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Balancing ecotourism and wildlife management through a conservation behavior approach

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Abstract

Ecotourism promises to reconcile wildlife conservation and human development if negative impacts of human visitation and associated infrastructure can be minimized. Animal behavior studies can be used to identify individual and population responses to anthropogenic impacts before other fitness consequences are documented. With input from professionals in animal behavior and ecotourism, we identified key questions needed to better understand the impact of ecotourism on wildlife. Activity budgets, foraging, movement, stress, habituation, and reproduction were themes that emerged from our survey. We highlight promising research on these themes and identify remaining behavioral research questions about conserving wildlife in the context of ecotourism. Although ecotourism activities often have detrimental effects on animal behavior, we highlight research needs that can inform management and ecotourist education to improve human behavior to be more compatible with sustainable use of nature.

KEYWORDS

anthropogenic, behavioral ecology, human wildlife conflict, tourism

1 | INTRODUCTION

Nature-based types of tourism, such as ecotourism, are growing exponentially with over 8 billion visitors to natural terrestrial areas each year (Balmford et al., 2015). Such high visitation rates create ecological impacts, particularly to the wildlife that is the main attraction for many tourists (Blumstein et al., 2017). However,

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ecotourism has the potential to reconcile wildlife conservation and human development because of its non-consumptive and non-extractive nature (Meletis & Campbell, 2007). By better understanding and mitigating impacts, ecotourism can grow sustainably with minimal effects on wildlife and mutual benefits for local communities and visitors.

When species respond with fear to humans as they do to predators (Frid & Dill, 2002), tourism could have deleterious consequences for the very animals that tourists seek to experience. Fear of humans even exceeds fear of lions for many taxa in South Africa's Greater Kruger National Park (Zanette et al., 2023), although non-lethal human activities do not always elicit fear-driven responses, which may be influenced by trophic level or history of human–animal interactions (Dsouza et al., 2024). Studies of animal behavior can identify the behavioral shifts that often occur early in response to environmental change and measure behavioral responses that likely indicate detrimental effects on population-level outcomes (Dimitri & Longland, 2018; Northrup & Wittemyer, 2013; Smith et al., 2024). To identify key behavioral research questions related to the potential effects of ecotourism on wildlife conservation, we surveyed professionals in the fields of ecology, conservation, and ecotourism (see Data S1 and S2, Supporting Information). We received 67 responses from professionals working around the world. During a 2022 workshop held by the Animal Behavior Society Conservation Committee with participation by ecotourism practitioners in Costa Rica, we prioritized answers from the global survey, focusing here on four behavioral themes: activity budgets and foraging, movement, stress and habituation, and reproductive behavior. For each of these themes, we describe the conservation concern in the context of ecotourism, providing examples, and present the primary research questions that should be investigated for each theme (Table 1).

1.1 | Activity budgets and foraging

An obvious indicator of ecotourism disturbance on animal behavior is change to the daily timing of behavior and to activity budgets, that is, the allocation of time to different behaviors. Many organisms alter timing of behaviors entirely, shifting from being diurnal to nocturnal under human presence (Gaynor et al., 2018). Such temporal shifts can be challenging to survival as they alter metabolic costs, foraging efficiency, antipredator strategies, and social behavior (Gaynor et al., 2018; Sih, 2013; Tuomainen et al., 2011). Through tracking trade-offs among behaviors such as vigilance and foraging, the ramifications of disruptive ecotourism on the individual and population fitness of animals becomes apparent. For example, woodland caribou (*Rangifer tarandus caribou*) exposed to tourists spend more time vigilant instead of resting and foraging (Duchesne et al., 2000), possibly leading to a less favorable energy balance. Although comprehensive activity budgets consist of all behaviors, most research on the effects of ecotourism and behavioral repertoires has focused on foraging and vigilance (Larson et al., 2016). Across all forms of ecotourism, animals tend to spend less time foraging and instead increase vigilance in response to humans (Bateman & Fleming, 2017). Vigilance and other anti-predator responses to non-lethal human ecotourism activities can be costly (Frid & Dill, 2002). For example, whale sharks (*Rhincodon typus*) engaged by ecotourists divert time from foraging to avoiding humans, impacting short-term health, long-term survival, and reproduction with repeated exposure (Quiros, 2007).

