors is expected to be sturdier in terms of climate, as compared to conventional meat, improving food security, which accordingly is one of the drivers for its development (Warner, 2019). The closed bioreactor environments may also contribute to a reduction in antibiotic use during meat production processes, which is a significant problem in conventional meat production due to the development of antibiotic resistance (Aires-de-Sousa, 2017). In relation to nutrition security, an important consideration is that meat is a protein source of the highest biological value, second only to egg and milk proteins (Hoffman and Falvo, 2004), while plant-based substitutes require more research and efforts to approach conventional meat amino acid value as human food. Cell-based meat offers additional advantages in comparison to conventional meat, as its proteins are coded by animal cell DNA, which tends to maintain conventional meat amino acid profile, and its final overall composition may be customized in a tailored way, such as low cholesterol risk by using mostly poly and monounsaturated fatty acids, for example. Finally, both meat alternatives offer virtually zero risk of zoonotic diseases, as pathogens are intrinsically absent in the production process. Thus, innovative meat products tend to significantly reduce human suffering and financial costs associated to both prevention and treatment actions required by the conventional meat chain regarding bacterial diseases, such as those caused by *Salmonella*, *Escherichia coli* O157:H7, methicillin resistant *Staphylococcus aureus* (MRSA), and bovine tuberculosis. In addition, dangerous virus mutations, such as the new subtypes H5N1 and H7N9 of Type A influenza virus, popularly known as bird flu, the subtype H1N1, known as swine flu, and the recent SARS-CoV-2, the coronavirus causing Covid-19, would be impossible with the consumption of alternative meats. This is a major benefit as these diseases are causing major human mortality and current control measures are seriously disrupting human society.

Unlike the classic plant-based substitutes for meat, which used whole vegetable ingredients such as peas and other beans, many of the new plant-based meat analogs are structurally similar to meat (Joshi and Kumar, 2015), as they are molecularly constructed. Even though they differ in composition, these substitutes preserve certain properties and sensory attributes of meat, such as texture and flavor (Dekkers et al., 2018). The process of formulating these products includes a comprehensive molecular analysis of plant proteins in search of compounds that simulate animal meat (Lagally et al., 2017). Another emerging technology is the use of genetically modified bacteria and yeasts to generate organic molecules for the production of gelatin, collagen, milk, egg white, etc. through fermentation (Stephens et al., 2018). To produce cell-based meat, the same fundamentals of tissue engineering technology that have been

perfected in the last few decades are used, including the proliferation and differentiation of specific stem cells for each tissue required to match meat compounds, such as muscle and fat (Datar and Betti, 2010; Post, 2012; Ben-Arye and Levenberg, 2019; Zhang et al., 2020). Thus, the resultant meat is potentially the same as that from farm animals but made through a slaughter-free process. Start-up companies working with cell-based technology may be considered disruptive as they use different and potentially fewer resources to develop an improved method of producing meat, which in turn may potentially transform the food chain. Thus, a new set of capabilities beyond the evident biotechnological knowledge required will characterize the cell-based meat global value chain (Reis et al., 2020). Furthermore, cell-based meat may change historical concepts, perceptions, and practices, in the context of human-animal relationships. The domestication of animals as sources of food over the last 10,000 years has changed human society and the role animals play in it. Recently, with the beginning of cell-based technology, a new domain is possible: the domestication of cells rather than animals (Shapiro, 2018; Tubb and Seba, 2019). Similar to the events of the first domestication, cells rather than animals may in future be genetically selected, raised, and fed an optimal diet.

The development of cell-based meat and other cellular agriculture techniques may therefore be considered "disruptive innovations," i.e., likely to remodel the different sectors of the industry or services (Christensen et al., 2015). These technologies also encompass the three attributes that define radical innovations (Dahlin and Behrens, 2005): uniqueness, novelty, and likely to influence future innovations. They employ unique and novel processes for producing meat, i.e., processes which are different from previous and current ones and may redefine the future technology used in the meat and agribusiness chains as a whole. In relation to animal products, a disruption may be dependent on whether consumers have attitudes that lead them to search for aspects beyond quality and price to include ethical aspects, regarding animal welfare and the environmental impact of meat, for example (Goddard, 2019). This occurs mostly in the early stages of the disruption, since in the medium-term product quality likely improves and acceptance tends to increase, especially if prices decline, which will almost certainly occur as new technologies are developed. If such a disruption to our food chain eventuates, a change in human-animal relationships is likely to occur, as for the first-time, it will be possible to challenge the concept of necessary animal suffering and killing without compromising meat consumption. Pressure from the animal production industry has been limiting the farm animal protection laws (Schwartz, 2020), which commonly prohibit only unnecessary suffering of farm animals. This is designed to shield harmful practices in animal production systems from inclusion in the list of crimes against animals, or even more deeply, from the very recognition of farm animal suffering and abuse. Most of all, the acceptance of the slaughtering of animals for food sets any debate about what is acceptable to do to animals at an extremely low bar. Many forms of animal abuse that are associated with legitimate goals, such as scientific experimentation and food production, are sustained by institutions with important social credibility. Therefore, it seems that society will allow certain contexts of animal cruelty without question (Flynn, 2012), because a genuine benefit from the practices is perceived.

Accordingly, cruelty to animals is often legally focused on the avoidance of unnecessary suffering (Radford, 2001), which is defined as avoidable and purposefully caused. This is considered to infringe moral principles (Hurnik and Lehman, 1982). In addition, there are many different interpretations of animal suffering, depending on the country, culture, and animal species in question (Lundmark et al., 2014), including which animal species are considered edible (Herzog and Foster, 2010; Joy, 2011). Although farm procedures causing pain and distress imply suffering, most policymakers interpret them as necessary, e.g., beak trimming of turkeys, laying hens, and castration of piglets (Lundmark et al., 2014), as they prevent behavior problems in high density stocking and consequently economic losses. Thus, legislation regarding animal suffering is contradictory due to the inconsistency in policymaker conclusions (Lundmark et al., 2018). This is one example of ways through which traditional meat production axioms tend to naturalize or even to extol animal suffering and killing; this normalization process may generalize and is likely not restricted to those animals used in food production activities. However, animal ethics is gaining unprecedented recognition in current western societies. The dilemma about how we use animals, and if we "use" them at all has become a major ontological, epistemological, moral, and political force, and it may be that a profound anthropological shift is underway (Burgat, 2015). It is our view that a basic hindrance for this anthropological shift is the persistent motivation to eat meat. Thus, the development of a system that makes meat production possible without animal suffering is likely to cause profound changes in the human-animal relationships.

In this paper, we discuss the ethical impacts of alternatives to conventional meat on human-animal interactions from an animal point of view, focusing on industrial meat production scenarios. Our hypothesis was that the insertion of plant-based and cell-based meats in the global meat market may alleviate farm animal suffering and partly restore habitat for wild native fauna, in addition to creating new possibilities for animal ethics and protection, as it relieves the need to accommodate the necessary animal suffering and killing that accompany modern animal production practices.

MATERIALS AND METHODS

Scenario Forecasting

The evidence suggest that alternative meat production methods will become a reality, leaving little room to speculate whether they will hold an important position in the food industry, rather only questions regarding time frame. The market share of plant-based meat substitutes has consistently increased since it was launched, with data from the United States showing that retail sales of plant-based foods grew 11.4% in 2019, within a context of overall food retail growth of 2.2% (Plant Based Foods Association, 2018), and more recently, the

Covid pandemic outbreak resulted in a further increase in sales of plant-based meat substitutes, likely caused by perceived high product safety regarding zoonotic diseases and the many difficulties related to Covid outbreaks within slaughterhouses. Regarding cell-based meat, even though it is not yet on the market, the increasing number of start-ups with robust and increasing investments dedicated to its development constitutes a sign of accelerated development. In the United States, the Food and Drug Administration (FDA) and the United States Department of Agriculture (USDA) have recently engaged in conversations regarding cell-based meat labeling and regulation, essentially to align on a joint regulatory framework between the two agencies (Congressional Research Service, 2018; USDA, 2019a). In Europe, newly developed foods, such as cultivated meat, are regulated under the Novel Food Regulation supported by the European Food Safety Agency (EFSA), with labeling regulations from Food Information to Consumers (FIC; Froggatt and Wellesley, 2019).

These movements by such institutions seem powerful indications of the relevance of this new industry. However, there are uncertainties as to the exact proportions of total meat market to be substituted, which are challenging for scenario forecasting. For instance, although recent research has shown that cell- and plant-based meat substitutes may be accepted or at least tried by consumers in a diversity of countries like Brazil, Germany, Italy, India, China, and the United States (Bryant et al., 2019; Mancini and Antonioli, 2019; Valente et al., 2019; Weinrich et al., 2019), some of those products do not exist so far (e.g., cell-based meat products), and more nuanced insights into the cultural and social barriers for introducing food innovation are still needed (Herrero et al., 2020), as they can challenge an exclusively technical understanding of dietary changes (Noack and Pouw, 2015). Thus, even though the need for a profound transformation of the food systems is recognized (Herrero et al., 2020), projections must be cautiously interpreted.

In line with the prevailing uncertainties, we employed a conservative estimation, one that is both cautious and moderate, of the cell-based meat contribution to the global meat market in the year 2040, to analyze its potential consequences for animal welfare and the human-animal relationships. As a recent scientific development, cell-based meat projections are scant in scientific literature; thus, our discussion is based on the prospective agribusiness disruption in global industry and economy for 2020–2030 and 2040 presented in reports by Tubb and Seba (2019), an independent team of technology, finance, and market experts, and the global consultancy group AT Kearney (Gerhardt et al., 2019), the only available documents with such projections. Due to the limitations in knowledge, at this point, a major emphasis on scale rather than absolute numbers seems warranted, thus reducing expectations of precision and error risks. Knowledge is limited and is curbing cell-based meat development, in terms of intrinsic factors such as animal-free culture medium ingredients, scaling-up challenges, and final product characteristics. A variety of extrinsic factors may additionally affect the development rate of meat substitutes and are difficult to predict. Examples of external relevant factors are climate change, water shortages, outbreaks of food-borne diseases, as well as the geographical distribution of these putative events, which may differently stress either a faster or a slower development for each plant- and cell-based meat alternatives. Furthermore, we highlight again that as potential consumers worldwide have socially engrained relationships to food (Herrero et al., 2020), expressed as established local habits and traditions, the acceptance of meat substitutes may not be straightforward. Considering all the complexities, however, it seems clear that a major disruptive change is on the horizon, which warrants forecasting efforts from a variety of perspectives. We are specifically interested in understanding how it will change human-animal interactions. For this, a preliminary scenario assumption in terms of the magnitude of the changes is required.

Tubb and Seba (2019) used data from the United States to calculate frameworks and information from The Good Food Institute, a non-governmental organization that supports cell-based studies, to reference their analysis of cell-based products. The report is focused on cattle; however, it includes some information on other food animal production systems, as well as information on clothing and cosmetics. It suggests that the ability of cell-based products to transpose the conventional systems is high, starting with ground meat and reaching afterward into the integral muscle tissue markets, such as steaks. Precision fermentation of genetic modified microorganisms may also be utilized to produce specific proteins needed for culture media and to provide animal products other than meat, such as milk and eggs. It is estimated that in the year 2030, 30% of the conventional beef in the United States will be substituted by cell-based meat, and the cost will be substantially less than that of conventional meat. Independently, Gerhardt et al. (2019) combined opinions from experts in the global agriculture, food, and meat industries to conceptualize what alternative sources of meat may be in use in the year 2040. They estimated that cell-based meat will represent 35% of the global meat chain in the year 2040 and plant-based meat another 25%. Thus, conventional meat may be reduced to 40% of total meat production by the year 2040.

For this paper, we used the statistics of Gerhardt et al. (2019) due to the report's worldwide analysis and more conservative perspective in terms of both percentages and time frame, comparing its 2040 scenario to the 2030 one considered in the Tubb and Seba (2019). Subsequently, we applied the expected reduction of 60% in traditional animal production for the year 2040, including 35% of cell-based and 25% of plant-based meat replacements (Gerhardt et al., 2019), to study the direct impact on number of animals involved and biomass distribution across terrestrial vertebrate animals. Our analyses considered the major production chains involving cattle, pigs, and chickens. The 60% was chosen as the most conservative prediction from an extremely limited choice between two publications and, as such, its interpretation is subject to the background consideration of the aforementioned relevant intrinsic and extrinsic factors at play. More extreme percentage substitutions of conventional meat may be considered as potential lower and upper limits. If technological challenges for cell-based meat development

prove too challenging, the respective 35% predicted market share will not be achieved within the considered time frame, which would leave the overall substitution by the year 2040 at around the 25% predicted for plant-based alternatives, assuming that there would not be a compensatory emphasis on plant-based developments. Another powerful restrictive condition is the launching of cell-based meat as an animal friendly product before the complete substitution of animal-derived ingredients in the cell culture media. If this occurs without due transparency to consumers, the consequences could include a strong backlash, with the attachment of a strong negative image to any future cell-based meat product. At the other extreme, much higher percentage substitutions may be achieved if technological breakthroughs present themselves before the year 2040 and if stricter animal protection laws come into effect as a consequence. Some restrictions to harmful animal use when alternatives exist are currently in place in many countries in other contexts, such as the use of animals in science. The same rationale may be put in place, considering the raising and killing of animals to produce meat, which would lead to levels of substitution closer to 100%, aided by legal restrictions on animal use, which are unlikely to be enacted simultaneously in different countries.

