Title: Ecological impacts of human-induced animal behavior change

Running title: Ecological impacts of altered animal behavior

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Statement of authorship: MW developed initial framework and figures and wrote the first manuscript draft. All authors provided detailed feedback on framework structure and presentation format and contributed substantially to manuscript revisions.

Data accessibility statement: No data were used in the production of this manuscript.

Keywords: behavioral effects, behavioral ecology, animal behavior, human impacts, human-wildlife interactions, ecosystem management

Article type: Reviews and Syntheses

Word count: 199 (abstract) and 6928 (main text)

Number of references: 196

Number of tables and figures: 5 (2 tables, 3 figures), with 2 supplementary tables

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Ecological impacts of human-induced animal behavior change

ABSTRACT

A growing body of literature has documented myriad effects of human activities on animal behavior, yet the ultimate ecological consequences of these behavioral shifts remain largely uninvestigated. While it is understood that, in the absence of humans, variation in animal behavior can have cascading effects on species interactions, community structure, and ecosystem function, we know little about whether the type or magnitude of human-induced behavioral shifts translate into meaningful ecological change. Here we synthesize empirical literature and theory to create a novel framework for examining the range of behaviorally mediated pathways through which human activities may affect different ecosystem functions. We highlight the few empirical studies that show the potential realization of some of these pathways, but also identify numerous factors that can dampen or prevent ultimate ecosystem consequences. Without a deeper understanding of these pathways, we risk wasting valuable resources on mitigating behavioral effects with little ecological relevance, or conversely mismanaging situations in which behavioral effects do drive ecosystem change. The framework presented here can be used to anticipate the nature and likelihood of ecological outcomes and prioritize management among widespread human-induced behavioral shifts, while also suggesting key priorities for future research linking humans, animal behavior, and ecology.

Ecological impacts of human-induced animal behavior change

INTRODUCTION

As human activities continue to expand in magnitude, number, and extent (Venter *et al.* 2016; Watson *et al.* 2016; Halpern *et al.* 2019), a growing body of literature has documented widespread human impacts on animal behavior across aquatic and terrestrial ecosystems (Wong & Candolin 2015; Larson *et al.* 2016; Shannon *et al.* 2016; Gaynor *et al.* 2018; Tucker *et al.* 2018; Samia *et al.* 2019; Suraci *et al.* 2019). Animal behavior underlies many critical ecological functions, including nutrient cycling, primary productivity, pathogen transfer, and habitat provision (Gribben *et al.* 2009; Barber & Dingemanse 2010; Palkovacs & Dalton 2012). By affecting both interspecific and intraspecific interactions, behavioral trait variation can alter population and community dynamics (Bolnick *et al.* 2011) and wildlife conservation outcomes (Festa-Bianchet & Apollonio 2003; Blumstein & Fernández-Juricic 2010; Berger-tal & Saltz 2019), yet we know little about whether the type or magnitude of human-induced behavioral shifts translate into ecological change. While many behavioral effect studies allude to the implications of their findings for populations, communities, and ecosystems, limited empirical and theoretical investigation as well as a lack of synthesis across existing literature spheres preclude us from knowing where and to what degree these impacts occur, limiting our ability to guide and prioritize management efforts. Without an enhanced understanding of the ecological consequences of human induced behavioral effects, we risk both overlooking important drivers of ecological change that are not addressed through traditional management strategies, and misallocating management resources to mitigating behavioral impacts that ultimately have little ecological relevance.

While recent frameworks and case studies have linked numerical declines of animal populations to ecological consequences (Estes *et al.* 2011; Dirzo *et al.* 2014), we lack a similar understanding of the behaviorally mediated pathways through which humans impact ecosystems. Here, we present a novel framework outlining the pathways through which human activities may modify ecosystems via changes in animal behavior. We begin by categorizing the mechanisms through which human activities affect animal behavior, synthesizing a broad literature on human-induced behavior change that previous reviews have segregated by ecosystem [e.g., forests (Marzano & Dandy 2012)], behavior [e.g., flight (Stankowich 2008)], or human disturbance [e.g., noise (Williams *et al.* 2015; Shannon *et al.* 2016)]. We then present detailed pathways linking documented animal behavior changes to established or hypothesized ecosystem consequences. While our integrative framework illustrates the potential for human-impacted behaviors to affect population dynamics, community interactions, and ecosystem functions, we identify numerous factors likely to dampen these various pathways and discuss the relevance of these factors for anticipating and managing the ecological consequences of behavior change. While much remains to be learned about the drivers of animal behavior change, we highlight comparatively large knowledge gaps around the actualized ecological impacts of many human-impacted animal behaviors that prevent us from drawing management recommendations from many existing studies. As this body of literature continues to grow, we advocate for an increase in empirical and modelling studies that go beyond documenting behavioral impacts to examine the potential for realized ecological implications of human-induced animal behavior change.

MECHANISMS FOR HUMAN-INDUCED ANIMAL BEHAVIOR CHANGE

Human activities are increasingly impacting the aquatic and terrestrial environments in which wildlife persist. In addition to our growing population and rising urban and agricultural development, technological advances enable us to access and modify previously remote environments (Ramirez-Llodra *et al.* 2011; Pertierra *et al.* 2017), and increased participation in outdoor recreation expands our anthropogenic footprint in natural areas once thought of as protected and pristine (Gonson *et al.* 2016; Watson *et al.* 2016). Even when not directly present, human disturbance permeates ecosystems through chemical and sensory pollution (Longcore & Rich 2004; Williams *et al.* 2015), habitat modification (Torres *et al.* 2016), trash deposition (Newsome & van Eeden 2017), human-facilitated invasive species

(Murphy & Romanuk 2013), and anthropogenic climate change (Rosenzweig *et al.* 2008; Hoegh-Guldberg & Bruno 2010).

