REVIEWS AND SYNTHESES

Ecological impacts of human-induced animal behaviour change

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Abstract

A growing body of literature has documented myriad effects of human activities on animal behaviour, yet the ultimate ecological consequences of these behavioural shifts remain largely uninvestigated. While it is understood that, in the absence of humans, variation in animal behaviour can have cascading effects on species interactions, community structure and ecosystem function, we know little about whether the type or magnitude of human-induced behavioural shifts translate into detectable ecological change. Here we synthesise empirical literature and theory to create a novel framework for examining the range of behaviourally mediated pathways through which human activities may affect different ecosystem functions. We highlight the few empirical studies that show the potential realisation 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 behavioural effects with little ecological relevance, or conversely mismanaging situations in which behavioural effects do drive ecosystem change. The framework presented here can be used to anticipate the nature and likelihood of ecological outcomes and prioritise management among widespread human-induced behavioural shifts, while also suggesting key priorities for future research linking humans, animal behaviour and ecology.

Keywords

Animal behaviour, behavioural ecology, behavioural effects, ecosystem management, human impacts, human–wildlife interactions.

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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 behaviour 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 behaviour 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, behavioural 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 2016), yet we know little about whether the type or magnitude of human-induced behavioural shifts translate into ecological change. While many behavioural 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 prioritise management efforts. Without an enhanced understanding of the ecological consequences of human-induced behavioural effects, we risk both overlooking important drivers of ecological change that are not addressed through traditional management strategies, and misallocating management resources to mitigating behavioural 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 behaviourally 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 behaviour. We begin by categorising the mechanisms through which human activities affect animal behaviour, synthesising a broad literature on human-induced behaviour change that previous reviews have segregated by ecosystem [e.g. forests (Marzano & Dandy 2012)], behaviour [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 behaviour changes to established or hypothesised ecosystem consequences. While our integrative framework illustrates the potential for human-impacted behaviours 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 behaviour change. While much remains to be learned about the drivers of animal behaviour change, we highlight

comparatively large knowledge gaps around the actualised ecological impacts of many human-impacted animal behaviours 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 behavioural impacts to examine the potential for realised ecological implications of human-induced animal behaviour change.

MECHANISMS FOR HUMAN-INDUCED ANIMAL BEHAVIOUR 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 behaviour by altering the conditions under which animals make behavioural decisions. Direct human presence and indirect impacts on an animal's surroundings can alter behaviour 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 behaviour change pathways more coherently. Selected examples for each empirically documented pathway are provided in Table S1.