Animal fear of ecotourists may be overcome through food provisioning that attracts wildlife for better viewing by tourists (Orams, 2002). It may seem beneficial to animals, but the long-term impacts can be negative. Food provisioning shifts foraging locations and alters activity patterns, often resulting in increased begging towards humans and a high density of individuals that can lead to increased aggression and greater parasite transmission (Corcoran et al., 2013). Spider monkeys (*Ateles geoffroyi*) increase interactions with humans but also suffer more agonistic behaviors from other monkeys when food is provisioned (Pérez-Galicia et al., 2017). Although American black bears (*Ursus americanus*) gain body mass by frequenting feeding areas (Ardiantiono et al., 2018; Massé et al., 2014), the food-conditioned bears have no advantage in litter size, and their cubs are 5.6 times more likely to be killed due to their association with developed areas (Mazur & Seher, 2008). Furthermore, food provisioning can alter activity budgets and diel patterns. Whitetip reef sharks (*Triaenodon obesus*) increase their daytime activity and reduce resting periods when tourist boats that fed the sharks were present (Fitzpatrick et al., 2011). Lastly, food provisioning might have demographic and community effects on wildlife; bolder or hungrier individuals, and omnivorous species (Ilarri et al., 2008), are more acutely affected by food provisioning (Moran et al., 2021).

Nevertheless, there are situations where provisioning has positive impacts on wildlife and may offer lessons for provisioning that benefits conservation while increasing wildlife viewing opportunities. Carrion provisioning helped recover populations of endangered Indian vultures (*Gyps indicus*; Gilbert et al., 2007). Moreover, provisioning can benefit wildlife when specific feeding practices are followed, such as considering the nutritional

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TABLE 1 Key themes and important questions in animal behavior research that could improve our understanding of impacts of ecotourism on wildlife and improve management questions.