These diverse human impacts can induce changes in animal behavior by altering the conditions under which animals make behavioral decisions. Direct human presence and indirect impacts on an animal's surroundings can alter behavior via changes in population densities, top-down effects, bottom-up effects, and changes in the physical environment (Fig. 1). We introduce these four mechanisms here, integrating previously disparate literature to establish a foundation for assessing human-induced behavior change pathways more coherently. Selected examples for each empirically documented pathway are provided in Table S1 in Supporting Information.

Population density effects

By changing the density of a given population, humans can alter numerous behaviors that are sensitive to population size. For example, reducing local wildlife abundances through culling has been shown to alter territorial behaviors and increase mixing between social units in *Meles meles* (Eurasian badger) populations (Carter *et al.* 2007). Reduced male to female ratios due to selective hunting of male *Saiga tatarica* (Saiga antelope) led to disruptions of harem breeding dynamics in which older females aggressively prevented subdominant females from mating (Milner-Gulland *et al.* 2003). Other social behaviors such as group foraging (MacNulty *et al.* 2012; Gil & Hein 2017) and shared vigilance (Beauchamp *et al.* 2012; Gil *et al.* 2017) have been established as sensitive to group size and could inferably be impacted by human-induced changes in population density, though these potential links have not been documented empirically.

Top-down effects

Humans can have top-down impacts on animal behavior by directly or indirectly altering how and where animals perceive risk [i.e., risk assessment (Stankowich & Blumstein 2005) and "landscapes of fear"

(Laundre *et al.* 2010; Gaynor *et al.* 2019; Suraci *et al.* 2019)]. Animals adjust their behaviors when they perceive direct human presence as a threat, even in response to benign activities such as hiking or boating (Larson *et al.* 2016). Humans play the ecological role of 'super predators' in many systems and can shift the behavior of even the highest trophic level species (Darimont *et al.* 2015), triggering fear effects that can differ from and exceed those of natural predators (Proffitt *et al.* 2009; Ciuti *et al.* 2012; Clinchy *et al.* 2016). Humans can also indirectly affect a prey's perception of risk by modifying the populations of their natural predators, either increasing or decreasing risk of predation. For example, exploitation and habitat conversion have led to global predator losses (Estes *et al.* 2011), while predator restoration programs [e.g., *Canis lupus* (gray wolves) in Yellowstone (Ripple & Beschta 2004)] and human-facilitated invasive species [e.g., *Carcinus maenas* (green crabs; Bertness & Coverdale 2013)] have increased predator abundances in some systems. Risk assessments and associated behavioral responses can change dramatically as a result of these human-induced changes in predator densities (Ripple & Beschta 2003; Madin *et al.* 2010). Top-down effects may be particularly prevalent in aquatic systems, where fluid environments enhance the transmission of chemical cues among species (Preisser *et al.* 2005; Mitchell & Harborne 2020).

Bottom-up effects

Human activity can also have bottom-up impacts on animal behavior by changing the availability and distribution of prey or resources (Monk *et al.* 2018). Intentional and unintentional anthropogenic food subsidies (e.g., provisioning wildlife for tourism purposes, trash availability in residential or recreational areas) can increase resource availability and modify resource distributions (Ditchkoff *et al.* 2006; Burgin & Hardiman 2015; Soulsbury & White 2015). Alternatively, hunting, fishing, land use change, pollution, and climate change can alter resource availability and drive changes in consumer foraging behaviors (Estes *et al.* 1998; Gutierrez *et al.* 2008; Tinker *et al.* 2008). While altering resource availability can of course have numeric effects on consumer populations, it also impacts the conditions determining animal behavior, including risk-foraging trade-offs, movement patterns, and habitat selection.

Physical environment effects

Anthropogenic activities that modify habitat structure or generate chemical or sensory pollution can alter animal behavior by changing environmental conditions and habitat suitability, and by altering sensory cues that inform animal decision-making. Noise and light pollution, for example, influence patterns of animal movement (Tuxbury & Salmon 2005; Castellote *et al.* 2012; Davies *et al.* 2013), feeding (Bird *et al.* 2004; Pirotta *et al.* 2014), and communication (Parks *et al.* 2010; Vargas-Salinas *et al.* 2014). Structural habitat modifications such as those associated with land or coastal development can have large-scale impacts on animal movement and distribution patterns (Leblond *et al.* 2013; Skarin & Alam 2017; Wang *et al.* 2017). Many aquatic organisms are sensitive to anthropogenic changes in water clarity and chemical concentrations, which have been shown to interrupt communication, mating, and schooling behaviors (Seehausen *et al.* 1997; Ward *et al.* 2008; Brodin *et al.* 2013). Changing climate is also reshaping the physical environment in unprecedented ways, many of which are likely to alter animal behavior, as explored more explicitly in other reviews (Wuethrich 2000; Knowlton & Graham 2010; Harmon & Barton 2013; Beever *et al.* 2017).

LINKING HUMAN-INDUCED BEHAVIOR CHANGE TO ECOLOGICAL FUNCTIONS

Animal behavior underlies many critical ecosystem functions by shaping interactions with conspecifics, other species, and the abiotic environment (Sih *et al.* 2010; Start & Gilbert 2017). These functions include nutrient cycling, primary production and carbon sequestration, habitat provision and regulation, pollination and seed dispersal, disturbance regulation, and pathogen transfer (Table 1). Humans can alter these functions by changing animal behaviors that directly facilitate them (e.g., altering animal movement may affect seed dispersal). Humans may also indirectly impact these functions by inducing behavior changes that alter individual fitness, population dynamics, and/or interspecific interactions that cascade to affect ultimate functions (e.g., changes in breeding behaviors of a seed disperser may indirectly affect dispersal through changes in population abundances). While human-induced behavior change has the potential to disrupt ecosystem functions, it can also enable functions to persist through adaptations to human-impacted conditions. We outline both documented and hypothesized pathways (Fig. 1, Table S2) that illuminate the potential implications of human-induced animal behavior change, and illustrate a needed shift in research priorities to evaluate ecosystem consequences to address numerous links that have not yet been investigated in human-impacted systems. We discuss existing evidence for various pathways through a novel synthesis of existing literature, highlighting pathways with both stronger and weaker empirical and theoretical links to ultimate ecological impacts. We end by outlining open questions for future research.