Population density effects

By changing the density of a given population, humans can alter numerous behaviours that are sensitive to population size. For example reducing local wildlife abundances through culling has been shown to alter territorial behaviours 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 behaviours 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 behaviour by directly or indirectly altering how and where animals perceive risk [i.e. 'landscapes of fear' (Laundre *et al.* 2010; Gaynor *et al.* 2019; Suraci *et al.* 2019)]. Animals adjust their behaviours 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 behaviour 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), whereas predator restoration programmes [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 behavioural 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 behaviour 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 behaviours (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 behaviour, 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 behaviour 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.* 2011; Vargas-Salinas *et al.* 2014). Structural habitat
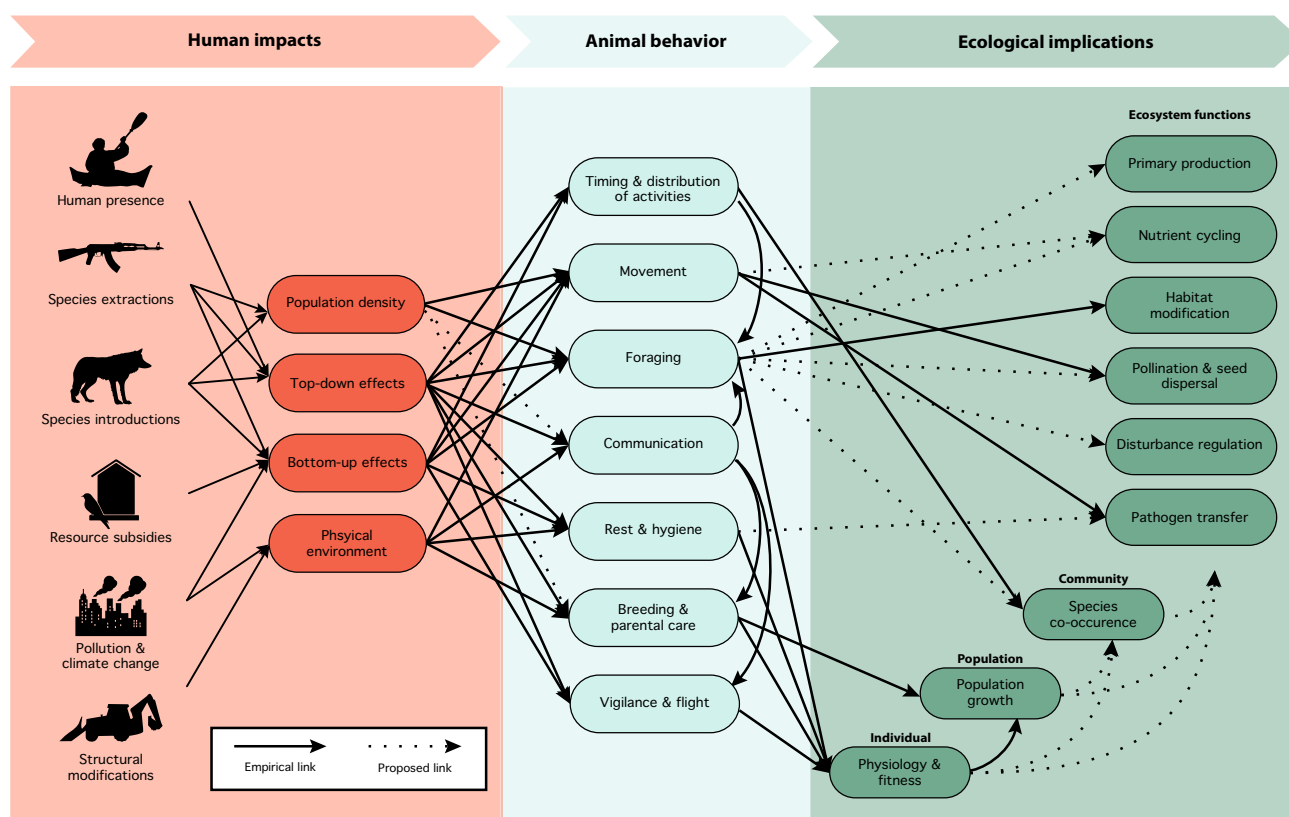
Figure 1 Diverse pathways in which human impacts may affect ecosystem functions through animal behaviour change. Solid arrows indicate links supported by one or more empirical studies explicitly linked to human impacts (see Table S2 for supporting examples). Dashed arrows indicate proposed links that have not been empirically documented in human impacted systems, but are supported by models and/or by our understanding of the role of animal behaviour in natural systems. While human impacts on animal behaviour are relatively well documented, many prospective links between animal behaviour 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 behaviour 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 behaviours will be interrelated due to trade-offs in time budgets, links among behaviours here represent behaviour changes that directly induce changes in subsequent behaviours of the same individual, conspecifics or heterospecifics.

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 behaviours (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 behaviour, as explored more explicitly in other reviews (Wuethrich 2000; Knowlton & Graham 2010; Harmon & Barton 2013; Beever *et al.* 2017).

LINKING HUMAN-INDUCED BEHAVIOUR CHANGE TO ECOLOGICAL FUNCTIONS

Animal behaviour 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 behaviours that directly facilitate them (e.g. altering animal movement may affect seed dispersal). Humans may also indirectly impact these functions by inducing behaviour changes that alter individual fitness, population dynamics, and/or interspecific interactions that cascade to affect ultimate functions (e.g. changes in breeding behaviours of a seed disperser may indirectly affect dispersal through changes in population abundances). While human-induced behaviour 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 hypothesised pathways (Fig. 1, Table S2) that illuminate the potential implications of human-induced animal behaviour change, and illustrate a needed shift in research priorities to evaluate ecosystem consequences and 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 behaviour changes come from systems where humans have directly and indirectly altered animal foraging behaviours. By modifying risk environments, top-down human disturbances can initiate behaviourally mediated trophic cascades in which changes in predator or prey behaviour 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, altering habitat suitability for other species and resulting 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 behaviours 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 behaviours 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), whereas consumptive behaviours 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 behaviours 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 behaviour 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), whereas 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 2 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.