Theme	Research questions	Examples from the literature related to or applicable to ecotourism
Activity budgets and foraging	1. How does human presence alter behavioral repertoires?	Ardiantiono et al. (2018), Bessa et al. (2017), Harris and Haskell (2013), Knight (2009), McKinney (2014), and Pérez-Galicia et al. (2017)
	2. How do vigilance and foraging interact under ecotourism?	Field et al. (2024), Montero-Quintana et al. (2020), Nevin and Gilbert (2005), Symons et al. (2014), Worrell et al. (2017)
	3. How can we alter human behavior/visitation to not interfere with circadian rhythms of wildlife species?	Bessa et al. (2017) and Corcoran et al. (2013)
	4. What long term consequences result from food provisioning?	Brunnschweiler et al. (2014), Foroughirad and Mann (2013), French et al. (2022), Heim et al. (2021), Hodgson et al. (2004), and Orams (2002)
	5. How can food provisioning benefit individuals and populations, and not become ecological traps?	Ardiantiono et al. (2018), Fitzpatrick et al. (2011), Gilbert et al. (2007), and Shutt and Lees (2021)
Movement	1. Which ecotourism activities draw wildlife in or push them away?	Corcoran et al. (2013), Duchesne et al. (2000), Orams (2002), and Radkovic et al. (2019)
	2. How do animals alter their movement in response to ecotourist activities or infrastructure?	Burger and Gochfeld (2007), Doherty et al. (2021), Stankowich (2008), and Tucker et al. (2018)
	3. Are conservation areas successfully promoting natural long-distance movement (i.e., dispersal, migration)?	Lopez Gutierrez et al. (2020) and Okello (2009)
	4. How can field measures of movement (e.g., flight initiation distance) be most effectively used to identify and reduce stress from ecotourism?	Hines (2011), Slater et al. (2019), and Stankowich (2008)
Stress and habituation	1. How does stress (e.g., measured through hormones or physiological response) change in response to ecotourism activities?	Barbosa et al. (2013), French et al. (2017), Palacios et al. (2018), and Wilson et al. (2015)
	2. Which human activities cause chronic or acute stress in wildlife?	Shutt et al. (2014) and Thiel et al. (2008)
	3. Are there fitness consequences of stress from ecotourism activities?	Bateman and Fleming (2017) and Müllner et al. (2004)
	4. Can wildlife habituate to ecotourist activities?	Cruz-Díaz et al. (2024), Higham and Shelton (2011), Saltz et al. (2019), and Webb and Mccoy (2014)
	5. How can ecotourism operators manage human activities (e.g., group size, proximity, frequency of visits) to minimize stress for wildlife?	Johns (1996), Knight (2009), and Shutt et al. (2014)
Reproductive behavior	1. How and why does human presence disrupt courtship behaviors of both males and females?	Buckley et al. (2016), Butler and Maruska (2020), Carney and Sydeman (1999), and DiNuzzo et al. (2020)
	2. How does human presence during breeding affect reproductive receptivity, output and offspring fitness?	Giglio et al. (2022) and Müllner et al. (2004)
	3. How do anthropogenic cues from ecotourism (i.e., light and noise) disrupt the circannual patterns of reproduction and affiliated behaviors?	Butler and Maruska (2020), Cianchetti-Benedetti et al. (2018), Dominoni et al. (2020), Nedelec et al. (2017), and Rising et al. (2022)
	4. How can humans observe reproductive behaviors and/or parental care without causing stress and altered behavior?	Kämpfer and Fartmann (2022)

Note: These emerged from a multiphase research prioritization process (see Data S1).

value of supplemented foods and reducing aggregations at food sources by providing infrequent food at unpredictable sites (Murray et al., 2016). Similarly, regulating the timing of human visitation can also help keep behavioral repertoires intact (Wakefield & Attum, 2006). By adopting evidence-based food provisioning and human visitation practices, ecotourism operators can potentially help tourists experience wildlife with less disturbance of activity patterns and foraging.

1.2 | Movement

By changing wildlife movement patterns, distances or rates, ecotourism disturbance might have negative effects on the persistence of animal populations. Species community composition may change as species that make long-range movements are excluded from regions with a high human disturbance footprint (Tucker et al., 2018). As a result, protected parks may be less effective at protecting biodiversity if surrounding human activity limits movement and connectivity through wildlife corridors despite suitable habitat (Okello, 2009).

Human activities typically cause wildlife to increase their movement and distance from people (Doherty et al., 2021). Increases in movement can lead to higher energy expenditure and greater mortality risk. For example, high intensity lights used in nighttime shrimp-watching tours disrupt the mass land-migration of parading shrimp (*Macrobrachium dienbienphuense*), driving many shrimp back to the water to be washed away by the rapids (Hongjamrassilp & Blumstein, 2022). To distance themselves from summer hikers, woodland caribou move out of preferred alpine meadows and into coniferous forests, where calf predation by coyotes and black bears rises markedly (Duchesne et al., 2000; Dumont, 1993).