Foraging

The best evidence for ecosystem consequences of human-induced animal behavior changes come from systems where humans have directly and indirectly altered animal foraging behaviors. By modifying risk environments, top-down human disturbances can initiate behaviorally mediated trophic cascades in which changes in predator or prey behavior cascade to affect downstream trophic interactions (Schmitz *et al.* 1997). For example, Hebblewhite and colleagues (2005) showed how changes in *C. lupus* distribution patterns to avoid human activity on hiking trails led to changes in *Cervus elaphus* (elk) grazing patterns and plant community composition, which altered habitat suitability for other species and resulted in changes in *Castor canadensis* (beaver) lodge density and riparian songbird diversity and abundance. Fishing-depleted piscivore populations have been shown to modify the foraging behaviors of herbivorous fish, contributing to seascape-level differences in algal distribution patterns (Madin *et al.* 2010, 2019; DiFiore *et al.* 2019). Direct human presence has also been linked to nutrient cycling in coral reef systems via models, where suppressed herbivore grazing observed in the presence of a spearfisher alters carbon and nitrogen flux in a corresponding simulation model (Gil & Hein 2017).

Beyond implications for habitat suitability and nutrient cycling, the potential ecological impacts of altered animal foraging behaviors are numerous and can be induced by a wide range of human impacts (Fig. 1).

Changes in the quantity, type, or location of resources consumed can alter seed dispersal (Beaune *et al.* 2013; Morán-López *et al.* 2020), while consumptive behaviors that alter plant or algal communities can drive changes in primary production and carbon storage (Silliman & Bertness 2002; Atwood *et al.* 2018), habitat suitability (Seabloom & Richards 2003; De Knegt *et al.* 2008) and disturbance regulation such as wildfire and flooding dynamics (Schmitz *et al.* 2008; Cherry *et al.* 2016). Changes in foraging behaviors that alter the type or quantity of resources consumed can also have impacts on body condition (Votier *et al.* 2010) that could potentially cascade up to population and ecosystem consequences, though evidence for these latter links is limited.

Movement

Another pathway through which humans can have ecologically-significant impacts on animal behavior is by altering movement (Spiegel *et al.* 2017). Top-down, bottom-up, and physical environment disturbances have driven widespread changes in animal movement patterns (Tucker *et al.* 2018), which have the potential to modify the transport of nutrients, pathogens, seeds, and pollen within and among ecosystems (Dougherty *et al.* 2018). Changes in *Bycanistes bucinator* (trumpeter hornbill) movement patterns due to habitat fragmentation have been linked to changes in seed dispersal ranges (Lenz *et al.* 2011), while changes in movement and aggregation patterns driven by anthropogenic food subsidies have been shown to increase disease transmission in both aquatic (Semeniuk & Rothley 2008; Burgin & Hardiman 2015) and terrestrial (Carter *et al.* 2007; Becker & Hall 2014; Forbes *et al.* 2015; Moyers *et al.* 2018) systems. Our framework points out the potential link between animal movement and nutrient dynamics, which has been well established in natural systems literature but not yet empirically linked to human impacts. For example, *C. lupus* movements while hunting can drive soil and foliar nutrient patterns by determining the distribution of *Alces alces* (moose) carcasses, leading to increased macronutrient content, microbial abundances, and leaf nitrogen that can persist for more than two years after a kill (Bump *et al.* 2009). Human disturbance can alter movement patterns of numerous predators that have been linked to nutrient transfer in separate natural systems studies, including *C. lupus* (Ashenafi *et al.* 2005; Hebblewhite *et al.* 2005), *Puma concolor* [pumas (Smith *et al.* 2016; Barry *et al.* 2019)], *Ursus spp.* [bears (Schindler *et al.* 2003; Nevin & Gilbert 2005; Zeller *et al.* 2019)], and *Carcharhinus spp.* [sharks (Brunnschweiler & Barnett 2013; Williams *et al.* 2018)], yet no studies have investigated the resulting links between human-induced changes in movement patterns and ecosystem nutrient dynamics.

Communication

By altering animal communication through top-down effects as well as impacts on the physical environment and population densities, humans have the potential to drive changes in population dynamics, interspecific interactions, and ultimate ecosystem functions. The transfer of information among individuals can play a critical role in determining mating success (Schmidt *et al.* 2015), foraging decisions (Gil & Hein 2017), competitive outcomes (Gil *et al.* 2019), and susceptibility to predation (Gil *et al.* 2017). Because animals often glean information from communication among heterospecifics (Magrath *et al.* 2015), impacts on communication can also alter information available to other species. While human impacts on animal communication have been documented for numerous species and systems, the ecosystem consequences of altered communication have been less investigated. Gil and Hein (2017) demonstrated the role of communication about fear and food in determining foraging behaviors of herbivorous fish, with modeled implications for algal consumption and nutrient flux. Altered environmental conditions can also negatively impact breeding via suppressed communication (Habib *et al.* 2007), while many other studies document the ability of individuals and species to adapt communication strategies to account for changing sensory environments (Parris & McCarthy 2013; Vargas-Salinas *et al.* 2014).

Timing and distribution of activities

Top-down, bottom-up, and physical environment effects of human activities may also alter ecosystem dynamics through shifts in the timing and distribution of animal activities, such as increasing nocturnality (Benítez-López 2018; Gaynor *et al.* 2018) and avoidance of or attraction to developed areas (Leblond *et* *al.* 2013; Soulsbury & White 2015). Because some species are more spatially or temporally displaced by or attracted to human activities than others (George & Crooks 2006; Erb *et al.* 2012; Ladle *et al.* 2018; Moll *et al.* 2018; Smith *et al.* 2018), human disturbance can impact community dynamics by altering co-occurence and interactions among species. Predators, for example, are often more displaced than prey species (Reed & Merenlender 2008; Muhly *et al.* 2011; Wang *et al.* 2017), and prey may actively seek human disturbance as a shield against natural predators (Berger 2007). Disproportionate predator and prey displacement can in some cases lead to changes in predator diets and subsequent trophic interactions (Smith *et al.* 2018). Spatial or temporal displacement may also alter competitive relationships by disproportionately displacing competitor species (Ladle *et al.* 2018; Moll *et al.* 2018) or by increasing niche overlap between species previously occupying separate niches (Smith *et al.* 2018). While changes in species co-occurrence could potentially impact various ecosystem functions, these ecological consequences have not been documented empirically beyond implications for individual species' survival (Vinne *et al.* 2019). Existing studies have largely measured shifts in activity levels but not in ecologically transferable behaviors (e.g., feeding), making it challenging to infer the ecological impacts of some of these spatial and temporal shifts (but see Smith *et al.* 2018).