Direct Impacts of Alternative Meats on the Environment and Vertebrate Terrestrial Animal Biomass Distribution

We considered the impacts of the replacement of conventional meat sources with 35% of cell-based and 25% of plant-based meats by the year 2040 on the environment, addressing land, water and energy use, as well as for the vertebrate terrestrial animal biomass. Then, we studied biomass impact, considering that biomass is the metric used to quantify carbon usage by different organisms. Based on the estimation of biomass distribution by Bar-On et al. (2018), which measures biomass in gigatons of carbon (1Gt C = 10^{15} g of carbon), we applied the estimated 60% (35 and 25%) reduction of livestock biomass by the year 2040 (Gerhardt et al., 2019), to estimate the potential biomass release.

Direct Impact of Meat Alternatives on Farm Animal Welfare

The estimation of the reduction in the number of individual farm animals as a consequence of the introduction of 35% of cell-based and 25% of plant-based meats was based on the predicted global beef, pork, and chicken meat production for the year 2040 and the current number of cattle, pigs, and chickens. Even though the highest number of individual vertebrate animals involved in food production is that of fish species, which supports the need for urgent action regarding their welfare, data on an individual animal basis are very difficult to estimate, and they were not included in this exercise. Fish are consumed in part because the meat is believed to confer health benefits, and as such, the opportunities to value-add by improving the health giving credentials of the meat are considered to be less than for terrestrial animals and, therefore, less likely to be a target for replacement.

First, we calculated the production for these chains using values from the years 2017, 2019, and 2020 (**Table 1**), which we considered represented current production. Then, we calculated the average of the published prospective world meat production for the years of 2027, 2030, and 2050, to estimate animal meat production for the year 2040 (**Table 1**). In this exercise, the potential dynamics of the interplay among the three terrestrial meat production chains across the next decade, namely cattle, pigs, and chickens, were considered stable, to reduce complexity in the calculations, even though some changes in proportions may occur, as chicken meat production is growing at a faster rate than cattle and pig production. However, we assumed that this dynamic character may not sufficiently change numbers to invalidate our conclusions.

Afterward, we calculated the average stock number for each species using published data from years 2017 and 2019 (**Table 2**). Two of the references cited did not present the quantities of pigs (FAO, 2019) and chickens (USDA, 2019b); therefore, we left this data out of the calculation. Also, for

TABLE 1 | Meat production estimation, in million tones for beef, pork, and chicken.

Production chain	Data source			Average
	FAO	OECD	USDA	
Beef	70.8 (2017)[1]	72.7 (2019)[2]	61.9 (2020)[3]	68.5
Pork	118.7 (2017)[1]	121.8 (2019)[2]	95.2 (2020)[3]	111.9
Chicken	120.5 (2017)[1]	125.3 (2019)[2]	103.5 (2020)[3]	116.4
Total	376.0 (2030)[4] 470.0 (2050)[5]	367.0 (2027)[2]	—	404.3 (2040)[6]

[1]FAO, 2018b; [2]OECD, 2018b; [3]USDA, 2019b; [4]FAO, 2003; [5]FAO, 2012; [6]Our estimation.

TABLE 2 | Estimation of number of individual animals, in billions, based on cattle, pig and chicken stock number published in four sources in 2017-2019, and in 2027-2050, after multiplying by the percentage increase in production growth calculated from total annual meat production per species as per **Table 1**.

Source		Animal species		
		Cattle	Pigs	Chickens
FAOSTAT (n.d.)	2017	—	1.41	27.82
STATISTA (n.d.)	2017	—	0.78	22.85
FAO, 2019	2017	—	—	18.30
USDA, 2019b	2019	0.99	0.77	—
Calculated average	2020	0.99	0.98	22.99
Forecast based on estimation for $2040^{1}\ \% = \frac{404.3 \times 100}{296.8}$	2040	1.34	1.34	31.32
Forecast based on 60% substitution by meat alternatives[2]	2040	0.54	0.54	12.53

Production levels after applying the anticipated reduction of Gerhardt et al. (2019) are also provided.
*[1]As calculated by (404.3 × 100)/296.8 (see **Table 1**) and weighed for the proportion of each animal species; [2]Gerhardt et al. (2019).*

cattle, most of the references present data from both the beef and dairy industries; hence, we selected the data from USDA (2019b), which referred only to beef cattle. Later, we calculated the percentage of production growth from the year 2020 to 2040 and applied this number to each previous animal individual population. Finally, we calculated the reduction of individuals in each animal species for the future, following the estimation of 60% by Gerhardt et al. (2019; **Table 2**). The decrease in the number of individual animals involved in meat production was considered a straightforward gain in animal welfare and in animal ethics. The animal welfare gains refer to the reduction of total animal suffering, composed of the summation of individual afflictions, as animals involved in intensive production systems suffer from severe space and consequent behavioral restrictions, health problems resultant from artificial selection for production traits, and submission to painful procedures and stressful management events, such as transport and slaughter (Harrison, 1964; Webster, 2005; Broom and Fraser, 2015). Gains in animal ethics include all the welfare gains, in addition to the proportional absence of breaches in animal integrity and dignity, which are inherent to the killing of each sentient individual. In other words, the killing of animals is an important moral issue because of the suffering involved (Višak and Garner, 2016).

Finally, we envisioned three possibilities for the individual animals that will remain involved in production in the year 2040: (A) the welfare and number of farm animals if conventional meat production was to remain the sole system in the year 2040; (B) the average welfare and number of the remaining farm animals if conventional meats were to compete with cell- and plant-based meats for low-priced products; and (C) the average welfare and number of the remaining production animals if conventional meats were to compete with cell- and plant-based meats for high-priced products. Scenario A is fictitious and presented only for comparison, as in 2020, plant-based alternatives to meat products can already be purchased in many supermarkets, as well as restaurants, including major fast-food chains, such as A&W, Burger King, Kentucky Fried Chicken, and Subway.

Indirect Impacts of Alternative Meats on the Human-Animal Relationship

The impact of increasing markets for cell-based and plant-based meats on the human-animal relationships was analyzed using two complementary rationales. The first is related to a reduction in the negative impact of conventional meat production on global animal welfare, particularly in intensive raising conditions and during slaughter, which is avoided every time conventional meat is replaced by an alternative product. The second rationale is that, due to the extinction of the meat paradox, there may be fewer people who are desensitized toward animal suffering. The meat paradox is defined by Loughnan et al. (2014) as the simultaneous emotion related to the fact that people tend to dislike hurting animals and, at the same time, to like eating meat.

Results and Discussion

According to our analysis of the reduction in the number of animals used in the production for the year 2040, we discuss the impacts of alternative meats on the environment and biomass distribution, on farm animal welfare, and on the human-animal relationships.

Environmental and Vertebrate Animal Biomass Consequences

Livestock production uses extensive areas of land and is responsible for the occupancy of 26% of the terrestrial land, as well as 33% of the total arable land, which is dedicated to crop production for animal feeding (Steinfeld et al., 2006). The expansion of grazing areas and crop planting to feed farm animals has been related to deforesting important ecosystems. For instance, 70% of the deforested area of the Amazon forest is occupied by pastures for grazing animals (Steinfeld et al., 2006). This decreases resources for wildlife (Steinfeld et al., 2006; Tuomisto and Teixeira de Mattos, 2011). According to studies of prospective high-volume cell-based meat production (Tuomisto and Teixeira de Mattos, 2011; Mattick et al., 2015), large amounts of land, up to 99% of that currently used, will be freed (Tuomisto and Teixeira de Mattos, 2011). The new system of producing meat will surpass the efficiency of land use even when compared to the intensive meat production involving pigs and chickens (Mattick, 2018). Since cell-based meat production will be conducted in bioreactors, it is likely that there will be major transformations in the industrial production landscapes, which are calculated to be much less dependent on land use. Therefore, some land space will be freed, and this may return to wildlife or be used for further expansion of the human population, or both. The latter seems unlikely as land availability does not appear to be a constraining factor on human population growth, with most growth occurring in the urban population (FAO, 1999).

Regarding water consumption, agriculture accounts for 92% of the human fresh water footprint and almost one-third of this relates to animal production (Gerbens-Leenes et al., 2013). Additionally, considering the continuous expansion of the livestock population for animal-derived products, any intensification of production may increase water use due to a greater dependence on concentrate feed (Mekonnen and Hoekstra, 2010). Tuomisto and Teixeira de Mattos (2011) estimated that there would be a reduction of 82–96% in water consumption for each kilogram of meat produced, comparing cell-based and conventional animal meat production systems. As with all estimations regarding cell-based meat, this number is dependent on assumptions, which are not yet all clear; however, the scale makes the estimations relevant, for both land and water use. Even if we consider some inaccuracy in the estimations, a major reduction seems probable. At the same time, as land and water use are likely to considerably decline, energy inputs may increase for cell-based meat production due to the greater demand for electricity by laboratories in all phases of the cultured meat production process (Tuomisto et al., 2014; Mattick et al., 2015). Hence, improvements in the efficiency of energy use, such as developing clean and renewable alternative sources

of energy, will remain an important requirement. As an overall effect of the reduction in the number of individual animals used for meat production, some of the released natural resources will be needed for biomass production for energy generation.

The biomass of carbon in livestock, concentrated in cattle and pigs, is much higher than that in wild mammals: ~0.1 Gt C, compared with 0.007 Gt C (Bar-On et al., 2018). That in domestic poultry, mostly chickens, is in turn greater than that in wild birds: 0.005 and 0.002 Gt C, respectively (Bar-On et al., 2018). Our assumption is that the reduction of 60% in the number of farm animals when cell-based meats and plant-based alternatives are developed may release 0.06 Gt of carbon biomass (**Figure 1**); this surplus is related to the increase in efficiency characteristic of the alternative forms of meat production. Additional studies describing the biomass requirement for alternative meats are required, since they may give a more precise idea of the carbon amount, which may be liberated, and thus available for either animal wildlife or expansion of the human population, or both. However, from the Figures presented here, it is apparent that today's biomass available for wild terrestrial animals, at around 0.009 Gt C, would be greatly augmented by the reduction in the number of farm animals, which may release 0.06 Gt C by the year 2040. In other words, the amount of carbon released due to the reduction in the number of farm animals is 6.7 times the amount of carbon currently available for all wild terrestrial animals. Even considering that part of this freed carbon will be sequestered in the form of cell-based and plant-based meats, the possibilities for partially restoring wildlife biomass seem encouraging.

