



Tourism and wildlife habituation: Reduced population fitness or cessation of impact?

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ABSTRACT

Habituation typically is viewed as a negative consequence of human interactions with wildlife (Higginbottom, 2004; Newsome, Dowling, & Moore, 2005; Shackley, 1996). While animal habituation commonly is used in the laboratory and field-based zoology studies, attempts to consider deliberate habituation specifically in a tourism management context (Shelton, Higham, & Seddon, 2004) has been received unsympathetically by biological scientists and wildlife managers on the grounds that habituation, by definition, is undesirable. This paper puts forward the case that the global and stable behavioural descriptor, *habituation*, is not the most useful way to formulate most observed lack-of-wildlife-response to visitor approach and observation. It presents an applied behaviour analysis of wildlife habituation that is situated within learning theory. This analysis differentiates between avoidance/approach behaviours, tolerance, habituation and sensitisation. This provides a formulative framework for human–wildlife interactions, that is then considered specifically in terms of tourism businesses seeking to provide sustainable visitor interactions with wild animals. A tourism management model derived from this critique of habituation is presented and discussed.

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1. Introduction

The concept of wildlife habituation traditionally has been treated uncritically within the field of nature-based tourism (Edington & Edington, 1986; Shelton & Higham, 2007). Typically the concept of habituation is accepted as a unitary phenomenon that is a negative possible consequence of tourist interactions with animals in the wild (Higginbottom, 2004; Newsome et al., 2005; Shackley, 1996). This global and stable behavioural descriptor, *habituation*, is an unhelpful way to formulate most observed lack-of-wildlife-response to human interactions. A more fine-grained behavioural and temporal approach to understanding wildlife habituation may be of considerable relevance to the optimal management of tourist interactions with wild animals.

This paper attempts two points of departure from established discourses on wildlife habituation. The first challenges the contrast between the use of habituation in zoological studies (e.g. to mitigate researcher impacts), and the treatment of habituation in tourism management as entirely undesirable (Seddon, Ellenberg, & van Heezik, in press). Second, it asks if in some instances habituation

may be deployed as a deliberate tourism management strategy in pursuit of cessation of visitor impacts upon focal animals (Nisbet, 2000). These discussions draw upon three sources; thousands of unstructured personal observations on the part of the authors derived from employment as wildlife tour guides in New Zealand; extensive *in situ* personal observations of human–wildlife encounters in New Zealand including New Zealand's sub-Antarctic Islands, and Ross Sea Dependency (Antarctica); and key empirical literature (e.g. Bejder, Samuels, Whitehead, Finn, & Allen, 2009; Ellenberg, Mattern, Seddon, & Jorquera, 2006; Johns, 1996; Knight, 2009; Romero & Wikelsi, 2002). The discussions that follow draw upon person observations unless indicated otherwise through reference citation.

2. Ecotourism and wildlife encounters

Wildlife viewing, once the domain of dedicated enthusiasts, or 'specialists' (Duffus & Dearden, 1990), has moved into the mainstream of commercial tourism (Knight, 2009). With this has come a proliferation and diversification of opportunities to encounter wildlife (Higham, Lusseau, & Hendry, 2008). This course of development has occurred despite an inescapable tension. Knight (2009: p. 167) identifies a fundamental contradiction in wildlife viewing in that "wild animals are generally human-averse; they avoid humans

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and respond to human encounters by fleeing and retreating to cover". A gradual reduction of such avoidance commonly is labelled *habituation*. However human–wildlife encounters represent a complexity of interaction stimuli that render the unitary term *habituation* problematic (Bejder et al., 2009). With this point in mind, it is surprising that wildlife *habituation* continues to be treated uncritically within the context of nature-based tourism and sustainable tourism management.

Successful commercial wildlife viewing requires that visitors are concentrated in well-defined locations where interactions with wild animals are predictable and constant (Whittaker, 1997). Usually, viewing wildlife takes place where sightings are most consistent, focal animals can be viewed in abundance or, where spectacular behaviours may be predictably observed and experienced (e.g. courtship and socialising behaviours). The critical nature of these sites, in terms of site ecology and wildlife behaviours, raises two important points; (1) That the behavioural state of wild animals varies significantly over time (e.g. across times of day, through different stages of the breeding cycle and across life course) and (2) that animal responses to external stimuli (e.g. the presence of tourists) is likely to vary over time, as influenced by these temporal determinants.