Vigilance and flight

A large number of studies on human-induced behavior change have focused on human impacts on vigilance and flight behaviors (Stankowich 2008; Weston *et al.* 2012). Changes in flight or vigilance can impact individual fitness via changes in physiological stress (Arlettaz *et al.* 2007; Tarjuelo *et al.* 2015) and susceptibility to predation (Arroyo *et al.* 2017). Human-induced stress has in some cases been linked to lower reproductive output (Pauli & Buskirk 2007; French *et al.* 2011; Arroyo *et al.* 2017) and reduced offspring survival (Mann *et al.* 2000; Phillips & Alldredge 2000), while other studies have documented population stability in spite of increased flight and vigilance behaviors (Reimers *et al.* 2009). Even if the costs of these anti-predator behaviors do add up to influence individual fitness and drive changes in population growth rates (Gomes & Sarrazin 2016), links to broader ecological consequences beyond the affected species remain unstudied (Fig. 1). Changes in flight and vigilance may also indicate tradeoffs with other behaviors [e.g., foraging (Cooper (Jr.) *et al.* 2015; Tarjuelo *et al.* 2015)] that could potentially alter ecosystem function, but these tradeoffs should not be assumed and instead measured explicitly (see "Measuring ecological outcomes of human-induced animal behavior change" section).

Rest and hygiene

Human activities can also affect rest (Naylor *et al.* 2009; Barnett *et al.* 2016; Déaux *et al.* 2018) and hygienic behaviors (Titus *et al.* 2015; Nedelec *et al.* 2017) through top-down, bottom-up, and physical environment effects. Hygienic behaviors such as personal, conspecific, or heterospecific grooming or the cleaning of an animal's habitat have been shown to affect pathogen transmission in natural systems (Spivak & Reuter 2001; MacIntosh *et al.* 2012; Duboscq *et al.* 2016), though these links have not been established in human-impacted systems. Human impacts on rest have been linked to physiological changes (Barnett *et al.* 2016), but population and ecosystem consequences have not been investigated.

Breeding and parental care

Human impacts on breeding and parental care behaviors can also lead to changes in population dynamics with uninvestigated impacts on ecosystem functions. Through top-down effects, perceived risk from human nest visits increased incubation breaks and reduced the probability of nest survival in *Anser albifrons* [greater white-fronted geese (Meixell & Flint 2017)]. Through bottom-up effects, provisioning from *Tursiops truncatus* (bottlenose dolphin) tour boats reduced the amount of time that mothers spent with their calves, which was associated with lower calf survival rates (Mann *et al.* 2000; Foroughirad & Mann 2013). By changing the physical environment, noise from road traffic had negative impacts on *Parus major* (great tit) clutch size (Halfwerk *et al.* 2011). Changes in population densities can also alter breeding behaviors, such as the *S. tatarica* example in which smaller herd size and skewed sex ratios lead to increased aggression among females, thought to have contributed to observed declines in reproductive rates (Milner-Gulland *et al.* 2003). Despite widely documented impacts on breeding and parental care behaviors and implications for population dynamics, links to broader ecosystem functions have not been established.

FACTORS INFLUENCING EXPECTED PATHWAY OUTCOMES

As described above, human activities have the potential to alter numerous ecosystem functions through diverse behaviorally mediated pathways. However, not all human disturbances will translate into changes in animal behavior, let alone ecological consequences. Human disturbances can also induce behavior changes that serve to maintain ecosystem functions. As demonstrated in Fig. 1, investigation of these complete pathways is extremely limited, giving us little information on the prevalence or strength of these pathways and the conditions under which they are realized. Here we draw on synthesized literature and theory to highlight several factors likely to affect the strength of these pathways (Fig. 2, Table 2), which may contribute to the overall lack of evidence for many ultimate links to ecosystem functions. These factors of interest can also be used as management intervention points and focal areas for future research.

Behavioral responses to human disturbance

Spatial and temporal distribution of human disturbance

The degree to which human activities modify animal behaviors – and the likelihood that these behavioral shifts could go on to affect ecosystem functions - will depend in part on the spatial and temporal distribution of human disturbance. Infrequent or highly localized disturbances can at times have dramatic immediate effects on animal behavior, but may not be persistent enough to affect larger ecosystem processes if animals resume behaviors during undisturbed periods (see *'Magnitude and persistence of behavior change'* below).

Chronic and spatially pervasive human disturbances – such as those caused by changes in population densities, top-down or bottom-up effects of altered predator or resource abundances, or changes to the physical environment – may have more persistent and widespread impacts on animal behavior. Indeed, some of the best evidence we have for ecosystem consequences of human-induced animal behavior change comes from systems in which human activities have had chronic impacts via alterations of natural predator abundance that persist beyond direct human presence (Ripple & Beschta 2004; Madin *et al.* 2010). In cases where animals perceive human disturbances as negative (e.g., hunter or fisher presence, increase in predator abundance) or positive (e.g., provisioning from wildlife tourism, human trash), increased exposure may increase sensitization to disturbance cues (Blumstein 2016). Conversely, when a human disturbance is perceived as non-threatening, chronic or repeated disturbance can facilitate habituation and tolerance (Rees *et al.* 2005; Rodríguez-Prieto *et al.* 2010; Wheat & Wilmers 2016).