Impact on Animal Ethics and Welfare

Animal ethics is the branch of ethics that relates to human-animal relationships and how human ought to treat other animals. Conversely, animal welfare is based on empirical science, informing humans of the quality of an animal's life, based on the extent of good and bad experiences that the animal is having, has had, or is expected to have (Phillips and Kluss, 2018). By definition, it is the state of an individual regarding its attempts to cope with its environment (Broom, 2011), and it is measurable by considering animal's physiology and behavior. Animal cells, extracted from livestock for the purpose of generating cell-based meat, cannot be said to have rights, in the same way as animals, because such rights are based on animals' interests (Beauchamp, 2011). However, the cells may be said to have their own needs, which give them maximum advantage. Animal rights protagonists may further argue that if animals have the right not to have their bodies or parts of their bodies used in biomedical research, because it challenges their body integrity, they may also have the right not to have their muscle cells extracted for cell-based meat production. However, from the perspective of the continuum of attitudes toward animal rights advocated by Beauchamp (2011), such views represent an attitude founded at the extreme end of the animal rights continuum, particularly if there are utilitarian benefits to the species or specific animals involved. Beauchamp (2011) suggests that rights only merit protection if the benefits accrue to the individual animals themselves, not the species; hence, the impact on the animal from whom the cells are extracted merits detailed consideration. In addition to extracted cells, fetal bovine serum is currently used to grow cell-based meat (Chauvet, 2018). This serum is an excellent source of nutrients and cell-growth factors, and it is collected from fetuses at abattoirs. During slaughter of the cow, the fetal heart is punctured to extract blood, and there is a concern that the fetuses may still be alive during the process, which may even be considered an advantage by some because it is possible to extract more blood if the heart is still beating (Phillips and Kluss, 2018); the blood thus collected is then processed for fetal serum production. Fortunately, it is realistic to expect a non-animal replacement for the fetal bovine serum in the near future (Chauvet, 2018). Fetal serum substitution is currently under development by adapting cells to chemically defined media, which are fully independent of animal-derived ingredients (Marigliani et al., 2019a). Fetal bovine serum is not the only animal ingredient used in cell culturing; a systematic review of 156 articles featuring 83 different cell culture methods identified the use of several animal-derived products from different species (Marigliani et al., 2019b). A major advancement in this issue came with the publication of the new Organisation for Economic Co-operation and Development (OECD) Guidance Document on Good *In Vitro* Method Practices (OECD, 2018a), discouraging the use of serum and presenting a list of serum-free media alternatives, including an

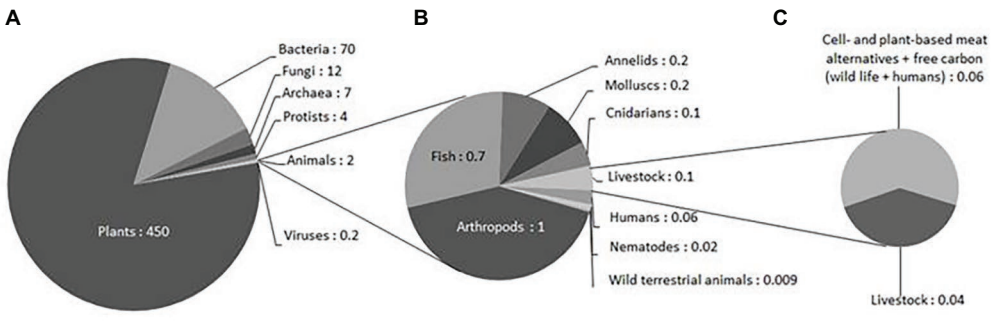

FIGURE 1 | Biomass distribution for kingdoms **(A)**, animal groups **(B)**, as per Bar-On et al. (2018) and the analysis of the impact of a 60% reduction in slaughter-based meat production **(C)** (Gerhardt et al., 2019) on the availability of biomass (1 Gt of carbon = 1Gt C = 10^{15} g of carbon).

animal-product-free media description. The challenges of offering meat that is really cruelty-free and that is also perceived to be so may likely be overcome by implementing technology for the use of culture media that is completely free of animal ingredients and by adopting strict transparency so not to risk a breakdown in consumer confidence.

A fundamental objection to the use of animal cells for the production of cell-based meat is that it promotes the concept that animals are a legitimate source of food, a view challenged by many animal rightists. Human cells could equally well be used to produce cell-based meat; however, they would be accepted by few consumers (Wilks and Phillips, 2017). Many surveys worldwide have demonstrated that most people would accept the use of animal cells in cell-based meat and would at least try the product (e.g., in the United States, Wilks and Phillips, 2017; in Brazil, Valente et al., 2019). The biggest impediments to its more permanent adoption are likely to be food neophobia, political conservatism, and a distrust of scientists (Wilks et al., 2019). A related concern, levied against the use of genetically modified animals, is that humans are "playing God and against Nature" (Savulescu, 2011). The concern derives both from a perceived attempt by humans to usurp the role of a higher being and also an overestimation of our ability to manage complex biological systems. The latter is related to people's distrust of scientists, when it comes to their ability to create new food sources safely (Wilks et al., 2019). A further concern is the slippery slope argument (Savulescu, 2011) that assumes that innovations such as cell-based meat will ultimately lead to more damaging innovations that will seriously degrade human society, for example, creating cell-based meat based on humans. This concern may be challenged by the idea that each step in our manipulation of life on earth is checked in terms of its benefits for society as a whole. Without central control by government, human life would be "poor, nasty, brutish, and short" (Hobbes, 1651). However faulty this system may be, it is undeniable that human intervention has improved human life quality and quantity throughout many centuries. It is possible and urgent that human interventions care for other sentient beings and for the environment in a more solid and straightforward manner.

Another concern is the detrimental impact that cell-based meat may have on existing livestock numbers worldwide. It has been assumed that cell-based meat would compete with high-value meats, not industrially produced low quality meats (Cole and Morgan, 2013). However, other possibilities must also be considered. In **Figure 2**, the number of individual animals involved in each of the three most relevant global meat chains is presented, and the scenarios B and C posit quite different responses of the animal production industries to the insertion of the alternatives to traditional meat in the global market. The validity of this ethical objection depends not so much on which scenario is correct, rather on the answer to the question of whether farm animals' lives are worth living at all. The "life worth living" concept, which emerged from considerations of the quality of human lives (Yeates, 2017) has been developing from a motivational framework, in which it appeared in its infancy (Webster, 2016), to a more robust concept that can be used to measure, or at least estimate, animals' quality of life (Mellor, 2016). If cell-based meat does compete with high-end meat products, appealing to the ethical consumer, these are likely to be derived from livestock with the best welfare, even considering the limited range of welfare for most farm animals. However, the market for inexpensive, mass produced meat has been growing at the expense of the quality product, and this market may well be one target of cell-based meat manufacturers, given that production costs are expected to decrease and to reach cost parity with conventional meat products in the next 5–10 years (Tubb and Seba, 2019). This mass-produced meat originates from intensive production systems, where it is debatable whether animal lives are worth living.

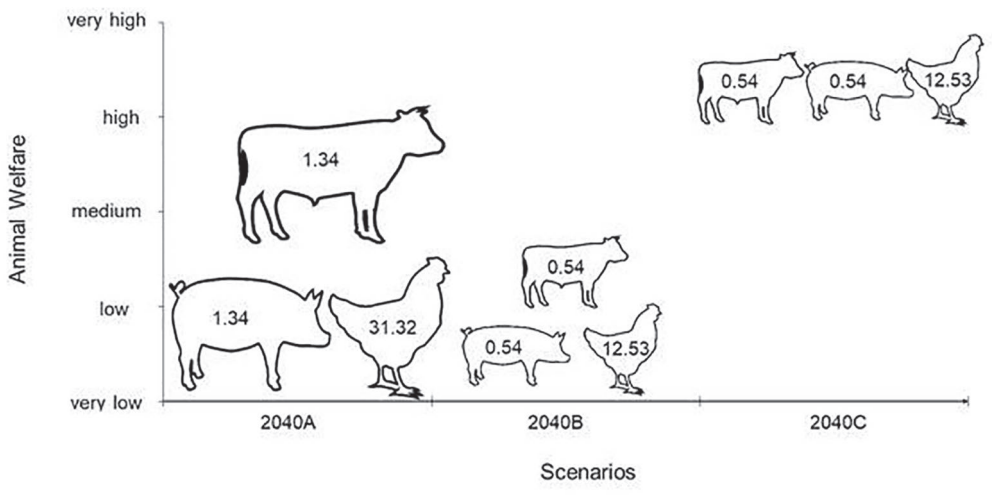

FIGURE 2 | Number of individual animals in each degree of animal welfare, in billions, considering the estimated total number of cattle, pigs, and chickens in 2040, assuming that total global meat production will be reduced to 40% of its 2019 level, following the projected insertion of 35% of cell-based and 25% of plant-based meat production (Gerhardt et al., 2019).

Furthermore, diminishing the use of agricultural land for animal production will free up land, where wildlife may be allowed to flourish.

Pressure on wildlife habitat from expanding agricultural production is at least partly responsible for the novel zoonotic wildlife diseases that are emerging (Wilkinson et al., 2018). This substitution of farm animals by other forms of life may dramatically change the distribution of vertebrate animal life on earth (**Figure 1**). Few comparisons of farm and wild animal numbers exist, but in the case of birds, the global biomass of domestic poultry is three times that of wild birds, as described above (Bar-on et al., 2018). Similarly, the biomass of humans and livestock outweighs that of terrestrial wild vertebrates. As it is widely acknowledged that the welfare of farmed livestock is poor (Phillips, 2015), replacement with wildlife that is subjected to fewer anthropogenic pressures is morally justifiable, even desirable from a utilitarian standpoint. From a deontological standpoint, there are additional concerns about the short lives of farm animals, infringing Tom Regan's concept of subject of a life (Beauchamp, 2011), the manipulation of their genetic inheritance as a species, and threats to their future existence caused by limitation of their biodiversity (Phillips, 2015), again suggesting that substitution with wildlife is desirable. There may be concerns that the welfare of wildlife, particularly of prey animals, is also compromised, but then Darwin (1861) had considerable insight: "we may console ourselves with the full belief that the war of nature is not incessant, that no fear is felt, that death is generally prompt, and that the vigorous, the healthy, and the happy survive and multiply." Today, this statement may be recognized as somewhat romanticized; however, it seems relevant to acknowledge animal ethics gains from decreasing animal suffering, which is directly anthropogenic.

Scientific assessment of animal welfare has been the object of many scientific papers and has now been summarized in protocols. The most used protocols for the animal species represented in **Figure 2** are the respective Welfare Quality protocols (Welfare Quality®, 2009a,b,c), and they include a variable number of specific measurable indicators for each of the four principles: good feeding, good housing, good health, and appropriate behavior. The measured levels for each indicator are composed of the degree of adherence to each principle, which in turn are integrated to calculate a final welfare level for the target situation. Recurrent animal welfare assessment has produced a relatively improved understanding of welfare status for the most common animal production systems. In general, giving livestock access to pasture improves most aspects of their welfare (Mee and Boyle, 2020) in contrast to increasing use of intensively confined systems employed for most of the pig and broiler chicken industrial farms. For this reason, in current practices involving most of the animal industry, it is possible to distinguish welfare levels of pastured cattle as relatively higher than those of indoor-raised pigs and chickens, as represented in **Figures 2A,B**. This approach simplifies complexities which are inherent to the many field variations that may be observed when assessment is performed and rather uses a concept of animal welfare potential of each system. However, it relies on our best assumptions of welfare, as per current knowledge. Although many scientific studies have proposed solutions to prevent animal welfare issues, they still persist and even major problems with simple solutions became normal in production systems (Grandin, 2018). The intensive systems of pig and chicken industrial production are often related to poor living conditions for the animals, such as high stocking densities and early growth diseases (Bessei, 2006), and even animal welfare certified systems may not present significant improvement for the animals (Souza et al., 2015; Reis and Molento, 2019). Therefore, even though there may also be issues related to the extensive production systems (Petherick, 2005), the intensification processes seem to intrinsically reduce the welfare of the animals. In addition, we have only considered straightforward conditions of animal raising and slaughtering and aberrant situations such as overseas live exports were not included; even though these situations are extremely relevant, their inclusion would have blurred the picture due to the level of details required. Thus, in **Figure 2A**, we have distributed cattle, pigs, and chickens according to their average animal welfare in industrial production systems described in a simplified but representative way, in terms of what happens to the greatest number of animals in each species, as well as the number of individuals predicted to be involved in the year 2040 if no alternative meats were to become significant in the global market.

Since plant-based and cell-based meat production strategies are virtually animal-free systems (Kadim et al., 2015), if the scale of the forecast turns out roughly correct, a substantial decrease in the number of animals involved in intensive raising practices and slaughter will occur, which will in turn significantly impact the total animal suffering. Even though animals may still be necessary for cell supply, the techniques available to induce cells to proliferate indefinitely or even selection of cells that express immortality may reduce or avoid the need for new samples (Stephens et al., 2018). Nevertheless, the welfare of animals involved must be considered (Croney et al., 2018). As the number of animals demanded will be only a fraction of that required for slaughter-based meat production, the animals providing cells will probably be kept at higher welfare standards, as measured by accepted assessment protocols (Welfare Quality®, 2009a,b,c) because of their extremely reduced numbers and their high value to the industry. As for the welfare of animals in the remaining conventional meat production in the year 2040, we present the total number of farm animals per main species and their position in terms of animal welfare, in the unlikely case of all meat being produced through conventional processes (**Figure 2A**), and we discuss two main scenarios for the year 2040 (**Figure 2**): (A) average farm animal welfare decreases due to a pressure for low-cost conventional meat and (B) average farm animal welfare increases due to a niche-market developing for traditional meat, and a consequent demand for high quality meat, including the addressing of environmental and animal welfare concerns.