These points raise the challenge of understanding and responding to the potential adverse impacts of human–wildlife interactions, not only for the sake of the focal animals, but also from an experiential standpoint with the aim of (1) reducing avoidance, flight or retreat responses and (2) mitigating adverse impacts on animals that may otherwise discontinue critical, site-specific behaviours e.g. by instigating site abandonment. Furthermore, increasingly tourists seek to be assured that their mere presence at wildlife viewing sites (and their associated behaviours) are not to the detriment of the animals that they seek to experience first hand, either in terms of the welfare of individual animals or wider population fitness (Higham & Lusseau, 2004; Muloin, 1998).

Such concerns on the part of tourists (and site managers) are well founded. Knight (2009) critiques the dichotomy between wildlife viewing and wildlife hunting as non-consumptive and consumptive respectively, highlighting that viewing and hunting wildlife have some fundamental similarities. First, both engage in locating and identifying target wild animals, which are generally "wary of human presence and reluctant to expose themselves to human eyes" (Knight, 2009: p. 169). Such wariness may be expressed through anti-predatory adaptations, both physical (e.g. camouflage colouration) and behavioural (e.g. concealment) to avoid detection. The directed, intensive and sustained tourist gaze offers a second parallel with hunting (and predation more generally), which also is likely to trigger alarm and anti-predatory responses in individual animals or groups of animals.

Tourist satisfaction is commonly associated with close-up, unconstrained and prolonged interactions with wild animals, the experience of critical behaviours (e.g. hunting, feeding, socialising and courtship) and, in some cases, immediate proximity extending to touch (e.g. Muloin, 1998). Although there are some exceptions to this rule (Orams, 2000), the importance of managing 'human–wildlife viewing interactions' (as opposed to 'non-consumptive viewing' – given the consumptive nature of pursuit, intensive gaze and proximal interaction) is evident. Knight (2009: p. 173) proposes that "there appear to be three main ways in which wild animals can be made available for human viewing: capture and confinement; habituation and attraction."

The first, *capture and confinement*, brings with it behavioural diminution associated with wild animals being physically removed from their natural ecosystem. Also, in many cases, the capture and confinement of 'charismatic' wild animals is illegal. The last, *attraction*, through interventions such as provisioning (i.e. feeding) is

equally unpalatable due to its association with manipulated wildlife distributions, compromised feeding (e.g. predator–prey) relationships, increased probability of aggressive behaviour (both towards animals and people) and consequential diminished behaviours (Orams, 1995). Attraction of animals through supplemental feeding, while affording close and enduring viewing opportunities, also compromises the notion of *wild*, creating indistinct dividing lines between animals that are wild and those that are confined, tamed or domesticated (Knight, 2009). Of the three approaches to making wild animals viewable, this leaves *habituation*.

Habituation has been defined as "a decrease in the strength of a response after repeated presentations of a stimulus that elicits that response" (Mazur, 2006). As such, habituation typically is viewed as a negative consequence of human interactions with wildlife due to the likely consequential reduction of population fitness arising from reduced danger flight response. However, habituation has been actively applied by zoological scientists in their field studies (i.e. in the wild), having been pioneered by primatologists such as Jane Goodall (Tanzania) working with chimpanzees (*Pan troglodytes*) and Dian Fossey (Rwanda) with gorillas (*Gorilla gorilla*) (Knight, 2009). Interestingly, Fossey's habituation of Gorillas made possible the development of Gorilla tourism as an alternative to Gorilla poaching (Shackley, 1995). Yet habituation has never been treated critically in the specific context of sustainable commercial wildlife viewing (Nisbet, 2000).