Table 1 Ecosystem functions affected by animal behaviours, 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	References
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)

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 & Hein (2017) demonstrated the role of communication about fear and food in determining foraging behaviours of herbivorous fish, with modelled implications for algal consumption and nutrient flux. Altered environmental conditions can also negatively impact breeding via suppressed communication (Habib *et al*. 2007), whereas 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 drawn 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 behaviours (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 behaviour change have focused on human impacts on vigilance and flight behaviours (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), whereas other studies have documented population stability in spite of increased flight and vigilance behaviours (Reimers *et al*. 2009). Even if the costs of these anti-predator behaviours 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 trade-offs with other behaviours [e.g. foraging (Cooper (Jr.) et al. 2015; Tarjuelo *et al*. 2015)] that could potentially alter ecosystem function, but these trade-offs should not be assumed and instead measured explicitly (see 'Measuring ecological outcomes of human-induced animal behaviour change').

Rest and hygiene

Human activities can also affect rest (Naylor *et al*. 2009; Barnett *et al*. 2016; Déaux *et al*. 2018) and hygienic behaviours (Titus *et al*. 2015; Nedelec *et al*. 2017) through top-down, bottom-up and physical environment effects. Hygienic behaviours 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 behaviours can 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 behaviours, 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 behaviours and implications for population dynamics and single-species conservation goals, 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 behaviourally mediated pathways. However, not all human disturbances will translate into changes in animal behaviour, let alone ecological consequences. Human disturbances can also induce behaviour 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 realised. Here we draw on synthesised 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.

Behavioural responses to human disturbance

Spatial and temporal distribution of human disturbance
The degree to which human activities modify animal behaviours – and the likelihood that these behavioural shifts could go on to affect ecosystem functions – will depend in part on the spatial and temporal distribution of human disturbance. Infrequent or highly localised disturbances can at times have dramatic immediate effects on animal behaviour, but may not be persistent enough to affect larger ecosystem processes if animals resume behaviours during undisturbed periods (see *'Magnitude and persistence of behaviour 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 behaviour. Indeed, some of the best evidence we have for ecosystem consequences of human-induced animal behaviour 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 sensitisation 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).
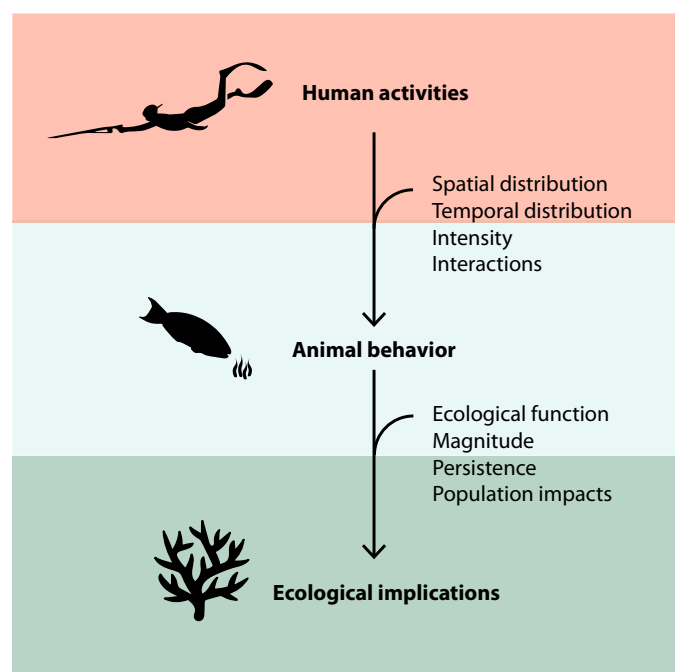
Figure 2 Factors influencing links among human impacts, animal behaviour and ecological implications. Linking human activities to ecosystem impacts via changes in animal behaviour. Human impacts on animal behaviour will depend on the spatial and temporal distribution and the intensity of human activities. Depending on the ecological function of a given animal behaviour, functional redundancy within a community and the magnitude and persistence of behaviour change, human-impacted animal behaviour may ultimately drive changes in ecosystem functions.

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 behavioural functions to persist alongside human disturbance (Sih *et al.* 2011). Some behaviours, 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 behaviours 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 behaviours likely to be sensitive to the timing or location of human disturbances.