The first scenario (**Figure 2A**) simulates the average total number of cattle, pigs, and chickens involved in farm production in the year 2040 and the welfare of each species. The second scenario (**Figure 2B**) represents a reduction of 60% of animal

use in meat production with a decrease in the average welfare of the remaining farm animals, due to a potential increase in economic pressure. Although cell-based meat is still very expensive and consequently generates high-cost products (Stephens et al., 2018), future large-scale plants and continuous cultivation of cells are expected to considerably reduce the price (Specht et al., 2018). Assuming that in the year 2040, cell-based meat will be widely accessible, and there may be a pressure for the remaining slaughter-based meat production to be at lower cost, to compete with the cell-based products. In this case, average farm animal welfare may decrease due to the increased market pressure for intensive cost-effective production. Hence, although the total size of slaughter-based meat production will be smaller, its proportional impact may be worse, both in relation to animal welfare, environmental issues, and public health matters, including increased disease risks (e.g., *Salmonella* and *Campylobacter*) and greater use of intensively-farmed land to provide the necessary feed (Tubb and Seba, 2019). In this context, the current grains and cereals used in animal production will still require extensive land (Steinfeld et al., 2006) even though they are directly edible by humans (Leitzmann, 2014; FAO, 2018c). This renders conventional meat from grain-based diets intrinsically inefficient in terms of reducing human hunger in the world. The projection for growth in cropped land use is colossal, reaching 3 billion tons of cereals in 2050 (FAO, 2012), in a scenario where alternative meats were not considered. In addition, the animal production sector has been engaged to improve feed conversion so that it is more efficient (Steinfeld et al., 2006), which may result in additional animal welfare problems. One last reason that may force a negative impact of cell-based meat establishment on animal welfare is a putative stimulation of higher global meat consumption, independent of origin (cultured or traditional; Stephens et al., 2018), resulting in increased meat demand regardless of production methods.

The third scenario (**Figure 2C**) represents higher welfare for the remaining farm animals through a dominance of cell-based meat in the market of low-priced meat and, consequently, high quality or niche demand for traditional meat. According to consumer acceptance studies, willingness to both try and regularly consume cell-based meats is related to its perceived positive impact on animal welfare and environment (Laestadius and Caldwell, 2015; Wilks and Phillips, 2017; Mancini and Antonioli, 2019; Valente et al., 2019), but lower costs for this product may also enhance its consumption (Gaydhane et al., 2018). Therefore, conventional meat may become more expensive, segmented as a luxury food (Post, 2012). Such products are frequently branded and labeled as green, environment and animal-friendly, and consumers are likely to pay premium prices for those attributes (Orsato, 2009) which, in turn, lead to production systems improvements. This may, consequently, allow for higher animal welfare on the remaining conventional farms. Reasons for higher welfare in this case are related to a greater possibility for the adoption of alternative systems for conventional meat production, such as those using free-range pigs and broiler chickens. Outdoor raising systems for pigs generally improve their health and behavior, since animals enjoy more space, access to natural resources, and social contact. It also improves pigs' mothering and reproductive ability, reduces piglet mortality and the number of pigs with poor leg conditions (Gourdine et al., 2010), as well as increases in social-play and decreased conflict behavior and stereotypies (Nakamura et al., 2011). However, it will still require improvements in pig growth rates (Park et al., 2017) if it needs to compete with confined systems as a low-cost production method. Thus, if traditional pork achieves higher prices as a consequence of cell-based pork availability, the pressure to reduce costs may decline. Likewise, free-range broiler chickens raised in open fields can enjoy improvements in their physical activities and behavioral diversity (El-Deek and El-Sabrout, 2019). Also, animal welfare assessment in free-range systems demonstrates better health and ambience, behavior and psychologic states, less pododermatitis and lameness, an absence of panting, increasing wing-flapping, and prevalence of positive emotional states (Sans et al., 2014). Chickens have been genetically selected for outdoor systems using the so-called "slow growth" lines, which automatically confer higher production costs for the fundamental characteristic of these animals: They grow slower. Using slow growth lines takes roughly double the time and other resources per kilogram of meat produced.

The most significant influence in terms of global animal welfare is, by far, the major reduction in the total number of individual animals involved in food production (**Figure 2**). This global decrease is in the order of hundreds of millions fewer cattle and pigs and of tens of billions fewer chickens per year. At this point, it is again important to consider the low precision of these calculations but their robustness in order of effects. In other words, even if future reality is 20 or 30% different than the assumptions accepted for our estimations, changes will be highly significant.

For the conventional animal food production that remains, further consideration is needed to understand which systems, either high, low, or intermediate welfare, will be retained and thus define the impact of the innovation on the average welfare of the remaining farm animals. It is likely that further development in farm animal welfare regulations and animal protection laws will remain important. In addition, a stronger focus on welfare regulations for wild animals is likely required in many jurisdictions, to ensure that the outcome of substitution of farm animals by wild animals is associated with less overall suffering and that no increase in human activities that cause wild animal suffering will be allowed. Additionally, it seems possible to foresee potential changes in the human-animal relationships when meat production is uncoupled from animal raising and slaughter, with the mitigation of relevant barriers to animal protection and a recognition of animals as subjects by legislation.

Impact on the Human-Animal Relationship

Eating animal meat sets inconsistencies in the human-animal relationships, as most people consider themselves animal lovers but, at the same time, they are causing suffering in non-human animals (Joy, 2005). In addition, meat eating tends to lead people to withdraw moral concern (Loughnan et al., 2010). It has further been postulated that the institution of animal

slaughter constitutes the basis of an implicit right to be violent, which may even be linked to a culture, where violence has a valued place (Burgat, 2017). If these views have validity, the development of meat which is uncoupled from slaughter will change human-animal relationships in a profound way.

Animal-based products often have had their names changed to create distance from their animal origin (e.g., beef and pork as opposed to cattle and pigs). Historically, the division between words for animals and their meat emerged because of the French-speaking nobility eating the meat of the animals raised by English-speaking workers (Quinley and Mühlenbernd, 2012). This cultural dissociation of conventional meat products from the animals from which they originate has increased recently, separating killing an animal to produce food from the stages of purchasing, distribution, preparation, and consumption (Buscemi, 2014). The divergent nomenclature is related to the concept of the absent referent, which is anything whose original meaning is undercut as it is absorbed into a different hierarchy of meaning; in this case, the original meaning of animals' fates is absorbed into a human-centered hierarchy (Adams, 2000). Even though references to the connection between animal and meat were reduced, many people still experience cognitive dissonance whenever something reminds them of the animal origin of meat (Harmon-Jones et al., 2009), which then evokes the meat paradox. To reduce the moral burden, people often minimize harm, deny responsibilities, and diffuse the identity implications of their acts (Bastian and Loughnan, 2017). Thus, as meat is detached from being raised under low welfare conditions and the killing of animals, this moral discomfort should disappear, allowing for unrestricted defense of animal welfare and animal life. This new freedom, in turn, may allow for the recognition that animals are morally relevant individuals, in other words, that they are subjects of a valuable life. Although a simple solution for these moral ambiguities is to follow a plant-based diet, meat consumption is strongly established into most global societies. Carnism is the ideology of meat consumption, where people, as omnivores, choose to eat meat even without the necessity of doing so (Joy, 2011). In this context, Monteiro et al. (2017) discuss two types of carnism: carnistic defense and domination. The first one relates to the meat paradox, supporting eating meat and denying animal suffering in the context of meat production. The carnistic domination is based on the hierarchy between humans and animals, justifying killing animals for human purposes and endorsing human superiority.

Independently of carnism type, the justification of killing animals to produce meat, which is a highly valued human food, may impair improvement of many areas of animal protection. The industrial meat production in typical western urban societies is associated with normalization of animals as having only instrumental value, and with killing animals. Thus, against this background, difficulties arise in recognizing the intrinsic value of individual animals and their rights to integrity and dignity. A right to integrity may be challenged by cell-based meat, confronting virtue ethics, which strives for excellence in character (Hursthouse, 2011) and deontological theory. In modern society, it becomes natural and somewhat necessary to treat animals as resources. This may relate to a generalization, which resides in the banalization of evil (Arendt, 1963). For instance, Giedion (1948) described as follows, the serial killing of animals in slaughterhouses: "What is truly startling in this mass transition from life to death is the complete neutrality of the act. One does not experience, one does not feel; one merely observes." Indeed, meat is, perhaps most of all, a relationship with animals that is essentially about killing (Burgat, 2017). Therefore, the processes related to meat production may be characterized as a type of desensitization in people (Schacter et al., 2011), because the exposure to dreadful experiences routinely may reduce emotional responsiveness.

If the expectations of price, taste, and appearance of meat can be achieved by cell-based meat, consumers may accept it as a regular food (Bryant and Barnett, 2018). Also, there is strong evidence of cell-based meat consumer acceptance because of its welfare benefits (Laestadius and Caldwell, 2015; Wilks and Phillips, 2017; Mancini and Antonioli, 2019; Valente et al., 2019). In addition, when potential consumers are further informed about environmental or animal welfare benefits – which improves their awareness about those benefits – their willingness to consume increases (Verbeke et al., 2015; Bekker et al., 2017; Weinrich et al., 2019). Thus, since willingness-to-pay regarding animal welfare is related to a social consensus that it has a moral value (Bennett and Blaney, 2002), knowledge about the positive impacts on animals provided by alternative meat production may result in an important contribution to the establishment of this product in the market. Therefore, besides the positive implications of cell-based meat for animals, there may be indirect animal ethics gains in terms of freedom to consider animals as an end in themselves.

In **Figure 3**, we represent a possible relationship between the consumption of cell-based meat and the awareness of its

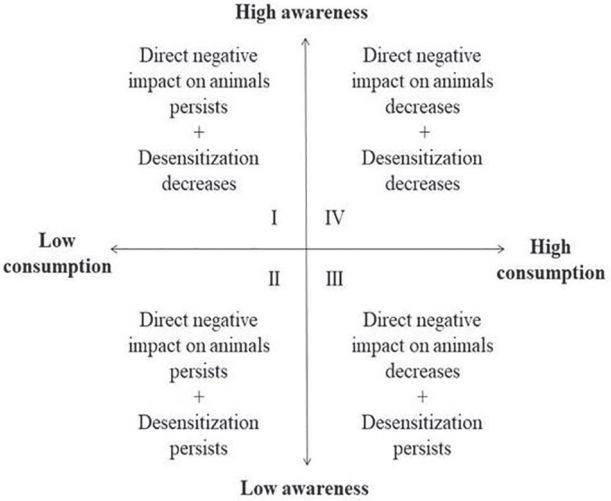

FIGURE 3 | Direct consequences to animals and indirect effects on animal ethics of different levels of cell-based meat consumption and awareness of its animal ethics consequences.

consequences in improving animal ethics issues. We projected four different contexts, which are represented anticlockwise from left to right: (1) low consumption of cell-based meat and high awareness (quadrant I) may maintain a direct negative impact on animals but may decrease the desensitization; (2) low consumption and low awareness (quadrant II) may also have a persistent direct negative impact on animals and continued desensitization; (3) quadrant III, with high consumption and low awareness, shows the direct negative impact on animals that may decrease, but the desensitization may persist; and (4) finally, quadrant IV presents high consumption of cell-based meat and high awareness, which may decrease both the direct impact on animals and desensitization.

As meat has traditionally required major animal inputs, resulting in significant impacts on their lives, from being selectively bred to being killed (Mouat et al., 2019), in addition to being closely confined, the consumption of cell-based meat may be a new determinant of animals' interests and the quality of their lives. Growing awareness, despite urbanization, of the practices of animal production has had an important impact on the ethics of what we eat (Mouat et al., 2019). Phillips (2015) has argued that it is not relative welfare that matters to animals, and therefore to us, but the absolute number of animals that are suffering worldwide. This is further argued by Phillips (2015) to be increasing, because more animal production uses small animals, so more are eaten; more are grown in developing countries without welfare standards and in intensive production systems (Reis and Molento, 2019); and demand for meat is increasing worldwide. While the major switch from slaughter-based to cell-based and plant-based meat consumptions will directly reduce farm animal suffering (quadrants III and IV), the animal ethics improvements will likely depend on decreasing the banalization of animal suffering (Singer, 1995), i.e., decreasing the present levels of desensitization regarding animals (quadrants I and IV). The important direct gains to animals from the decision to buy alternative meats, even when based on non-animal related reasons such as price or human health issues (quadrant III), deserve proper recognition, since from an animal point of view, what matters is not what we think or feel, but what we actually do (Webster, 2016). This recognition does not exclude the importance of striving for decreased desensitization, since this is essential if broader and more permanent gains for animal welfare are to be achieved. In other words, the improvement of the relationship between human and non-human animals in a broad sense seems to be dependent on increasing both the consumption of alternatives to conventional meat and the levels of awareness regarding the role of alternative meats in uncoupling meat from animal suffering and slaughter (quadrant IV).

Our hypothesis is that alternative meats may diminish desensitization toward animals, since people will not have to tolerate the necessary animal suffering and killing for the sake of meat consumption. From a broader perspective, the concepts of animal rights and animals as subjects-of-a-life (Regan, 2004) may find more overall support when meat production is uncoupled from the need to kill animals. However, this may require specific actions to increase awareness of animal ethics issues, since other factors may lead the transition to alternative meats. Thus, even though the transition from traditional meat to cell-based meat will have an intrinsic direct positive impact on farm animals, the promotion of awareness may increase the human-animal relationships in a more generalized sense.