The relationship between tourists and wild animals is extremely complex (Bejder et al., 2009). Duffus and Dearden (1990) contend that this complexity arises from the interplay of three key components of the wildlife experience; site users, focal wildlife species (both individual animals and local animal populations) and the wider ecology of the viewing site. Given these components, considerations of habituation in ecotourism can be contemplated only in terms of site users (e.g. visitor management, guiding practice), the focal wildlife population (i.e. species-level variables and characteristics of individual animals) and the wider ecology of the focal species (e.g. spatio-temporal ecology) (Higham et al., 2008). Duffus and Dearden (1990) highlight also the temporal dimension in so far as tourist interactions with wildlife animals vary within diurnal, seasonal and life course timeframes, a point that has been inadequately addressed in academic discussions of habituation (Bejder et al., 2009). Following Duffus and Dearden (1990) then, some species of wild animals, and some individual animals, demonstrate a well-established response of inquisitiveness to humans or signs of human activity. Others are intensely private, remain concealed from onlookers, and flee readily from human interaction. In terms of inquisitiveness and active interaction, gulls are a ubiquitous example but rarely are gulls the focal species of interest to ecotourism operators and their visitors (Shelton & Higham, 2007). Useful approaches to the task of analysing the behaviour of species that are of tourist interest should, however, prove to be of considerable value.

Applied behaviour analysis, based on the notion of stimulus control and situated within learning theory, is well suited to provide a formative framework for those human–wildlife interactions that are of interest to commercial tourism operators. In this respect, the term habituation has been described as any situation where wildlife come to tolerate the presence of humans without any obvious signs of physiological or behavioural response (Shackley, 1996). Under this definition, habituation may be considered a mitigation or cessation of impact. The use of the term habituation in tourism and recreation has been applied also when animals approach people, or scavenge for food (Newsome et al., 2005). Park managers in North America attempt to educate the public not to engage in behaviours that will merge habituation and approach-for-food, particularly in the case of deer (The National Park Service, 2006a, 2006b) and bears (Davis, Wellwood, & Ciarniello, 2002).

To be as useful as possible, habituation must be distinguished from foraging or increased approach behaviour, even though the three phenomena regularly occur together (Davis et al., 2002). The starting point for such an undertaking is a critical behavioural analysis of wildlife habituation. In response to this need, a critical discussion of animal responses to human presence is presented, in order to achieve a more fine-grained understanding of habituation in all of its complexity. This critique provides a platform from which then to consider habituation within the context of sustainable wildlife tourism management.

3. A behavioural formulation of wildlife habituation

A behavioural formulation of wildlife habituation should begin by acknowledging the poor fit between observable animal behaviour and internal state (Ellenberg et al., 2006). In other words, the apparent tolerance of some wildlife species to approach and observation may not necessarily mean that these wild animals are not being impacted. Bejder et al. (2009) explain that wildlife tolerance of human stimuli may arise from various factors including:

- (1) Displacement: e.g. less tolerant individual animals may be displaced, resulting in a bias towards more tolerant animals that remain at a given site.
- (2) Physiology: e.g. reduced responsiveness to human stimuli due to physiological impairment.
- (3) Ecology: e.g. lack of suitable adjacent habitat to which animals may otherwise relocate.

This poor fit has been demonstrated in the case of penguins (Ellenberg et al., 2006) where artificial eggs placed under incubating birds record elevated heart rate in birds that outwardly appeared to be unaffected when approached (Nimon, Schroter, & Stonehouse, 1995). An understanding of habituation must acknowledge both the presence and absence of specific behaviours, and that impacts of significance at both the individual and species level may arise from both behavioural classes. The presence or absence of behaviours may vary at different scales of analysis, from individual animals to

entire populations (Bejder et al., 2006; Lusseau, 2003; Shelton & Higham, 2007), and is dynamic over time. Following Bejder et al. (2009), a behavioural formulation of habituation in the specific context of wildlife-based tourism may be presented in four parts; 1. Avoidance/approach behaviours, 2. Tolerance, 3. Habituation and 4. Sensitisation (Table 1).