Many human activities are restricted to or peak in intensity at certain temporal cycles (e.g., diurnal human activity cycles, hunting or recreation seasons) or locations (e.g., roads, recreational trails), often allowing animals to shift activities into less disturbed times or places (Rode *et al.* 2006; Leblond *et al.* 2013; Bateman & Fleming 2017; Gaynor *et al.* 2018). These shifts can alter species co-occurrence, as discussed in the previous section, but can also enable other behavioral functions to persist alongside human disturbance (Sih et al. 2011). Some behaviors, however, may be more sensitive to spatial and temporal displacement (Wilmers *et al.* 2013). Because the condition of an animal likely varies in time and space, the timing and location of human disturbances may also have differing effects on behaviors that are state-dependent. For example, *Ursus americanus* (black bears) have been shown to forage most heavily on anthropogenic food sources during seasons when natural food production is low and individuals are presumably hungrier (Lewis *et al.* 2015). Disturbances at critical times or locations such as breeding events, along migration routes, or at key resource locations may have elevated population or ecosystem impacts relative to equal disturbance levels occurring at different locations or times of day or year. While many species conservation efforts already include restrictions on human activity at sensitive times or locations (e.g., breeding grounds), we recommend adapting this approach for ecosystem management based on ecologically critical behaviors likely to be sensitive to the timing or location of human disturbances.

Intensity of human disturbance

The intensity of human disturbance also likely plays a role in determining if and to what extent animals alter behavior (Leblond *et al.* 2013). However, these relationships can exhibit numerous nonlinear forms [Fig. 3 (Tablado & Jenni 2017; Gaynor *et al.* 2019)]. Behavioral alterations often come at a cost for animals (Frid & Dill 2002; Eldegard *et al.* 2012; Lamanna & Martin 2016), and may only occur if human disturbance reaches a certain threshold level (Bejder *et al.* 2006; Scillitani *et al.* 2010; Beyer *et al.* 2013; Tablado & Jenni 2017; Smith *et al.* 2019). For example, *Sus scrofa* (wild boars) maintained relatively constant social dynamics and movement patterns as hunter presence increased from low levels, but abandoned former territoriality and dramatically altered mobility across the landscape when hunter presence surpassed a certain threshold (Scillitani *et al.* 2010). Similarly, Smith and colleagues (Smith *et al.* 2019) identified a threshold in housing density that creates barriers for *P. concolor* movement. Threshold effects relative to human disturbance levels may also occur when animals learn positive associations with human activities, such as anthropogenic food subsidies. When the availability of food from humans reaches a certain level or consistency, animals may abandon prior foraging behaviors and adopt strategies centered around anthropogenic food sources (Yirga *et al.* 2012; Lewis *et al.* 2015). Conversely, habituation to human activities may dampen or decelerate impacts on animal behavior as human activities intensify when animals perceive these activities as neither threatening nor beneficial (Higham & Shelton 2011; Jiménez *et al.* 2011; Soldatini *et al.* 2015; Titus *et al.* 2015).

Interacting human disturbances

Given the vast global human footprint, animals are likely experiencing not one, but many forms of direct and indirect anthropogenic impacts that might have additive or interactive effects on animal behavior. For example, hunting pressure has been shown to exacerbate the behavioral impacts of road traffic on migrating elk (Paton *et al.* 2017). Environments where threatening and nonthreatening human activities mix - such as areas used by both hunters and hikers, spearfishers and recreational divers, etc. - may be of particular concern as they can prevent animals from accurately assessing risk and adjusting behavior appropriately (Coleman *et al.* 2008). In cases where animals do habituate to non-threatening human interactions, they may be more susceptible to hunters or poachers (Januchowski-Hartley *et al.* 2013; Geffroy *et al.* 2015). Direct human impacts on animal behavior are likely accompanied by additional indirect effects such as altered predator or resource abundances and changes in habitat suitability, though the behavioral and ecological implications of these overlapping disturbances remain uninvestigated.

Ecosystem consequences of animal behavior change

Ecological function of animal behavior

Regardless of the magnitude or persistence of animal behavior change, resulting ecological outcomes will ultimately depend on the ecological importance of a given behavior. While every species is inherently linked to ecosystem function, the behaviors of some - such as keystone species or ecosystem engineers - are far more critical than others for overall ecosystem function. For example, changes in beaver foraging behaviors could have disproportionately large consequences for ecosystem function by changing local water distributions, while changes in foraging behaviors of other rodent species may not trigger any detectable ecological changes. While human-induced behavior change often has a negative connotation, changes in some behaviors may actually be acting to preserve behaviors with direct ecosystem functions. For example, changes in the timing of activities to avoid human interactions may allow beavers to maintain foraging impacts despite human disturbances. Monitoring behaviors that are directly transferable to ecosystem function (e.g., foraging) as opposed to or in addition to those that could have indirect implications (e.g., flight behaviors, which may or may not impact foraging) will be more valuable in anticipating ecosystem impacts. Ecosystem managers can prioritize management efforts by identifying ecologically foundational or keystone behaviors in a given ecosystem context. The pathways illustrated in this framework can guide the mitigation of human disturbances likely to alter these critical behaviors as well as the monitoring of downstream ecological effects.

Population impacts of behavior change

As introduced above, behaviorally mediated changes in species abundances also have the potential to impact ecosystem function. While population impacts for any species will be important from a conservation perspective, those with unique ecological roles will be more relevant to ecosystem function than others. By altering the contexts in which animals make decisions, human impacts can uncouple formerly reliable environmental cues from actual outcomes. In these ecological traps, animals elect seemingly adaptive behaviors that actually prove to be maladaptive and can lead to population declines (Schlaepfer *et al.* 2002; Battin 2004). For example, while *Bison bison* (American bison) repeatedly choose to forage on agricultural lands due to bottom-up human impacts on resource distributions, they are subject to increased hunting in these habitats which has contributed to a nearly 50% population decline in less than a decade (Sigaud *et al.* 2017). Conversely, ecological traps can also arise when animals fail to change their behavior in human impacted scenarios. For example, antipredator responses such as grouping or schooling that are effective for natural predators may actually increase susceptibility to hunters or fishers (Proffitt *et al.* 2009; Hamilton *et al.* 2016).