CONCLUSIONS

The development of a slaughter-free meat chain will have significant practical and animal ethics impacts on our relationship with non-human animals, which are wider than the *prima facie* benefits to farm animals. This is supported by utilitarian, deontological, and virtue ethical principles applied to animals. Considering the many uncertainties involved, especially those regarding the rate of substitution, which is dependent on acceptance levels of alternative meats by different societies, the resolution of technological challenges, and the need for transparency to avoid significant drawbacks, it is highly likely that a major disruptive change is on the horizon. Gains in environmental resources such as land, water, and biomass are likely to be very significant, while energy costs per kilogram may remain high for cell-based meat. More research is needed to understand the consequences of new meat alternatives for the welfare of the remaining farm animals, since it will depend on economic pressures and the strategies that will be adopted by the conventional meat chain. Finally, alternative meats may diminish desensitization toward animals, since people will not have to allow for some kind of necessary animal sufferings for the sake of meat consumption. Thus, there may be indirect animal ethics gains in terms of freedom to consider animals as an end in themselves. Our relationships with non-human animals may be about to change to a more respectful, mutualistic relationship, for the benefits of all concerned.

AUTHOR CONTRIBUTIONS

MH contributed to conceptualization, investigation, methodology, writing, review, and editing. CM contributed to project administration, supervision, conceptualization, investigation, methodology, writing, review, and editing. GR and CP contributed to conceptualization, writing, review, and editing. All authors contributed to the article and approved the submitted version.

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Are All Conservation Measures for Endangered Species Legitimate? Lines of Thinking With the European Hamster

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When dealing with the protection of an endangered species, it appears more and more important to address the ethical limits and the societal perception of the implemented conservation measures. This will be illustrated here through the example of conservation programs of the European hamster (*Cricetus cricetus*) in France. The main threats for this critically endangered rodent are the impoverishment and fragmentation of its habitat due to recent changes in agricultural practices and urbanization. Thus, the status of this species changed from harmful to endangered in only a few decades. This must lead to acceptance of the species by citizens and especially farmers paid to destroy this species until the 1990s while nowadays to protect it. To stem the decline, several measures have been taken through the last 20 years including population reinforcement, wild animal tracking, and implementation of suitable habitats. One can, therefore, discuss the efficiency of these measures and their integration in the entire socio-ecosystem. Population reinforcement and the questions that can arise from it will first be addressed. Secondly, *in situ* animal monitoring and implications of the methods used will be discussed. Third, we will deal with agricultural practices favorable to the species. Finally, we will highlight the links between European hamster conservation measures and wider problematics.

Keywords: population reinforcement, animal monitoring, agriculture, conservation measures, animal ethics, environmental ethics, *Cricetus cricetus*

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INTRODUCTION

Conservation Measures for Animal Populations' Protection

Human beings currently impose a very strong selection pressure on organisms, forcing them to adapt, move away, or die. The impact of our species on the environment is particularly visible among other things by the creation of urban areas (Alberti et al., 2017), the fragmentation of the territory (Cheptou et al., 2017), the increase in global temperatures (Beaumont et al., 2011), the introduction of pathogens (Rogalski et al., 2017), or the loss of native biodiversity by the introduction of invasive species (Colautti et al., 2017). Thus, *Homo sapiens* become the main evolutionary force at the global level (Palumbi, 2001; Hendry et al., 2017). We have entered the sixth mass extinction crisis with a higher rate ever compared to earlier mass extinctions. The acceleration of the disappearance of fauna and flora caused by human activities is an assertion often used to alert

people. Then, every informed person agrees that protecting biodiversity in all forms is a priority, just like reducing global warming.

Protecting the habitat of species, in particular by reducing the threats that affect it, is a first so-called *in situ* conservation measure. It aims at maintaining populations in the environment where the distinctive characteristics of the species have developed and in which they can continue to evolve with their prey or food resources, predators and parasites. In addition, by reinforcing populations in their environment, conservation measures appear to allow a long-term success. Their importance was underlined in international conventions and legislation (e.g., Convention on Biological Diversity, Rio Earth Summit of 1992).

However, in theory as in practice, whether natural or encouraged by humans, the restoration of biodiversity is not always self-evident. Indeed, when considering the animals and the ethics devoted to it, two concepts emerge. *Animal ethics* itself considers the animal as an individual and will then refer to the study of the moral responsibility of humans regarding animals taken as beings. It therefore poses "the classic questions of human duties toward animals, possible animal rights, and more generally, moral judgements to be made on our current treatment of animals" (Vilmer, 2008). Next comes *environmental ethics* which considers animal species as a whole, as building blocks of the ecosystems in which they live (Vilmer, 2008). These two ethics devoted to animals are different and are often brought to clash. Indeed, in a lot of situations, the interests of the individual appear to be opposed to the interests of the collective (e.g., population, species or ecosystem), since the protection of habitat may be the cause of deleterious actions on individuals. A perfect example is the plan of the Australian government to kill about 2 million feral cats by 2020 to preserve the native Australian fauna from a high level of predation due to felines. On the other hand, we cannot minimize the suffering of these cats that are shot, poisoned, or trapped. The case of Australia is extreme, but protecting biodiversity often leads to conflicts of interest between different social groups or ecosystem users. In France, a striking example of such conflicts is the return of the gray wolf (*Canis lupus*) from Italy, which has become a real "sensitive case" in the light of a very strong public opinion on this issue. Indeed, the French gray wolf case is a natural recovery and was not the subject of any reintroduction or population support plan. From an ecological point of view, a return to equilibrium is possible, but some believe that the wolf has not its place any longer because of its role of top-level predator and, thus, possible human competitor. Some lobbies do not hesitate to blame the carnivores for livestock slaughters leading to the rise of authorized shoots to 19% of the population of wolves in 2020.

Another example of ethics disagreement—and purpose of this paper—is the captive breeding of endangered species for the preservation of biodiversity. In Alsace (Northeast of France), several programs have been launched to preserve, reinforce, or reintroduce animal emblematic species [white stork (*Ciconia ciconia*), Eurasian lynx (*Lynx lynx*), Western capercaillie (*Tetrao urogallus*), European otter (*Lutra lutra*)] of the region including the European hamster (*Cricetus cricetus*). Its case perfectly illustrates the gradient of consideration that humans can apply toward animals, from animal ethics to environmental ones. On one hand, the conservation plan aims at obtaining the recovery of the wild populations, thanks to the release of hundreds of individuals bred in captivity—such action irrefutably affects the individuals—and the improvement of their living conditions by the establishment of "hamster-friendly" cultures. On the other hand, these actions need to be sustainable by implementing practices that can reconcile not only environmental but also economic interests. However, the stakeholders here are numerous (scientists, NGOs, policymakers, farmers, citizens) and accession is not always easy. Thus, the ethical or environmental concerns of some may come up against others' view of the world that differed from the one they would have wished to promote more locally, notably within rural areas.

Through the European hamster case, we will here question different points to determine whether all conservation measures for endangered species are legitimate. At first, we will address population reinforcement and the questions that can arise from it. Secondly, *in situ* animal monitoring and implication of the methods used will be discussed. Third, we will deal with favorable agricultural practices that can be developed and the elements that can slow them. Finally, we will expose the interconnections of conservation measures for endangered species with other problematics and the benefits we can expect from them.

The European Hamster Case: From Agricultural Pest to Flagship Species of Alsatian Biodiversity

The European or common hamster is a small hibernating rodent found from Russia to the East of France, and more precisely in Alsace. European hamsters live in burrows dug in agricultural fields. It is a solitary species that only shows social interactions for the reproduction period from April to August. At the end of the summer, European hamsters prepare their next hibernation period—from October to April—hoarding food in their burrows.

Since the 1990 Bern Convention on the Conservation of European Wildlife and Natural Habitats, the European hamster is a strictly protected species (Annex II of Bern Convention). The common hamster was also included in the Annex IV of Habitats Directive (92/43/EEC) in 1993. Listed as Least Concern at the global level in the IUCN red list of Threatened Species, European scientists urgently requested its reclassification as Vulnerable species for many years (24th International Hamster Workgroup meeting; Surov et al., 2016). It is only in 2020 that the common hamster obtained the status of Endangered Species (Banaszek et al., 2020). Indeed, its range has declined in almost all areas it was present during the last century, especially in Western Europe but also more recently in Central and Eastern Europe (Stubbe and Stubbe, 1998; Surov et al., 2016). This is for example the case in Poland and the Czech Republic where populations have already significantly decreased (Ziomek and Banaszek, 2007; Tkadlec et al., 2012). The common hamster has already disappeared or regressed in many provinces of Eastern Europe and Russia where it was present, and if the evolution of populations continues in the same way, more than 70% of the population could disappear in these provinces (see Surov et al., 2016). In the western part,

for example in the territory regrouping Belgium, the Netherlands and the German land of North Rhine-Westphalia, the hamster has declined by more than 99% in recent decades (La Haye et al., 2012). Agricultural practices, habitat fragmentation, fur trapping but also the impact of climate change and urban pollutions on the rate of reproduction of females have been identified as possible causes of such decline, even if the mechanisms are still difficult to identify for some (Stubbe and Stubbe, 1998; Monecke, 2014; Surov et al., 2016).

In France, the common hamster is only present in Alsace where hamsters' trapping and killing were common until the 1990s. Since one individual can hoard up to more than 10 kilograms of food in its burrow for hibernation (Nechay et al., 1977) and with the explosion of population documented during the twentieth century, one may understand that the European hamster was considered as an agricultural pest causing crop damage. At this time, farmers' children even earned pocket money for hamsters' fur. But during the 1970s, the habitat of the European hamster in Alsace began to change: agricultural practices evolved to single-crop farming, small villages expanded their urbanization plans, and more and more road infrastructures appeared dividing the landscape. All of these factors converged to disastrous consequences on hamsters' populations in Alsace. The common hamster has disappeared from the vast majority of its historical Alsatian range and is now only present in 18 municipalities compared to the 329 municipalities in 1972 (**Figure 1**).

Moreover, the plans of protection (breeding program and two National Action Plans) implemented in France at the beginning of the 2000s were considered as not sufficient by the European Union Court of Justice (EUCJ) which condemned France in 2011 for the non-respect of Habitats Directive (Case C-383/09). Indeed, as a Directive State Member, France has the obligation to take all the measures necessary to establish a system of strict protection in their natural range of the animal species listed in this annex (O'Brien, 2015). Then, from the most hated animal in Alsace, the European hamster became the most protected one by international (Bern Convention), European (Habitats Directive) and national legislations in only a few decades. The European hamster was and is still the target of National Action Plans (NAP): a total of four NAPs cumulating 21 years of actions of conservation from 2000 to 2028 (**Figure 1**). Moreover, the status reversal of the common hamster has been so radical that feelings of human populations living with the hamster (farmers and citizens) were hatched, leading the European hamster to become without any doubt the most controversial species in Alsace (Losinger et al., 2006; Méchin, 2007, 2011, 2013).

Alsace is one of the most agricultural regions of France counting 40% of exploited lands (Agreste, 2020). The maize culture is one of the most important, not only for alimentation or seeds but also for biofuel or bioplastic (Méchin, 2011). Yet, it has been shown that maize as monoculture negatively impacts the survival of European hamsters not only by a lack of protective cover part of the year but also the behavior of mothers who killed their pups at parturition because of a lack of vitamin B3 and essential amino acids (Tissier et al., 2016a, 2017). Then, farmers were and are still the most impacted by conservation plans for the European hamster. However, the top-down policy-making process did not facilitate the relations between the different local actors since the animal as its protection was mostly felt as being imposed by others' decisions (politics and scientists) instead of being fully appropriated by farmers (Losinger et al., 2006; Méchin, 2013). Of course, the appearance of such group-conflicts and reactance processes are well-known to challenge the success of conservation plans (Lüchtrath and Schraml, 2015). On a larger scale, with larger mammals such as the European otter or the Eurasian lynx in France, the limiting factor appears to be only anthropic (Laurent, 2014). In these examples, fishers and hunters, respectively, do not accept the presence of those whom they regard as their direct competitors; stakeholders as well. This led to a major ethical issue: shall we favor humans or animals? Why is it so difficult to favor both? And more importantly, how do we even get to the question of our legitimacy to choose between both?

When considering the protection of a species and more generally biodiversity, two approaches are possible. The first consists in the establishment of protected areas in which human activities are strongly regulated or prohibited, leading to land-use conflicts. There is no doubt that in any case, it will require permanent protection of animals and their habitat. A second approach involves integrating the protection of biodiversity and ecosystems into human socio-economic activities. Both strategies have been applied in the case of the European hamster.