Not all species will increase their movement in response to humans. For example, boat and swim-with-the-dolphin tourism activities can cause bottlenose dolphins (*Tursiops aduncus*) to decrease traveling movement, leading to a shift in habitat use, and decreased nursing of calves (Stensland & Berggren, 2007). Within a species, individual variation can also influence how wild animals respond to human presence. A study of elk (*Cervus canadensis*) found differences in behavioral flexibility predicts which individuals are more likely to habituate to people and remain in human-disturbed areas, even ceasing migration (Found & St. Clair, 2017). Thus, although movement is a conspicuous behavior that can serve as an indicator for level of stress, and observing and quantifying changes in movement can provide important management strategies, caution in interpretation is necessary. A meta-analysis of ungulates, for example, found animals respond by fleeing faster when they perceive the approaching humans as more threatening (people with quicker, more direct approaches) (Stankowich, 2008). This study also found that animals flee more readily from open habitats compared to closed, wooded habitats. General management rules about movement changes in response to wildlife viewing opportunities for tourists can only come from comprehensive, analytical review (Buchholz & Hanlon, 2012).

1.3 | Stress and habituation

Generally, physiological stress is considered a natural and adaptive response to a challenging or threatening situation associated with a cue that acts as the stressor. Ecotourism may cause both acute and chronic physiological changes to an animal's stress response, which can lead to inappropriate behavioral responses in the short- and long-term (Ellenberg et al., 2007). Some species may be unable to adapt or habituate to stress associated with tourism (Burger, 1981; Müllner et al., 2004), and chronic stress responses to human activity can decrease disease resistance and fitness (Cohen et al., 2007). Thus, repeated or chronic stress caused by a stressor such as ecotourist visits to natural habitats are often inferred as the cause of maladaptive outcomes for wildlife. For example, Magellanic penguins (*Spheniscus magellanicus*) and Indian tigers (*Panthera tigris*) subjected to increased tourism exhibit lower reproductive fitness (Palacios et al., 2018; Tyagi et al., 2019). Are these necessarily due to physiological constraints due to stress?

Differentiating between chronic or acute stress can be difficult, and each type of stress can result in fundamentally different responses by wildlife and subsequent conservation approaches (Francis & Barber, 2013). Changing levels of stress hormones (i.e., corticosterone or cortisol) between time points, before and after tourist disturbance, or between populations, are often used as a proxy for quantifying stress. For example, tetra fish (*Odontostilbe pequira*) with chronic exposure to tourism experienced a population shift to individuals that produced more cortisol and showed increased behavioral signs of stress compared to non-exposed conspecifics (Geffroy et al., 2018). The long-term consequences for population viability are not clear cut in this case, but surely greater stress is an animal welfare issue of concern to ecotourists.

Habituation and habituation-like processes lead to decreased behavioral responses to a stimulus and may occur in individual animals (see Čapkun-Huot et al., 2024 for review). When stimuli are harmless, a lack of behavioral response is adaptive, so individuals do not exert unnecessary energy or mount a costly stress response. Magellanic penguins and marine iguanas (*Amblyrhynchus cristatus*) exposed to frequent tourism had reduced corticosterone levels (Romero & Wikelski, 2002; Walker et al., 2006). For tourism, great apes are systematically habituated until they no longer perceive humans as a threat. In this case, significant reduction in the acute stress response to humans through habituation can take up to 8 years (Shutt et al., 2014). However, habituation can have negative consequences by increasing vulnerability to human–wildlife pathogen transmission (Woodford et al., 2002) and to predators (Geffroy et al., 2015; Mccleery, 2009).

The strength and frequency of stimulus presentation are important mechanisms in mitigating stress and habituation processes, and they can be important tools for managing human behavior and activities to minimize impacts on wildlife. Chimpanzees (*Pan troglodytes*), for instance, show signs of habituation for groups of five tourists but increase vocalization rate in response to larger groups (Johns, 1996). Habituated western lowland gorillas (*Gorilla gorilla gorilla*) increase their physiological stress responses when tourists approached closer than the allowed 7 m distance (Shutt et al., 2014), and reduce behavioral alterations when humans remain more than 10 m away (Klailova et al., 2010). By understanding the positive and negative aspects of habituation (Ampumuza & Driessen, 2021) and dishabituation (Rodríguez-Prieto & Fernández-Juricic, 2005), the frequency of tours could be optimized for the benefit of both tourists and wildlife.