Ecological traps can lead to demographic Allee effects, in which maladaptive behaviors are unconstrained or exasperated at low population densities and lead to further population declines (Kokko & Sutherland 2001). By depleting local species abundances, humans can also induce information-mediated Allee effects where insufficient communication at low densities impede critical processes such as breeding habitat selection (Schmidt *et al.* 2015) or foraging (Gil *et al.* 2017), potentially compounding population declines and increasing extinction risk for already threatened species (Gil *et al.* 2019). Conversely, the communication of social information can also rescue populations from spiraling demographic declines (Kokko & Sutherland 2001; Schmidt *et al.* 2015; Gil *et al.* 2019). While behaviorally-mediated Allee effects can have dramatic consequences for populations, ultimate cascading impacts on ecosystem functions will depend on the role of the species, as well as on current population size.

Magnitude and persistence of animal behavior change

Even when human activities alter animal behaviors, the magnitude or persistence of the resulting changes may not be substantial enough to affect ecosystem functions. Many human-impact studies focus on acute effects, or behavior changes that occur while humans or human disturbances are immediately present, but provide little clarity as to if and how immediate responses translate to more enduring behavioral shifts with consequences for physiology and fitness, and ecosystem function. For example, while coral reef cleaner shrimp *Ancyclomenes pedersoni* reduce cleaning interactions by over 50% in the presence of SCUBA divers, these behavioral shifts likely have little ecological impact if divers are present for only a small fraction of the day and shrimp resume cleaning behaviors during undisturbed periods or habituate to human presence over time (Titus *et al.* 2015). Despite numerous short-term studies documenting acute disruption of shark behavior when SCUBA divers are present (Quiros 2007; Smith *et al.* 2010; Cubero-Pardo *et al.* 2011), a long-term study found no persistent effects of SCUBA diving on sharks (Bradley *et al.* 2017), highlighting a potential disconnect in the implications of some acute and chronic effects studies. Many animals resume normal behaviors relatively quickly when human disturbance ceases or diminishes (Neumann *et al.* 2010; Higham & Shelton 2011; Titus *et al.* 2015), though lag effects in systems exposed to hunting or provisioning can sustain behavioral shifts for up to months or even years after hunting or provisioning stops (Kitchen *et al.* 2000; Pauli & Buskirk 2007; Smith *et al.* 2008; Foroughirad & Mann 2013; Januchowski-Hartley *et al.* 2013)**.** Some animals have been shown to compensate for behavioral shifts during low-disturbance periods, such as birds that reduce feeding during weekends when human activity is highest but compensate with increased foraging on subsequent mornings (Tarjuelo *et al.* 2015). Explicitly documenting animal behavior beyond just periods of acute or novel human disturbance is needed to determine ultimate implications for individuals, populations, and ecosystems.

One mechanism through which human impacts can induce persistent behavioral change is by selecting for certain behavioral traits that ultimately alter behavioral phenotypes within a given population. For example, a long-term study of *Circus pygargus* (Montagu's harrier) populations found increases in boldness towards humans and a gradual disappearance of shy individuals, with an observed negative relationship between human disturbance levels and nest success for shy parents but not bold ones (Arroyo *et al.* 2017). By selecting for certain behaviors that are adaptive in response to human disturbance, humans can drive broader shifts in behavior that may extend beyond just human-impacted scenarios. These behavioral syndromes, or groups of correlated behaviors, can be adaptive in some situations but maladaptive in others [e.g., boldness in response to human vs. natural predators (Geffroy *et al.* 2015)] and may affect intra- and interspecific interactions as well as ecosystem functions (Sih *et al.* 2004).

While increasing the magnitude of animal behavior change would arguably increase associated ecological impacts, these relationships are not necessarily linear and can take a variety of forms (Fig. 3). Many ecosystems exhibit tipping points or thresholds beyond which small increases in a disturbance lead to rapid shifts in ecological condition (Holling 1973; Scheffer & Carpenter 2003). In these systems, behavioral shifts – or population changes that alter the number of individuals performing an ecological function - would have to reach a certain threshold level before having any substantial impact on ecological function. For example, herbivory on coral reefs is thought to have nonlinear impacts on coral health and recruitment, driving a shift between coral- and algal-dominated states (Knowlton 1992; Karr *et al.* 2015). Changes in herbivore feeding behavior may therefore have little effect on coral reef ecosystems until grazing is driven below a certain threshold level at which algae is not sufficiently controlled (Karr *et al.* 2015). Potential threshold dynamics may mask the ecological relevance of some human-induced animal behavior changes and make them more challenging to detect at low disturbance levels.

SHIFTING OBJECTIVES FOR FUTURE RESEARCH

As the human footprint expands, human activity will likely have a growing impact on animal behavior, increasing the likelihood of cascading ecosystem consequences and the need to understand and anticipate them. However, our review of existing literature highlights significant knowledge gaps around the prevalence of these pathways and their underlying dynamics, which hinder our ability to prioritize management efforts among ever-increasing human-wildlife interactions and mitigate negative consequences of human activity on ecosystems where applicable. Here we discuss key objectives for future research, challenges faced, and approaches to address them.