Studies and surveys of hamsters' populations have been carried out in several European countries including Germany, Poland, Czech Republic, Netherlands, Belgium, Austria, and France. The decrease of most of the populations led to the setting of protected areas. For example, in 2002, protected areas have been created in the Netherlands to reintroduce a hamster population in a favorable habitat (Müskens et al., 2005; La Haye et al., 2010). Such conservation plans (habitat protection and restocking measures) have also been carried out in Belgium (Verbeylen et al., 2007; Verbist, 2007), in Poland where wild animals from Czech Republic have been released as genetic support for the Polish population of Jaworzno (NAP 2019–2028), as well as in Germany (please see Weinhold, 2009 for an inventory of measures for each Federal states). In Alsace, population reinforcements of European hamsters are carried out since 2000 in three priority restocking areas with animals coming from breeding facilities. Releases performed in these areas lead to good results and hamster population grew the first years, but after this time hamster population decreased again and remained still low. The reasons for this partial failure seem to be an attraction of predators since hamsters were concentrated in a small area but were absent elsewhere (Villemey et al., 2013). Thus, these areas appeared for some as sanctuaries allowing protection managers to conduct their actions but also allowing the out-of-area farmers to be not concerned by the hamsters' protection following the Not-In-My-BackYard (NIMBY) principle (Méchin, 2011).

A second and more hand-in-hand—or at least holistic—strategy has been developed in France in 2013 with the beginning of the European granted LIFE+ Alister project. Until its end in 2019, different actors such as farmers, scientists, NGOs, and policymakers operated together not only to conduct discussions with hamster opponents, to breed and release individuals,

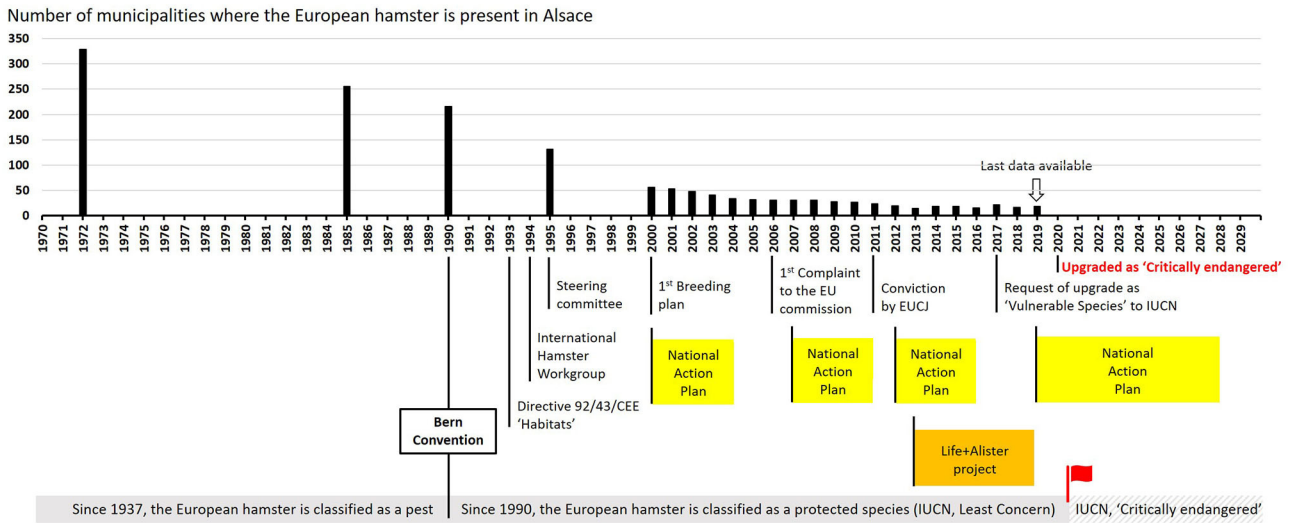

FIGURE 1 | Hamster conservation in Alsace: from the evolution of its presence to conservation plans between 1970 and 2028. Bars represent the number of municipalities where the European hamster is present in Alsace (France). The lower part of the figure represents the timeline of principal events concerning conservation measures and decisions for the species.

to study the ecological needs and biology of the species, but also to investigate the social dimension of the ongoing hamster conservation plan and improve the popularity of the species. A similar strategy was established in Germany with the Feldhamsterland program led by the NGO Deutsche Wildtier Stiftung which aims at targeting the best measures to protect the German hamsters' populations in collaboration with farmers and citizens.

In Alsace, at the beginning of the LIFE+ Alister project, an important step was to identify negative and positive trends considering the public opinion concerning *Cricetus cricetus* and its protection plan. Indeed, even if the term "pest" has been banned from the French legal vocabulary—and has been replaced by the classification "susceptible to cause significant damages (…)"—it is still a common word used by citizens to qualify the European hamster. Micoud (1993) already asked the question "How to get rid of so-called pests?." A first process proposed by the author is the animal's rehabilitation, meaning that its social representation must change positively. This step was and is still not easy considering the European hamster history in Alsace.

A first study focused on the image of the European hamster in articles of regional newspapers and websites (ACTeon, 2013). When concerning the European hamster, 52% of the articles showed positive arguments considering its protection, whereas 37% appeared more negative about the rodent and 11% were neutral considering land and territory use mostly. People entailed in the protection of the European hamster also did not demonstrate the same level of perception. While the agents of its conservation kept the distance and stayed neutral, the European hamster was considered as a disaster for politics and as a victim for the NGOs representatives (ACTeon, 2013). Still today, the European hamster is the figurehead of actions carried out by environmental NGOs or the totem of the eco-friendly "tribe" as Méchin (2011) pointed it out. In 2014, a second study using questionnaires and interviews focused more on Alsatians' perception and knowledge about the European hamster (ACTeon, 2015). Results showed that a large majority of the population questioned (90%, 700 persons) knew about the European hamster's critical situation, but only one person on five was aware of the different protective action plans. More interestingly and in detail, elder people knew the European hamster (96% of the more than 60 yo) but not its critical situation, conversely to the youngest people who knew the animal less (66% of 18–30 yo) but its situation better (ACTeon, 2015). Benefiting from this knowledge, LIFE+ Alister project partners conducted actions of communication toward civilians living close to the European hamster, notably targeting young public such as children. Regrettably, at the end of the program, the social image of the European hamster did not evolve so much, but one may protest that 3 or 4 years is too short to measure the impact of the conducted actions at such big scale (ACTeon, 2019).

POPULATION REINFORCEMENT

When the conservation status of a species becomes very bad somewhere or if populations are quickly decreasing, it can be necessary to reinforce them to avoid local extinction of the species. The reinforcement can occur in the residual area where individuals still survive, to increase their probability to subsist across time. It can also be done in the area between two sub-populations to maintain the connectivity between them and to increase the area of the presence of the species.

When talking about species conservation and especially with population reinforcements, genetic considerations have to be taken into account. Genetic diversity in populations has to be

preserved to keep at a high level the fitness of the endangered species. For instance, it has been demonstrated that the habitat fragmentation of a small rodent-like the European hamsters can lead to low diversity in the population and threaten the species locally (Reiners et al., 2011). If genetic diversity decreases too much, it can be necessary to introduce animals from other phylogeographic groups to improve the survival chances of the population (Melosik et al., 2017). But to be successful, there are other several prerequisites for population reinforcements to fulfill. We will examine these prerequisites in the next section and expose what has been done for the European hamster and the results that were obtained.

Pre-releasing Requisites

The main goal of all wildlife release programs is to put back into their natural habitat animals that will be able to survive in suitable conditions with long-term resources and a minimum of disturbances. To achieve this goal, two pre-requisites appear of major importance: animals "ready" to be released and suitable habitats. But before even thinking of releasing animals, we should give regard to the ethical question: are captive animals really able to return to the wild and thrive? Of course, we are not talking here about animals that spend their all lives in captivity in zoos or circus, but about animals that are specially bred to be freed, not or little used by humans. Even bred during a short period, animals can become more or less habituated to humans despite the efforts taken to avoid such a situation. Then, it might be important to consider (1) to only release individuals that are not habituated—or at least less habituated—or (2) to disaccustom individuals before the release. The first strategy seems adequate when considering young individuals shortly after weaning, mimicking a natural dispersion from their native burrow. For its part, the second strategy involves multiple stages. The animals can be released into temporary enclosures with vegetation to hide and with some additional food or preys to hunt. Another advantage is that the fences protect them against natural predators or disturbance. Ideally, these enclosures should be installed in natural reserves or at least in protected and controlled areas. Thus, the animals will have time to gradually get used to their new life. Some may even breed in the enclosures and produce wild offspring never handled by humans that can be released on other plots afterwards. Depending on the species, this step will take more or less time. In larger mammals, especially social animals, this step is essential to create groups. Solitary animals can spend a shorter time in the pre-release enclosure. In the case of the European hamster, releases were done in fields with unharvested wheat and surrounded by electrical fences, to provide food and limit predation during the first weeks of their free life. Unfortunately, sometimes these enclosures can become deadly traps if predators find their way in (Villemey et al., 2013).

Furthermore, all species cannot be released the same way. If we talk about mammals, it might seem easier to free thousands of rodents with high reproduction rates than a few large mammals whose reproduction rates are lower. At the individual level, most rodents will certainly not survive very long, but the species as a whole will probably make it out, whereas the large mammals will be more successful in the short term but with an uncertain future, mainly due to human pressure (notably illegal hunting). In the case of the French European hamster, it is clear that one may ask why such a rather prolific species (1–3 gestations a year of 3–12 young) remains endangered after 20 years of conservation measures and more than 3000 individuals released.

The answer to this question leads us to the second pre-requisite: the suitability of the habitat. Finding a natural environment suitable for released animals appears to be a real challenge nowadays in a continuously human-disturbed world. Living in crops, European hamsters' survival is clearly linked to agricultural management, notably the presence of vegetation cover to protect them against predators and provide food resources. This is only possible if farmers modify their agricultural practices (see the specific section below).

Reinforcement or Habitat Improvement: Where Is the Priority?

The mortality of released European hamsters is still too high to allow a sustainable increase in the population. We can then question ourselves on the merits of such action knowing that freed animals will die massively because habitats are not suitable. Should we not first improve all habitats sustainably before releasing hundreds of individuals? On the other hand, habitat improvement is a long process. Can we do nothing to save the species in the meantime? Certainly not. Even if not easy, it seems preferable to strike the balance between both issues, animal and environmental ethics. Keeping the species under passive dependence preventing it from disappearing while working on environmental improvements is precisely what is done by the French hamster programs (LIFE+ Alister and NAP). Moreover, reinforcing populations while gradually improving habitat has many advantages and seems more suited to current societal constraints (see **Table 1**).

When populations have totally disappeared, the strategy may be different. Let us consider for example a well-studied species, the European otter (*Lutra lutra*). The French otter population underwent a continuous decline during the second part of the last century due to illegal hunting, habitat loss, and water pollution (Kuhn and Jacques, 2011). The reintroduction of animals from remote geographical origins is not recommended because of a risk of outbreeding depression and potential reduction of the fitness and long-term survival of the population (Randi et al., 2003). Thus, in this case, it appears more suitable to restore habitats and increase connectivity among residual animals via natural corridors. In the case of European otters, efforts to protect and rehabilitate such habitats have paid off, and otters recolonized areas throughout France over the past 20 years with regional variations (Lemarchand et al., 2016). But could this strategy of recolonization be applied to hamsters? Although the French hamster population is isolated from other residual European populations living in very different habitats, the solution could be similar on a local scale: protecting residual wild population nuclei and improving the surrounding habitats little by little to allow a natural recolonization. Again, the key issue is to change agricultural practices to find suitable crops for both hamsters (i.e., ecologically durable) and farmers (i.e.,

TABLE 1 | Pros and cons of the strategies considering different priorities for population reinforcement and habitat improvement.

	Population reinforcement while improving habitat	Habitat improvement followed by population reinforcement
PROS	May be seen as a first "trigger" step resulting in: - the maintenance of the population (no genetic loss) - a better perception/acceptance compared to a reintroduction if population extinct during this time - the maximization of the partners involvement (political and societal)	Derived from the necessity to solve the causes of the decline before reinforcing (otherwise it leads to a failure) resulting in: - a better perception of the conservation plan (seen as holistic instead of species-focused) - the maximization of the conservation efforts
CONS	Need to continue until the habitat has been sufficiently improved resulting in: - a possible long time before seeing positive or lasting effects of the reinforcements - a possible dispersion of actions and resources	May lead to the complete extinction of the population/species in the wild resulting in: - the ↓ of genetic diversity - the ↓ of politics stakes - the ↑ of administrative obligations - the ↓ of motivation of local actors - the ↓ of habits to live with this species

economically viable). This is what research is focusing on even if such strategy can take decades and requires considerable human and financial investments.

Problems Risen by Releasing Programs

Releasing animals is accompanied by many constraints or problems. First, some people are strongly opposed to breeding in captivity. They consider that captivity is not acceptable and/or that breeding conditions in cages are not optimal. Secondly, the mortality level after release can be considered as too high from the animal ethics perspective, as already exposed above. Finally, the high number of individuals that reinforce core populations might pollute or dilute the genetic pool present in the wild population and may be seen as a potential threat for its survival. These questions have to be kept in mind to minimize as much as possible potential problems but have not been identified as prohibitive for European hamster restocking programs in France.