3.1. Avoidance/approach behaviour

An important starting point for any critical discussion of habituation is an understanding of the complexity of avoidance and approach behaviours. The avoidance behaviours of cetaceans when engaged in interactions with tourist vessels have been particularly well researched (Baker, Perry, & Vequist, 1988; Corkeron, 1995; Lusseau, 2003; Salden, 1988;). Although responses to boat traffic vary between species, some show signs of active avoidance, ranging from altered movement patterns (Bejder, Dawson, & Harraway, 1999; Campagna, Rivarola, Greene, & Tagliorette, 1995; Edds & MacFarlane, 1987; Nowacek, Wells, & Solow, 2001; Salvado, Kleiber, & Dizon, 1992), increases in dive intervals (Baker & Herman, 1989; Baker et al., 1988; Blane, 1990; Janik & Thompson, 1996; MacGibbon, 1991) and increases in swimming speed (Blane & Jackson, 1995; Williams, Trites, & Bain, 2002). Avoidance behaviours in Bottlenose dolphins (*Tursiops truncatus*) have been shown to vary at an individual level (Lusseau, 2003), where male animals show a greater propensity to avoid boat traffic than females with calves (see Higham & Lusseau, 2004).

These studies present clear evidence of animal avoidance behaviours, not only as a result of the presence of boats, but also arising from the manoeuvring of boats, including sudden changes in vessel speed and rapid approaches (Constantine, 2001; Gordon, Leaper, Hartley, & Chappell, 1992; MacGibbon, 1991). In 2006, the International Whaling Commission reached agreement that “there is compelling evidence that the fitness of individual odontocetes repeatedly exposed to whale-watching vessel traffic can be compromised and that this can lead to population-level effects” (IWC, 2006). This consensus has been reached in light of recent studies that suggest avoidance responses from cetaceans when

Table 1
A critical behavioural formulation of the unitary term *habituation*.

Concept	Variables	Cases
1. Avoidance/approach behaviour	Avoidance response (e.g. pre-emptive avoidance)	Male Bottlenose dolphins (<i>Tursiops truncatus</i>)
	Response behaviours (e.g. generalised vigilance, concealment, discontinuation of critical behaviours)	Male Bottlenose dolphins (<i>Tursiops truncatus</i>)
	Stimulus control (i.e. group and individual behaviours)	Adele penguins (<i>Pygoscelie adeliae</i>); Little penguins (<i>Eudyptula minor</i>); Bottlenose dolphins (<i>Tursiops truncatus</i>)
	Exploratory approach behaviour Opportunistic approach behaviour	Elephant seal (<i>Mirounga leonine</i>) Buller's mollymawk (<i>Diomedea bulleri</i>); Giant petrel (<i>Macronectes giganteus</i>)
	Discriminative stimulus	Fantail/piwakawaka (<i>Rhipidura fuliginosa</i>); Southern Royal albatross (<i>Diomedea epomophora</i>)
2. Tolerance	Intrinsic tolerance	Little penguins (<i>Eudyptula minor</i>); Spotted shags (<i>Stictocorbo punctatus</i>); Stewart Island shags (<i>Leucocorbo chalconotus</i>); Little shags (<i>Phalacrocorax melanoleucos</i>)
	Selective tolerance	New Zealand sea lion (<i>Phocarcos hookeri</i>)
	Seasonal tolerance	New Zealand wood pigeon/kereru (<i>Hemiphaga novaezealandiae</i>)
3. Habituation	Approach habituation	New Zealand dabchick (<i>Poliocephalus rufopectus</i>)
	Spatio-temporally bound habituation	Colonial breeding female New Zealand fur seal (<i>Arctocephalus forsteri</i>).
	Socially acquired absence of avoidance behaviour	New Zealand fur seal (<i>Arctocephalus forsteri</i>) neonates
	Socially acquired habituation	Female New Zealand fur seal (<i>Arctocephalus forsteri</i>) (e.g. new colony recruits)
	Reduced physiological arousal	Northern Royal albatross (<i>Diomedea epomophora sanfordi</i>)
	Reduced avoidance behaviour	Yellow-eyed penguin (<i>Megadyptes antipodes</i>)
4. Sensitisation	Sensitisation	Stoats (<i>Mustela erminea</i>) (i.e. in the laboratory)
	Paradoxical sensitisation	Galapagos marine iguana (<i>Mblirhynchus cristatus</i>)

tourist vessels are present, and that those responses disrupt the behavioural budgets of affected animals. Repeated disturbance can then lead to displacement from preferred habitat and reduced fitness at the population level (Bejder et al., 2006) as opposed to any evidence of habituation.