1.4 | Reproductive behavior

Animals can be most attractive to tourists at precisely the part of their life cycle when they are most vulnerable to the negative effects of tourism, that is, during reproduction. Reproductive behavior includes behaviors related to sexual selection and mating, birth or hatching, and parental care. Many animals breed more successfully away from human activities (Kämpfer & Fartmann, 2022; Steenhof et al., 2014). The number of courtship displays by male sand fiddler crabs (*Leptuca pugilator*) decreased by 0.5% with each additional car that passed (DiNuzzo et al., 2020). In the presence of noise, male shore crabs (*Carcinus maenas*) were less likely to respond to female mating pheromones (Rising et al., 2022), while female blue tits (*Cyanistes caeruleus*) became choosier about their mates (Reparaz et al., 2014). Lower sexual receptivity may be connected to the stress response often elicited by tourism, since cortisol inhibits reproductive hormones in many groups (Siegel, 1980). For breeders with resource-limited windows of receptivity, ill-timed tourist disturbance of mating opportunities can delay reproduction for an entire ovulatory cycle (Milich et al., 2014).

As with courtship and copulatory behaviors, specific components of ecotourism, such as noise, roads, or artificial light at night, can affect mating and parental care depending on individual variation, breeding experience and/or sex of the parent (Grunst et al., 2023; Ng et al., 2019). Bowers et al. (2019) found already stressed female house wrens (*Troglodytes aedon*) take longer to resume nestling care (feeding and brooding) after a camera is placed near the nest. Males of a reef-living fish (*Acanthochromis polyacanthus*) reduce offspring care in reaction to motorboat noise, resulting in failure of 36% of broods exposed to noise in one study (Nedelec et al., 2017). Anthropogenic cues can also interfere with natural stimuli used to inform reproductive decisions. Year-round food provisioning can extend the breeding season for some species (Lowry et al., 2013). Globally, nesting marine turtles are repelled by artificial light, resulting in lower nest density (Brei et al., 2016; Mazor et al., 2013). Additionally, individual variation within a species may influence susceptibility. Nest visits by humans results in no decrease in nesting success of bold Montagu's harrier (*Circus pygargus*), but shy parents flee their nest more readily in response to human activities, reducing their number of fledglings. Shy individuals disappeared from one population within 4–5 generations, resulting in a more behaviorally homogenous population (Arroyo et al., 2017). The long-term consequences of this reduction in behavioral variation on population viability remain to be determined.

Although negative impacts are more frequently documented, ecotourism can benefit wildlife by facilitating the protection of key breeding areas. A 30-year study of endangered Tibetan macaque (*Macaca thibetana*) in a nature reserve found increases in both the wild population and ecotourism over the study period (Li et al., 2022). The authors noted that revenue from tourists benefitted the local economy and increased suitable wildlife habitat, allowing populations to expand outside of concentrated ecotourists areas. Ecotourism can have minimal impacts on some breeding species, such as incubating brown noddies (*Anous stolidus*) nesting on oceanic islands that habituate quickly to brief, harmless human activity (Martin et al., 2020). Additionally, research into reducing anthropogenic sensory pollution has developed best practices for reducing behavioral impacts (Dominoni et al., 2020), which has broad applications to ecotourism practices. Erring on caution would advise stricter regulation of human activities at key periods of the reproductive cycle and limiting humans to a subset of a breeding area to preserve species for future generations of ecotourists.

2 | FUTURE DIRECTIONS AND DESIGNING SOLUTIONS

Shifts in wildlife behavior are one of the first and most visible indicators of negative effects of a changing environment or stressors (Dimitri & Longland, 2018; Northrup & Wittemyer, 2013). Tourism, like other nonlethal human activity, can elicit antipredator responses from wildlife. Fear-induced behavioral shifts can impose fitness costs on the species responding, or on other species in the community through behaviorally mediated trophic cascades (Smith et al., 2024). Although additional research on the demographic consequences of behavioral shifts is needed more broadly (Smith et al., 2024), intensive tourism has been related to declines in nesting and reproductive behavior (Bessa & Gonçalves-de-Freitas, 2014), decreasing natality; and to altered predator response (Geffroy et al., 2015) and greater pathogen transmission in human-habituated populations (Fagre et al., 2022), increasing mortality.