Measuring ecological outcomes of human-induced animal behavior change

As shown in Figure 1, the central gap in our understanding of human-induced behavioral effect pathways is centered around the ecological outcomes of human-induced animal behavior changes. A key hurdle in linking altered behaviors to downstream ecological consequences is the implicit challenge in isolating the effects of behavior on complex, larger-scale ecological dynamics. Distinguishing behaviorally mediated effects from density-mediated effects can be especially tricky as they often occur in tandem (Bolker *et al.* 2003; Schmitz *et al.* 2004; Trussell *et al.* 2006). For example, changes in predator abundance, resource availability, and habitat quality will likely impact both the behavior and the overall abundance of a given species, while direct impacts on a species' abundance can have additional behavioral consequences, making it difficult to determine the relative ecological importance of these different mechanisms and to anticipate ecological outcomes. The behaviorally mediated nature of the iconicized Yellowstone wolf cascade has been challenged for this reason, with some researchers questioning the relative effects of changes in *C. elaphus* behavior as opposed to simply changes in *C. elaphus* density as a consequence of wolf reintroduction (Kauffman *et al.* 2010). Furthermore, ecological responses generally occur over much longer time scales than immediate behavioral responses to human activity. For example, Cherry and colleagues (Cherry *et al.* 2016) could readily measure the effects of *Canis latrans* (coyote) exclusion on deer grazing behaviors, but impacts on plant community dynamics were only apparent over the course of ten years. As our anthropogenic footprint expands, it also becomes harder to find adequate control sites that are not impacted by some sort of human activity, especially as humans become more drawn to 'wilderness' areas (Gonson *et al.* 2016).

Predicting ecological outcomes of human-induced animal behavior change

The challenges associated with measuring ecological outcomes empirically call for further incorporation of modelling approaches into behavioral effects literature. While the behavioral effect pathways linking human activities to ecosystem consequences may seem overwhelmingly complex, we provide a theory-supported framework for forecasting ecological outcomes that can be directly adapted into models (Fig. 1). Several studies have used models to infer the consequences of behavior change for populations (Christiansen & Lusseau 2015; Pauli *et al.* 2017; Gil *et al.* 2019; Smith *et al.* 2019) and, to a lesser extent, ecosystem functions (Becker & Hall 2014; Gil & Hein 2017). While models can help predict the ecological outcomes of human-induced behavior changes, they still require empirical data on how human activities affect behaviors with inferable ecological functions. This is a significant limitation in existing literature, which often measures human impacts on behaviors that are not easily translated into ecological outcomes. For example, a large number of human-induced behavioral effects studies have focused on measuring flight initiation distances (Stankowich 2008; McLeod *et al.* 2013), which are a useful indicator of risk assessment (Stankowich & Coss 2007) and tolerance to human disturbance (Blumstein 2016) but are less informative for models predicting ecosystem consequences. Even when a species plays an established ecological role, measurement of the wrong behavioral responses will limit our ability to estimate ecological implications. For example, herbivory can affect numerous ecological functions, including primary productivity and habitat provision, yet many studies measuring human impacts on herbivores have monitored flight or timing of activities instead of actual foraging behaviors (e.g., grazing amount, distribution, selectivity) that could inform models of downstream implications (see Gil & Hein 2017). A key step in progressing the behavioral effects field is to broaden the range of behaviors that are monitored and prioritize those hypothesized to be most relevant to ecosystem function. Particular opportunity exists around pathways linked to foraging and movement, which have myriad potential consequences including nutrient cycling, primary production, and habitat modification that have not been sufficiently investigated but have substantial support from natural systems theory. Future studies may consider specifically investigating the ecological consequences of human impacts on keystone species behaviors as these are more likely to result in detectable ecological change and could provide an upper bound in terms of anticipated outcomes of other behavioral effects pathways.

Another current limitation in existing literature is a lack of information on the persistence of human-induced behavioral effects. Many existing studies only measure acute behavioral shifts while human disturbances are present but do not investigate whether or not these behavioral impacts are sustained over time, limiting the utility of these data for models of ecosystem consequences. Additionally, some behavioral impact studies measure responses to novel anthropogenic stimuli, which risk overestimating behavioral impacts as they do not allow for animals to process and adapt to these disturbances as they would in situ (Peers *et al.* 2018). Increased studies monitoring behavioral responses over time would be extremely beneficial in inferring the actual ecosystem consequences of human-induced behavioral effects.

Differentiating impacts among human disturbance scenarios

As introduced above, nonlinearities between human activity levels, animal behavior change, and ecosystem processes can greatly impact the ultimate outcomes of behavioral effect pathways. In particular, initial studies have demonstrated both accelerating and dampening relationships between levels of human activity and resulting animal behavior change in different contexts. To better understand these relationships, more studies are needed that move beyond solely comparing behavioral responses in disturbed and undisturbed scenarios and instead quantify gradients of human activity levels against which behavioral responses are measured. More information is also needed on potential interactions between concurrent human activities in terms of impacts on animal behavior, specifically with regards to overlapping lethal and non-lethal human activities. Eliminating human disturbance in most ecosystems is unrealistic if not impossible, leaving managers with options to restrict certain types or levels of activities based on anticipated implications for animal behavior and ecosystem function. While our framework provides a foundation for connecting different human activity categories to behavioral effect pathways, effective management decisions will require an enhanced understanding of the effects of different activity levels, types, and combinations, which can also inform models predicting ecological outcomes of different human disturbance scenarios.

CONCLUDING REMARKS

As human and wildlife activities increasingly overlap in space and time, it is critical that we evaluate and quantify the potential for human-induced changes in animal behavior to impact ecosystem structure and function. While investigation of these behavioral effect pathways has been limited, some existing studies have demonstrated that human impacts on animal behavior can drive or contribute to substantial ecological consequences, making our ignorance of behavior change outcomes in other scenarios concerning. Other studies documenting human-induced animal behavior change allude to ecosystem implications despite contextual factors likely to dampen their ultimate ecological effects.