Table 2 Factors hypothesised to influence the strength of pathways linking human impacts, animal behaviour 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 behaviour 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 → behavioural responses		
Temporal distribution of human disturbance	• Chronic • Unpredictable	• Infrequent • Predictable
Spatial distribution of human disturbance	• Widespread • Continuous • Unpredictable	• Localised • Non-continuous • Predictable
Intensity of human disturbance	• High intensity	• Low intensity
Behavioural responses → Ecosystem consequences		
Ecological function of animal behaviour	• Critical ecological function of impacted behaviour (e.g. keystone species, ecosystem engineers)	• Functional redundancy of impacted behaviour
Population impacts of behaviour change	• Ecological traps and maladaptive behaviour change • Behaviourally mediated Allee effects • Overlapping threatening and non-threatening human activities	• Adaptive behaviour change • Habituation and tolerance
Magnitude of animal behaviour change	• Large behavioural shifts	• Small behavioural shifts
Persistence of animal behaviour change	• Lag effects • Behavioural adaptations	• Behavioural recovery • Compensatory behaviours

Intensity of human disturbance

The intensity of human disturbance also likely plays a role in determining if and to what extent animals alter behaviour (Leblond *et al.* 2013). However, these relationships can exhibit numerous nonlinear forms [Fig. 3 (Tab lado & Jenni 2017; Gaynor *et al.* 2019)]. Behavioural 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; Tab lado & 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 behaviours and adopt strategies centred around anthropogenic food sources (Yirga *et al.* 2012; Lewis *et al.* 2015). Conversely, habituation to human activities may dampen or decelerate impacts on animal behaviour as human activities intensify when animals perceive these activities as neither threatening
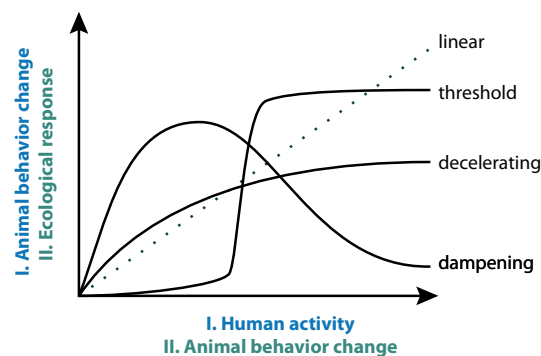

Figure 3 Examples of potential nonlinear relationships between human activity levels and animal behaviour change (I) and animal behaviour change and ecological responses (II). In relationships between human activities and animal behaviour (I), threshold effects can occur when behaviour change is costly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

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 behaviour. For example hunting pressure has been shown to exacerbate the behavioural impacts of road traffic on migrating elk (Paton *et al.* 2017). Environments where threatening and non-threatening 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 behaviour 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 behaviour are likely accompanied by additional indirect effects such as altered predator or resource abundances and changes in habitat suitability, though the behavioural and ecological implications of these overlapping disturbances remain uninvestigated.

Ecosystem consequences of animal behaviour change

Ecological function of animal behaviour

Regardless of the magnitude or persistence of animal behaviour change, resulting ecological outcomes will ultimately depend on the ecological importance of a given behaviour. While every species is inherently linked to ecosystem function, the behaviours 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 behaviours could have disproportionately large consequences for ecosystem function by changing local water distributions, while changes in foraging behaviours of other rodent species may not trigger any detectable ecological changes. While human-induced behaviour change often has a negative connotation, changes in some behaviours may actually be acting to preserve behaviours 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 behaviours 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 behaviours, which may or may not impact foraging) will be more valuable in anticipating ecosystem impacts. Ecosystem managers can prioritise management efforts by identifying ecologically foundational or keystone behaviours in a given ecosystem context. The pathways illustrated in this framework can guide the mitigation of human disturbances likely to alter these critical behaviours as well as the monitoring of downstream ecological effects.

Population impacts of behaviour change

As introduced earlier, behaviourally 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 behaviours 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 behaviour 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 behaviours 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 spiralling demographic declines (Kokko & Sutherland 2001; Schmidt *et al.* 2015; Gil *et al.* 2019). While behaviourally 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 behaviour change

Even when human activities alter animal behaviours, 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 behaviour 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 behavioural shifts with consequences for ecosystem function. For example while coral reef cleaner shrimp *Ancyclomenes pedersoni* reduce cleaning interactions by over 50% in the presence of SCUBA divers, these behavioural shifts likely have little ecological impact if divers are present for only a small fraction of the day and shrimp resume cleaning behaviours during undisturbed periods or habituate to human presence over time (Titus *et al.* 2015). Despite numerous short-term studies documenting acute disruption of shark behaviour 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 behaviours 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 behavioural 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 behavioural 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 behaviour 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 behavioural change is by selecting for certain behavioural traits that ultimately alter behavioural 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 behaviours that are adaptive in response to human disturbance, humans can drive broader shifts in behaviour that may extend beyond just human-impacted scenarios. These behavioural syndromes, or groups of correlated behaviours, 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 behaviour 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, behavioural 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 behaviour 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 behaviour 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 behaviour, 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 prioritise 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 these challenges.