Animal behavior studies can provide important insight for managers and regulators to improve ecotourism sustainability. There are many opportunities for collaborations across ecotourism practitioners, regional and species experts, and behavioral ecologists to contribute to conservation. Multiple organizations help to train ecotourists as community scientists, which ideally provides tourists with the opportunity to both contribute to conservation research and have a fulfilling experience. While studies of fitness at a population or community scale may be more feasible for academic researchers and contribute to federal or range-wide conservation regulations, local studies of tourists' impact on animals can be critical for preserve managers or ecotourism operators. A challenge in designing research-based management solutions is that rules-of-thumb can be difficult to identify, and many results are dependent on the taxa, geography, or specific context. Both local studies and meta-analyses are needed to further our understanding of broad patterns, and greater equity of taxonomic representation of different animal taxa will be necessary in studies of ecotourism-mediated disturbance for best practices to be adopted (Buchholz & Hanlon, 2012).

Procedures already in the animal behavior toolbox could be adapted to fit the priorities, concerns, and research needs of ecotourism approaches. For example, behavioral indicators of tourist impact, such as flight initiation distance (FID), could inform managers on how stressed focal animals are, allowing for real-time alteration of human behavior. FID is considered an easy-to-use and reliable method of evaluating anthropogenic stressors (Tarlow & Blumstein, 2007). Technology may be another partner for conservation. Deploying hydrophones to perceive whales and dolphins from farther away and using camera traps or night-vision goggles to observe nocturnal animals without bright lights (Wolf & Croft, 2012) could reduce disturbance.

As we have highlighted above, research can identify tourism's impacts on wildlife behavior and help develop best practices to minimize the negative effects of ecotourism. However, adherence to best practices can be a challenge. On-site education about the species, the environment, and the appropriate tourist behavior to avoid affecting target species will not only better protect the animals but may also promote a better tourist experience as a part of conservation efforts (dos Santos & Bessa, 2019). Furthermore, best practices may need to be modified over time because of improved information from regular study.

3 | CONCLUSIONS

Wildlife tourism is likely to continue to grow; managing its negative impacts on the well-being and population viability of wildlife is key towards a sustainable future. The economic value of ecotourism can serve as an incentive to stop habitat destruction and prevent biodiversity loss, thereby protecting animals and their ecosystems (Stronza et al., 2019). Ecotourism's benefits can outweigh its impacts (Buckley et al., 2016). To realize these net benefits, ecotourism must alleviate negative behavioral impacts, particularly those we illustrated on activity budget and foraging, movement, stress and habituation, and reproduction. For that, we may apply on-site education, tourist-training initiatives, technology, and sustained behavioral monitoring through a conservation behavior approach. Behavioral research can offer tourism managers opportunities to improve sustainable and economically beneficial ecotourism while also prioritizing animal conservation.

AUTHOR CONTRIBUTIONS

Chock and Seymoure organized the workshop that resulted in this study and coordinated the manuscript. Arteaga-Torres, Baker, Buchholz, Clucas, Nuñez, Pinho, and Schulte co-led the workshop and manuscript drafting. Bessa, Blumstein, and Kitheka contributed to conceptual development of the manuscript. All authors helped develop and/or participated in the workshop and extensively contributed to the writing and revision of the manuscript.

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DATA AVAILABILITY STATEMENT

All data are available within the manuscript and table.

ETHICS STATEMENT

This perspective piece followed all ethical protocols and guidelines set forth by the Animal Behavior Society and no animals were directly involved in this work.

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