Another problem that can be encountered with releasing programs is the regulation of predators. For prey species like the hamster, predation pressure is a key determinant of their survival (Kayser et al., 2003; La Haye et al., 2010; Villemey et al., 2013). Since many efforts are needed to breed and release animals, some people may ask for predator regulation to limit predation on released animals. Such a measure can be taken even though predation is a natural process, i.e., part of the food chain, and despite its low efficiency. Indeed, predator regulation has generally no significant and durable effect on the global predation rate of the prey (La Haye et al., 2008; Treves et al., 2016). The killing of predators can, however, be considered in programs like NAP since they result in the participation of many stakeholders, including hunters (Virion and Thouvenot, 2019). It is sometimes a wiser choice to consider this possibility—while trying to convince to never apply it—than showing strong opposition to it, leading to group reactance.

Results of Hamsters' Releasing Programs

Since the early 2000s hamsters are bred in France to participate in restocking programs. On one side, given the drop in hamster population at this time and since the species is now still present in three distinct areas of the region, we can consider that it is a success. Furthermore, releasing allowed maintaining the species in the region and conserve genetic diversity (Reiners et al., 2014). On the other side, populations are still not really increasing because of a high predation rate of released animals on some plots. An improvement of release protocols is currently under study. One way would be to limit the impregnation of the animals during captivity or prepare them for wildlife in pre-release enclosures (Virion and Thouvenot, 2019).

We cannot predict the situation we would face without this program, but we know that only one small part of the presence area in Alsace did not need and benefit from any restocking program, i.e., the area close to the city of Obernai. These last years, the Alsatian population started slightly to increase. However, this is not a demonstration of a general improvement of the situation since the area of presence of the species is still not increasing. Population increases only in a few areas where population reinforcements have been accompanied by habitat improvement during several years. This illustrates the benefits of a conjugate use of those two conservation measures, and a wider application is now needed.

Another illustration is the restocking programs that occurred in the Netherlands (Müskens et al., 2005; La Haye et al., 2010). There, the species was extinct in the wild in 2002, and restocking programs started the same year. Some hamsters' releases occurred in farmland reserves, i.e., fields bought by the government and managed by nature conservation organizations. Other ones occurred on fields where farmers signed a contract to implement measures favorable to hamsters. Both releases led to a nice increase in hamsters' population already during the first years.

IN SITU ANIMALS' MONITORING

While studying an endangered species, monitoring individuals in the wild is often a necessity for several reasons. It can first help to assess the size and characteristic of the residual populations. It allows also evaluating the benefits of the measures taken to protect the species. Last but not least, it is an important tool when studying a population *in situ* to better understand its biology or ecology, which is helpful to better protect it. The impact and a cost-benefit assessment have, however, to be evaluated, including ethical considerations. Kletty et al. (2019) summarized and compared the different methods available to monitor small mammals like the European hamster. Hereafter, we discuss some of them and their implications.

Capturing and Tagging Animals

The capture of an animal is a way to gather many data or information about it. It can be weighed and measured, and samples of feces, hair, or blood can be taken for later analysis. At the same time, individual identification can be done to allow recognizing it later. Different methods can be used: (i) photo-identification, if the species have fur or skin patterns that differ from one animal to another like with some felines or amphibians; (ii) external tags like rings, bands, ear punches, toe clipping, tattoo; and (iii) internal systems like passive integrated transponders (PIT) for radiofrequency identification (RFID).

Almost all these methods can have an impact on animals since they require animals to be trapped. This can cause stress but also prevent the animal to perform its natural activity during the time of capture. The issue can be dramatic especially when they have newborns that need protection, thermoregulation, or regular feedings. The capture of an animal can also modify or prevent some behaviors at key periods like reproduction or disturb social groups (Minteer et al., 2014). Even photo identification in some cases needs the capture of animals to take good pictures or specific parts of the body (like the belly of some amphibians).

The stress generated by handling procedures can be increased if there is additional pain linked to the method, and this can also affect other biological parameters like body condition or survival (Tamarin and Krebs, 1969; Pavone and Boonstra, 1985). However, knowledge about the biology of organisms and pain increase, encouraging scientists to question continuously the existing procedures.

In this sense, the use of PIT-tags is an interesting method. It is no more painful than a syringe injection, easy to use, and works for life. Another advantage of PIT-tags is that it can be combined with automated identification recorders to monitor the presence or movements (e.g., wildlife underpasses or burrows), biological parameters (i.e., coupled with a weight-watcher), or behavior (coupled with camera) of animals, without requiring their recapture (Tissier et al., 2018a; Kletty et al., 2019). Dying and ringing are other ways to gather information on the presence or behavior of specific individuals since it allows a direct or indirect (*via* cameras) recognition. However, even if these methods are painless, they can sometimes bother the survival or fitness of individuals, as it has been shown in penguins (Culik et al., 1993; Froget et al., 1998; Saraux et al., 2011).

All these methods of individual identification allow performing capture-mark-recapture (CMR) studies, which consist of capturing, tagging, releasing, and trying to recapture animals later. CMR is interesting for collecting longitudinal information on individuals and evaluate survival and population size or dynamics (by integrating the rate of unknown individuals and performing statistic corrections or modeling) (Pradel, 1996; Bohec et al., 2007).

Field studies on hamster populations in France are done with such CMR approach where all individuals captured, released, or participating in experiments are identified with PIT-tags, with the use of RFID automatic antennas in different studies and situations. Earrings have also been used in a specific study to recognize individuals on camera traps pictures. At the time of capture, body mass and tibia length are measured, and material like feces or hairs can be collected for genetic analysis. During periods where females can be lactating, special attention is given to minimize the time between the trapping of the animal and its release.

Transmitters to Follow Animals

Knowing the localization of specific individuals in the wild can provide valuable information, like home range or reproductive success. However, some ethical questions can arise with logger-transmitter equipment, especially intra-abdominal implantation of transmitters. The proximal issue with implantation is surgery that can cause suffering or even death. After surgery, implants can also affect the long-term behavior and the survival of animals. These questions have been assessed by Koehler et al. (1987) in a study carried out on four species of small rodents: they show a mortality risk with surgery (14% in their study but they indicate how to improve it), but a good survival after the release (more than 94% after 1 month). Nowadays, survival after surgery is now much better and can reach 100% after implantation of transmitters for hamsters (Capber, 2011). Furthermore, some of the transmitters in Koehler et al. exceeded 10% of the mass of animals while it is now recommended not to exceed 3–5% (Macdonald and Amlaner, 1980; Theuerkauf et al., 2007). In France, European hamsters are only implanted when their body mass exceeds 150 g. The transmitter weighing 6.5 g does not therefore exceed 4.3% of the body mass of the hamster and, thus, never exceeds the recommended range. It explains partially the good tolerance observed in the field. Furthermore, the transmitters do not seem to impair gestation (Capber, 2011). Thus, it is possible to implant loggers and transmitters without marked impact on the survival of individuals or on a population. However, since it is an invasive protocol—even moderate—it has to be used when expected benefits are high enough for the monitoring of equipped individuals, and only when necessary.

The use of external transmitters is also possible and does not require surgery, but it can have adverse effects on animals, like handicap (especially collars for hamsters, since they have cheek pouches), perturbation of its behavior, or survival impairment (Webster and Brooks, 1980; Theuerkauf et al., 2007; Kletty et al., 2019). Thus, if internal transmitters can be used, it seems to be a more suitable option.

Transmitter implantation and animal tracking may affect and disturb animals. On the other hand, the information gathered by such monitoring appears crucial in protecting endangered populations and improve conservation measures. Once again, enlightened choices have to be made and the balance must be found to minimize the effects on individuals and the protection of the population.

MODIFICATION OF AGRICULTURAL PRACTICES

In Alsace, intensive agriculture from the 1950s onwards led to the degradation of the agricultural ecosystem and the loss of biodiversity. As an illustration, the decline of the European hamster can be mainly attributed to the lack of protective and

nutritional cover part of the year. Therefore, it is primordial to restore habitat quality to increase hamster populations, and this ideally before the reinforcements (see **Table 1**).

What Are Hamsters' Needs?

The European hamster is an omnivorous rodent that can feed on a wide variety of food and that can adapt to different environments (Nechay et al., 1977; Tissier et al., 2019b). Despite this flexibility, nutrition requirements are often not met in its habitat to allow good development of the population. Maize cropping is deficient in essential amino acids and vitamins, whereas wheat monoculture that is however considered as a favorable crop does not contain enough proteins to ensure a proper reproduction of hamsters (Tissier et al., 2016a, 2017, 2018b; Weitten et al., 2018). Protein-rich plants (legumes) or animals (invertebrates, voles, *etc.*) are interesting food supplies that cover these deficiencies. A diversity of food resources is therefore a key issue to restore hamsters' reproduction and increase the population.

The crop in which they live provides hamsters also a protective cover against predators. However, this cover can be reduced or removed by the work of farmers, like harvesting, mowing, or plowing, resulting in increased exposure to predation (La Haye et al., 2010, 2014). It has also been observed that such removing of the cover leads to an increased emigration of hamsters out of the concerned plots, threatening their survival (Kayser et al., 2003; Kourkgy, 2019).

Last, the expansion of anthropogenic infrastructures especially roads, linked to unsuitable agricultural habitat like plowed fields, limit the movement of animals and the connection between different sub-populations (Tissier et al., 2019a). To improve that, underpasses for wildlife have been constructed under highways and then improved with anti-predation devices to secure the crossing of small mammals (Tissier et al., 2016b). To be more efficient in reconnecting residual populations safely, these underpasses need also to be surrounded by favorable habitats. Thus, agricultural practices have without doubt a key role in this habitat connectivity.

How to Implement Suitable Habitats?

To offer to hamsters the diversity and quality of food they need, a first way could be to use less or no pesticides in the considered fields. Indeed, these products can have negative effects on hamsters' survival and reproduction, but also alter their food resources. Pesticides kill adventive plants and also other organisms, from soil bacteria and fungi to invertebrate macrofauna (Edwards and Thompson, 1973; Joy and Chakravorty, 1991), therefore reducing the diversity of food sources for hamsters and impairing their reproduction.

A second way to improve hamsters' habitat is to foster epigeous and endogenous fauna through adapted agricultural practices bringing them protection and food. Soil disturbance reduction (like plowing or tillage suppression or reduction) can be important to increase soil organisms' biomass (Norris et al., 2016; Chen et al., 2020). This can be achieved by covering the soil with mulch or living cover, and the holding or the promotion of a maximum of carbonated matter on the fields (non-exported straws, manure, increased cover crops…). Promoting the presence of different crops at a reduced distance is also a solution (Sirami et al., 2019). This is especially true since the home range of a female is only 0.2 ha (Ulbrich and Kayser, 2004). The implementation of strips of two (or more) different crops on the same plot (allowing mechanization and crop diversification at the same time), or simply creating long but small plots seeded with different crops, would increase plant diversity at a small scale. It would be also interesting to consider other innovative practices like relay cropping and crop associations, which bring diversity on a smaller scale (less than a meter). All of these possibilities would bring shelter for hamsters by the time of mowing or harvesting.

As mentioned above, the persistence of a cover along time is important for hamsters, as much for the shelter as for the food it brings. This can be achieved by seeding intercrop cultures like the ones seeded to catch nitrogen residuals. However, such crops usually grow too late to be beneficial for hamsters. The practice can be improved either with early implantation of the intercrop just after the harvest or by seeding directly a cover crop in an already growing one (e.g., clover under-seeded in wheat or maize).

What kind of agriculture functioning at a large scale could provide the different services and integrate the methods exposed above? Some of them can be filled with organic agriculture, which is moreover already well integrated by citizens. However, it still usually (but not always) works with monospecific crops and bare soils, especially for weed control. Other types of agriculture are rising and aim to develop healthier soils and more biodiversity in agricultural systems. We can find it under different names like soil conservation, conservation agriculture, agroecology, biodiversity-based agriculture, or ecologically intensive agriculture. Even if there are many variations in concrete applications of these innovative agricultures, they all rely on the same principles of improving soil quality, increasing the diversity of plants and habitats along time and space, and integrating in a holistic approach the relations between the multiplicities of organisms living in the ecosystem (Duru et al., 2015; Wezel et al., 2018; Chabert and Sarthou, 2020).

Why Is It so Difficult to Modify Agricultural Practices?

We know a lot of elements and practices that may be beneficial for hamsters, but the aim is not to implement them only on restricted areas, whereas, its habitat is impoverished everywhere else. Instead, social and economic context should be taken into account to develop at a large scale, practices that would benefit all parties, including biodiversity and farmers.

First, it is necessary to understand that the solutions beneficial for farmland biodiversity are based on the modification of the actual agricultural practices. As with any change in habits, this is not easy to achieve. This is especially the case when it comes to change the relation a farmer has with its soil, when its management and especially plowing are questioned. It has indeed been shown that this relation is a key element for farmers since it is one of the last element they still control, while many

other competencies are delegated to external operators (Christen, 2011).