Measuring ecological outcomes of human-induced animal behaviour change

As shown in Figure 1, the central gap in our understanding of human-induced behavioural effect pathways is centred around the ecological outcomes of human-induced animal behaviour changes. A key hurdle in linking altered behaviours to downstream ecological consequences is the implicit challenge in isolating the effects of behaviour on complex, larger scale ecological dynamics. Distinguishing behaviourally 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 behaviour and the overall abundance of a given species, while direct impacts on a species' abundance can have additional behavioural consequences, making it difficult to determine the relative ecological importance of these different mechanisms and to anticipate ecological outcomes. The behaviourally mediated nature of the iconicised Yellowstone wolf cascade has been challenged for this reason, with some researchers questioning the relative effects of changes in *C. elaphus* behaviour 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 behavioural 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 behaviours, but impacts on plant community dynamics were only apparent over the course of 10 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 behaviour change

The challenges associated with measuring ecological outcomes empirically call for further incorporation of modelling approaches into behavioural effects literature. While the behavioural 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 behaviour 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 behaviour changes, they still require empirical data on how human activities affect behaviours with inferable ecological functions. This is a significant limitation in existing literature, which often measures human impacts on behaviours that are not easily translated into ecological outcomes. For example a large number of human-induced behavioural 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 behavioural 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 behaviours (e.g. grazing amount, distribution, selectivity) that could inform models of downstream implications (see Gil & Hein 2017). A key step in progressing the behavioural effects field is to broaden the range of behaviours that are monitored and prioritise those hypothesised 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 behaviours as these are more likely to result in detectable ecological change and could provide an upper bound in terms of anticipated outcomes of other behavioural effects pathways.

Another current limitation in existing literature is a lack of information on the persistence of human-induced behavioural effects. Many existing studies only measure acute behavioural shifts while human disturbances are present, but do not investigate whether or not these behavioural impacts are sustained over time, limiting the utility of these data for models of ecosystem consequences. Additionally, some behavioural impact studies measure responses to novel anthropogenic stimuli, which risk overestimating behavioural 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 behavioural responses over time would be extremely beneficial in inferring the actual ecosystem consequences of human-induced behavioural effects.

Differentiating impacts among human disturbance scenarios

As introduced earlier, nonlinearities between human activity levels, animal behaviour change and ecosystem processes can greatly impact the ultimate outcomes of behavioural effect pathways. In particular, initial studies have demonstrated

both accelerating and dampening relationships between levels of human activity and resulting animal behaviour change in different contexts. To better understand these relationships, more studies are needed that move beyond solely comparing behavioural responses in disturbed and undisturbed scenarios and instead quantify gradients of human activity levels against which behavioural responses are measured. More information is also needed on potential interactions between concurrent human activities in terms of impacts on animal behaviour, 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 behaviour and ecosystem function. While our framework provides a foundation for connecting different human activity categories to behavioural 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 behaviour to impact ecosystem structure and function. While investigation of these behavioural effect pathways has been limited, some existing studies have demonstrated that human impacts on animal behaviour can drive or contribute to substantial ecological changes, making our ignorance of behaviour change outcomes in other scenarios concerning. Other studies documenting human-induced animal behaviour 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 behavioural effects and outlines priorities for future research. While it is valuable to document behavioural 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 behaviour change, we risk situations in which ecologically important behaviour changes go unrecognised and traditional management efforts are ineffective in controlling ecological outcomes. Conversely, we also risk wasting valuable management resources on mitigating behaviour changes with little ecological relevance. While human impacts on animal behaviour often have a negative connotation, behavioural 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 behavioural changes are negatively impacting populations, communities or ecosystems, we should strive to mitigate these impacts through effective management that addresses behavioural effects. In other cases, behaviour 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 behaviour change literature continues to grow, our framework calls for an increase in studies that go beyond documenting human-induced animal behaviour change to investigate ecological impacts and the factors that influence these ultimate outcomes.

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.

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