Our proposed framework provides a novel foundation for examining and anticipating the ecological impacts of human-induced behavioral effects and outlines priorities for future research. While it is valuable to document behavioral shifts in response to human activities, incorporating this information into ecosystem management requires an understanding of whether or not these shifts are likely to drive detrimental ecosystem change. Without untangling the ecological consequences of human-induced animal behavior change, we risk situations in which ecologically-important behavior changes go unrecognized and traditional management efforts are ineffective in controlling ecological outcomes. Conversely, we also risk wasting valuable management resources on mitigating behavior changes with little ecological relevance. While human impacts on animal behavior often have a negative connotation, behavioral shifts may in many cases be helping animals adapt to unavoidably human-dominated landscapes (Sih *et al.* 2011; Soldatini *et al.* 2015; Wheat & Wilmers 2016; Bateman & Fleming 2017; Vinne *et al.* 2019). In cases where behavioral changes are negatively impacting populations, communities, or ecosystems, we should strive to mitigate these impacts through effective management that addresses behavioral effects. In other cases, behavior change that allows an animal to persist in our increasingly human-impacted world may be something to allow for, if not encourage. As the human-induced behavior change literature continues to grow, our framework calls for an increase in studies that go beyond documenting human-induced animal behavior change to investigate ecological impacts and the factors that influence these ultimate outcomes.

ACKNOWLEDGEMENTS:

We thank Owen Liu, Dan Ovando, and Karly Miller for their feedback on the initial framework structure and early manuscript conceptualization, and we thank Mike Gil and two anonymous reviewers for their thoughtful comments. MWW was supported by a National Science Foundation (NSF) Graduate Research Fellowship Program (GRFP) award. KMG was supported by Schmidt Science Fellows in partnership with Rhodes Trust.

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TABLES:

Table 1 Ecosystem functions affected by animal behaviors, with select examples from natural systems. While these impacts are well established in natural systems, only links to habitat modification, pollination and seed dispersal, and pathogen transfer have been empirically documented in human-impacted systems.

Ecosystem function	**Example**	**Reference**
Primary production	Herbivore grazing alters plant communities, primary production, and carbon storage.	(Silliman & Bertness 2002; Schmitz *et al.* 2008)
Nutrient cycling	Predators distribute carcasses throughout a landscape, with consequences for soil nutrient composition.	(Palkovacs & Dalton 2012; Leroux & Schmitz 2015)
Habitat modification	Woodpecker foraging provides nest holes for other species.	(Cockle *et al.* 2011)
Pollination & seed dispersal	Animal movement affects seed dispersal ranges.	(Russo *et al.* 2006; Beaune *et al.* 2013)
Disturbance regulation	Herbivore foraging moderates wildfire potential by altering groundcover composition.	(Cherry *et al.* 2016)
Pathogen transfer	Animal movement and interactions facilitate disease transfer.	(Hawley *et al.* 2011)

Table 2 Factors hypothesized to influence the strength of pathways linking human impacts, animal behavior, and ecological implications. These hypotheses can be tested in future studies across systems with varying degrees of disturbance to better understand when human impacts are likely to impact animal behavior and/or ecosystems. Many relationships may also exhibit nonlinearities, which could be further illuminated through future studies.

Mediating factor	**Traits expected to strengthen pathway**	**Traits expected to weaken pathway**
Human disturbance → behavioral responses		
Temporal distribution of human disturbance	• Chronic • Unpredictable	• Infrequent • Predictable
Spatial distribution of human disturbance	• Widespread • Continuous • Unpredictable	• Localized • Noncontinuous • Predictable
Intensity of human disturbance	• High intensity	• Low intensity
Behavioral responses → Ecosystem consequences		
Ecological function of animal behavior	• Critical ecological function of impacted behavior (e.g., keystone species, ecosystem engineers)	• Functional redundancy of impacted behavior
Population impacts of behavior change	• Ecological traps and maladaptive behavior change • Behaviorally mediated Allee effects • Overlapping threatening and non-threatening human activities	• Adaptive behavior change • Habituation and tolerance
Magnitude of animal behavior change	• Large behavioral shifts	• Small behavioral shifts
Persistence of animal behavior change	• Lag effects • Behavioral adaptations	• Behavioral recovery • Compensatory behaviors

FIGURE LEGENDS:

Figure 1 Diverse pathways in which human impacts may affect ecosystem functions through animal behavior change. Solid arrows indicate links supported by one or more empirical studies explicitly linked to human impacts (see Table S2 for supporting examples). Dashed arrows indicate proposed links that have not been empirically documented in human impacted systems but are supported by models and/or by our understanding of the role of animal behavior in natural systems. While human impacts on animal behavior are relatively well documented, many prospective links between animal behavior change and ecosystem functions have not been investigated in human-impacted systems - likely in part due to the complexity of many of these pathways. Studies have documented the effects of human-induced animal behavior change on individuals, populations, and communities, though cascading effects on ecosystem functions remain relatively unexplored. Potential links from individual, population, and community dynamics to numerous ecosystem functions are consolidated into single arrows here for clarity. While nearly all of an individual animal's behaviors will be interrelated due to tradeoffs in time budgets, links among behaviors here represent behavior changes that directly induce changes in subsequent behaviors of the same individual, conspecifics, or heterospecifics.

Figure 2 Factors influencing links among human impacts, animal behavior, and ecological implications. Linking human activities to ecosystem impacts via changes in animal behavior. Human impacts on animal behavior will depend on the spatial and temporal distribution and the intensity of human activities. Depending on the ecological function of a given animal behavior, functional redundancy within a community, and the magnitude and persistence of behavior change, human-impacted animal behavior may ultimately drive changes in ecosystem functions.

Figure 3 Examples of potential nonlinear relationships between human activity levels and animal behavior change (I) and animal behavior change and ecological responses (II). In relationships between human activities and animal behavior (I), threshold effects can occur when behavior change is costly and may not be induced until human disturbance reaches a certain intensity, after which behavior shifts relatively dramatically. Threshold dynamics have also been documented in cases when animals perceive a human disturbance as beneficial but can only shift behavior once this disturbance is sufficiently consistent or substantial, such as the switching of animal foraging behavior in response to anthropogenic food subsidies. Dampening trends may be exhibited when a human disturbance is initially perceived as threatening or bothersome but is eventually habituated to. Deceleration of behavioral responses may occur when behavior change becomes increasingly costly relative to actual disturbance from human activities, but some level of altered behavior is still perceived as beneficial. Threshold dynamics are relatively common in ecosystem responses to disturbance, suggesting that many relationships between animal behavior change and ecosystem change (II) may exhibit similar patterns.