Developing innovative practices is also difficult since no turnkey solution exists, and while farmers are advised by agricultural consultants to perform conventional agriculture and use pesticides. To leave this system, they have to break away from usual structures and to adapt what is known to their specific context and then try to find the best solutions. This implies a good understanding of ecological processes at work on the agricultural ecosystem. In general, only farmers with advanced agronomic knowledge develop agroecology-based practices. Anyway, the transition between conventional and biodiversity-based agriculture takes time, since it relies on long-term processes like soil biodiversity and carbon stock enhancing, or predator-prey balancing. The first years of transition can thus be particularly difficult for farmers since they face the disadvantages of the new practices but still not all the advantages (Fiorini et al., 2020). Therefore, there is an associated risk and a cost to think outside the box.

Negative externalities in agriculture (i.e., indirect cost associated with agriculture like water pollution or biodiversity loss) (Catarino et al., 2019) are generally not supported by farmers. Thus, agricultural practices that limit such externalities generally do not benefit from associated retributions for the efforts performed. There are exceptions for organic farming since it is well recognized and receive financial support especially for the conversion period to such agriculture (even if it is not always considered as sufficient). It would be interesting to extend such programs to farmers involved in agroecology since the positive externalities can be important and because the cost paid by farmers to change the system is high.

To implement more biodiversity at a landscape scale and help hamster population to survive, farmers have also to work together, which can modify their habits. They have indeed to decide together upon crop rotation of a defined area to maximize the surface of favorable crops where hamsters subsist and maintain coherence across space and time. Furthermore, the specific material that can be needed for conservation agriculture (like specific seed drills) is expensive and sometimes requires farmers to gather to reduce the associated cost. For those reasons, modification of practices to better integrate biodiversity can lead to a modification of the relations between farmers, which is not always easy and can require specific coordination.

Finally, the last hurdle we can talk about is associated with social perception. In our societies with task repartition, we delegate to farmers the production of our food. In that context, we can wonder if it is the consumers and not the farmers that would have the biggest responsibility in the ecological implications linked to agriculture. On one hand, farmers think usually that their actions are limited since they have to follow the law of the market, so it should be consumers that have to pay the right price if they want ecology to be considered. On the other hand, consumers think that farmers are responsible for diverse pollutions and should take the responsibilities linked to what and how they produce. Thus, an opposition develops between different groups: consumers and farmers, but also environmentalists, hunters, scientists, politics, *etc.* This is linked to the social identity theory and psychological reactance, as illustrated by Lüchtrath and Schraml (2015) in the context of hunters' opposition to large carnivores. They show that the different groups are in reactance with what can be proposed by others, to protect their social identity. Thus, it seems particularly important to build positive relationships to avoid such reactions of different groups of actors.

In the context of European hamster preservation in France, many of the difficulties cited above have been limited by the measures developed. The programs have been conducted with a great implication of farmers. They are not set aside while other stakeholders decide what has to be done, but they are involved in the studies, participate in the decisions, try new practices, or propose possible improvements. Group-working needed to perform favorable crop rotation or agricultural trials lead to good relations, discussions, and sharing between farmers and with other stakeholders. Furthermore, specific demonstrations or formations have been proposed in relation to conservation agriculture, especially with the help of the Agriculture Chamber of Alsace that is also implicated. Farmers are also encouraged by financial support especially for favorable crop implementation and specific material to share. They are also now encouraged to promote hamsters' presence rather simply developing the means in favor of biodiversity, since a bonus is given for each favorable crop containing hamsters' burrows. Thus, the protection of a small rodent helps to initiate or develop a transition toward more sustainable agriculture and a change in practices and states of mind.

The European Union: A Leverage or a Barrier for the Conservation of the European Hamster?

The European Union offers financing tools for the preservation of biodiversity, such as Life programs. After the condemnation of France by EUJC in 2011, the common hamster benefitted from such European funding (LIFE+ Alister program from 2013 to 2019) which, in our case, aimed to improve the habitat of the species, to find new areas favorable to the reintroduction of the species, and whose educational component to make the species known and welcomed by Alsatians was very important.

However, there were still obstacles to the implementation of some environmental measures that emerge from these programs, including the concern of not meeting consumers' demand and economic targets. Indeed, in their economic study, Eppink and Wätzold (2009) demonstrated that the measures for the protection of the common hamster in Mannheim area (Germany) implied important hidden costs notably linked to changes in development plans, the invisible costs being even higher than visible ones—directly associated with conservation measures. Moreover, the delay taken in the protection of the common hamster not only had a cost for the survival of the species but also a financial one. Indeed, proactivity in conservation domain (i.e., to start a program of conservation before a species is endangered) allows saving a non-negligible amount of money compared to simple reactivity (Drechsler et al., 2011). It is therefore not only a question of preserving a living

territory in terms of biodiversity but also in terms of economy. Thus, the LIFE+ Alister has sought to structure the protection of the common hamster not only around the ecological but also economic and social development of the Alsace area.

Biodiversity has long been considered as a source but also as a constraint of economic activities, notably when considering the EU's Common Agricultural Policy (CAP) (please see the review of Simoncini et al., 2019). Despite an ambitious EU Biodiversity Strategy to 2020 (European commission, 2011), the elaboration of the 2014–2020 CAP did not enable the incorporation of suitable measures to fulfill the objectives (Pe'er et al., 2014); 77% of the €86 billion EU budget for biodiversity during this period came from the CAP, but this was not sufficient to stop the decline of farmland biodiversity (European court of auditors, 2020). Biodiversity was until recently not considered to be part of agricultural areas, but this is slowly changing. The post-2020 CAP integrates more and new agro-environmental measures: farmers will be encouraged firstly to design eco-schemes at the level of agricultural landscapes, i.e., to implement hedges, rows of trees, field copses, ponds or fallow lands on a minimum of 10% of agricultural land (1st pillar of CAP post-2020) and, secondly, to implement measures that preserve the environment, such as reducing the use of fertilizers (2nd pillar). However, this still does not correspond to a real transition toward a sustainable and biodiversity-friendly agricultural model. We recommend the implementation of policies that specifically promote the development of already identified agricultural practices and farming models that allow a simultaneous consideration of food production, biodiversity, and human well-being (see for example Duru et al., 2015; Valenzuela, 2016; Boeraeve et al., 2020; Chabert and Sarthou, 2020). Concerning the French European hamster, studies and conservation plans, including the Life+ Alister program and agro-environmental measures, played a crucial role in the subsistence of viable populations and in the development of a more general context, such as improving the farmland habitat and enhancing hamster perception through society awareness. This gives us an optimistic glimpse into the future.

What About a Successful Increase in the Population?

Such successful increase is what happened with the bird symbol of Alsace, the white stork. This species was protected in the 1970s since the survival of the regional population was severely questioned. A reinforcement program occurred and was a success, since there are now more than 400 pairs. Despite this success, the white stork is still a subject of conversation because the now numerous individuals leaving near humans cause disturbances, like infrastructure damages, noise, or dropping nuisances. If the same success occurs with European hamsters, one can fear to come back to the previous situation when it caused important damages to crops. However, we have now an improved knowledge about predator-prey dynamics and ecosystem balancing, leading us to consider that overpopulation can be avoided with natural regulation by predators. Ecosystem balancing seems thus especially important in that scope to promote biodiversity while maintaining the production and other services provided by farmland ecosystems.

Other Issues, Same Problems, Same Solutions

Conservation measures and studies that have been carried out allowed a better knowledge of the biology of the European hamster and its habitat, its needs, and threats. In addition, gathering information improved knowledge in many other scientific fields like ecology or nutrition that can be transposed to other species (Monecke, 2014). Even if the French European hamster preservation plan can sometimes be viewed as a lot of energy and money spent for only a "small rodent," one may recall the convergence with problems and solutions encountered in a large variety of domains.

The European hamster is not the only species endangered in agricultural areas. Many farmland bird populations are decreasing since several decades (Donald et al., 2001; Heldbjerg et al., 2018; Stanton et al., 2018; Department for Environment Food Rural Affairs, 2019; Gaget et al., 2019). Invertebrate species are also concerned, with insects suffering a massive drop potentially linked to unsustainable agricultural practices (Benton et al., 2002; Shortall et al., 2009; Hallmann et al., 2017). Therefore, conservation measures are widely developed to protect farmland species or taxa, involving various stakeholders. In France, this can be illustrated by the development of different specific national action plans (NAP) like the one for the little bustard (*Tetrax tetrax*) (Poirel, 2019), the one for pollinators (Gadoum and Roux-Fouillet, 2016) or the one for adventive plants (Cambecèdes et al., 2012). During the last European hamster NAPs, conservation measures for hamsters and associated innovative practices have been identified to be highly beneficial not only for hamsters but also for a lot of other species including the above-cited ones (Wilson et al., 2005; Liu et al., 2015; Norris et al., 2017; Zellweger-Fischer et al., 2018).

Furthermore, these measures may also help to reduce soil erosion. This issue is of particular importance for farmers since the soil is the first support to their production. Ground runoffs and mudflows can happen in sloping areas during rainy periods and also affect people outside the crops (material damages, water quality, safety) (Bronick and Lal, 2005; Heitz et al., 2009). Soil erosion can be limited or avoided by improving soil quality and coverage, i.e., increasing soil biota, soil organic carbon content, and protecting it, thanks to mulch or cover crops (Bronick and Lal, 2005; Seitz et al., 2018). All these practices join the ones that are beneficial for the European hamster conservation.

Drinking water can be affected by nitrogen concentration and by a multiplicity of pesticide residuals as well, sometimes at high levels (APRONA, 2020). Surprisingly, water pollution is usually not the most negatively perceived by citizens, since it is not visible. Pesticides application is much more feared by people, especially when it occurred at the vicinity of habitations. Thus, agriculture with moderate or no use of pesticide would not only be beneficial for hamsters' biotope but also for its human neighbors, from a health and a sociological acceptance perspective.

Both citizens and hamsters need the development of an agriculture with more plant diversity, more cultivated or spontaneous biodiversity on crops, and more cover crops. Indeed, this participates in the creation of more attractive landscapes, thus increasing people's wellness (Hasund et al., 2011).

The proportion of farmers in the population is getting smaller and smaller, and the difficulties they meet are going in the opposite direction. It is especially true since they face more and more extreme climatic conditions due to global climate change (Rosenzweig et al., 2001; Fischer et al., 2002). Conservation or biodiversity-based agriculture can be beneficial for that too, since it relies on the operation of many ecosystem services that increase the resilience of the agroecosystem (Armand et al., 2009; Dainese et al., 2019; Montoya et al., 2020).

If innovative agricultural practices can help to adapt to climate change, they can also be beneficial to limit it. As explained previously, soil improvement is a key factor for the agricultural systems, and it relies on the increase of soil organic carbon. This organic carbon comes from the photosynthesis of plants, taking carbon dioxide from the air. This mechanism is important enough to have a significant effect on atmospheric CO_2 concentration. This is for example what is promoted through the 4 per 1000 initiative since an increase of soil carbon of 0.4% each year in the 30–40 first centimeters of all agricultural soils would allow compensating global annual CO_2 emissions (Rumpel et al., 2020). This does not mean that we found the solution to solve the atmospheric CO_2 problem or that we have not to reduce carbon emissions, but it shows that agriculture can significantly contribute to slow down the global change.

CONCLUSION

Conservation measures for endangered species are undoubtedly of great importance. It is crucial to take into consideration animal ethics as a societal need in order to be as beneficial as possible. Furthermore, they have a much broader impact than only protecting the considered species or habitat. To be successful, they have to include the multiplicity of stakeholders concerned with the covered topic. This is well illustrated with the case of the European hamster whose rescue deeply depends on modified and innovative agricultural practices developed by farmers. Moreover, these modifications consisting in more integration of biodiversity, soil, and natural processes are not only a solution for species' protection but also an entire improvement of farmers' socio-economic conditions, as well as citizens' well-being, and contribute to the planet health for sure. All of this implies taking into account the externalities (positive or negative) of the practices as their implementations, leading to the most holistic view possible. We recommend to stakeholders to use, to foster, and to develop all the measures available that can promote agricultural biodiversity, and to assist in the development of a new agricultural model. These measures must also be taken at the level of several territories or countries. Concerning the common hamster, exchanges of experiences and ideas take place every year during the International Hamster Workgroup meeting, between scientists and field operators from countries where the species is present, which makes it possible to improve conservation actions and develop collaborations. This year, a first joint conservation program between France and Germany will be submitted to Europe, in order to implement on a larger scale measures to restore population levels and improve agricultural habitat.

AUTHOR CONTRIBUTIONS

FK and MP equally contributed to this work as the first author. All authors brought constructive thoughts and participated in the elaboration of this review. All authors contributed to the article and approved the submitted version

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