3.1.1. Stimulus control

The presence or absence of avoidance/approach behaviours might usefully begin with the treatment of *stimulus control*. This term may be used to describe naturally-occurring wild animal behaviours that are resistant to modification. Adele penguins (*Pygoscelie adeliae*) launching from an Antarctic ice floe engage in grouping and rushing behaviours, presumably to reduce the likelihood of fatal attack by predators such as Leopard seals (*Hydrurga leptonyx*). The same stimulus control applies to Little penguins (*Eudyptula minor*) at tourist sites such as the Philip Island Penguin Parade (Victoria, Australia) and Oamaru Blue Penguin Colony (New Zealand). In this instance proximity to the landing site and grouping induces a rushing response which is unchanged despite millions of unchallenged landings over many generations of birds (Houston & Russell, 2000). This failure to habituate to coastline proximity has no obvious evolutionary cost to the species. The lighting, public address systems and grandstands full of visitors at these sites do not deter the birds from landing where they have, in recent history, always landed. This lack of avoidance response has not changed over time and is uniquely characteristic of this species of penguin which does not demonstrate habituation of approach or avoidance behaviour.

Another relevant case involves cetaceans. Lusseau's (2003) study of Bottlenose dolphins (*Tursiops truncatus*) in Doubtful Sound (Fiordland, New Zealand) found that these marine mammals entertained visitors on tour boats with their bowriding and leaping out of the water, such that it might be assumed that dolphins engage in this behaviour by choice. Power boats, though, act as a stimulus for dolphins not to rest; that is, bowriding and leaping are more likely to be under stimulus control and therefore not the result of choice. There are clear potential negative impacts of decreased resting on this species, including a disrupted energy budget and likely compromised reproductive success (Lusseau & Higham, 2004).

Repeated exposure to tourist vessels does not seem to reduce the strength of the dolphins' approach responses and this situation clearly demonstrates the difficulties inherent in referring to stable or increasing approach behaviour as habituation. Lusseau and Higham (2004) suggest the spatial segregation of non-permitted boats and Bottlenose dolphins through multi-level zoning. An additional management strategy could, in this case, include *inducing* habituation via stimulus mitigation; that is, reducing the dolphin's responsiveness to the presence of tourist vessels through the close management of key stimuli (e.g. boat speed and noise) so as to counter the stimulus control that these animals appear to act under.

3.1.2. Exploratory approach behaviour

A further manifestation of approach/avoidance behaviour, with an apparent temporal (i.e. life course) dimension may be termed *exploratory approach behaviour*. Elephant seals (*Mirounga leonine*) on sub-Antarctic Campbell Island may be exposed fleetingly to two or three groups of visitors per year at North West Bay (and not at all elsewhere on Campbell Island). Juvenile Elephant seals will approach and investigate tour parties at close range. The lack of similar interest on the part of adult Elephant seals very probably reflects a decreasing exploratory behaviour as a consequence of maturation rather than through habituation (i.e. repeated exposure to humans) where tourist encounters are so uncommon.

This change in responsiveness raises important questions around the naturally-occurring contingencies and physiological processes that operate to reduce exploratory behaviour during maturation from neonate through juvenile to adult. Repeated non-consequential exposure to a range of human behaviours should be situated somewhere in this process. On mainland New Zealand, where tourist encounters are more common, adult Elephant seals will rest ashore, selecting where possible confined and inaccessible resting sites, and demonstrating complete indifference to approach, based on a confidence of remaining unmolested. This indifference may be understood as reduced exploratory approach behaviour rather than habituation.

3.1.3. Opportunistic approach behaviour

The term *opportunistic approach behaviour* may be used to address approach stimuli linked to an individual's energy budget. Offshore boat-based tourist encounters with some seabird species such as Buller's mollymawk (*Diomedea cauta eremita*) may result in close but fleeting observations of birds derived from what may be described as 'investigatory fly past'. Opportunistic approach behaviour may be a generalisation from the birds' habit of following fishing boats whose crews routinely engage in gutting offshore. Giant petrels (*Macronectes giganteus*) also will engage in this behaviour. Distinct from provisioning and scavenging, these birds approach in response to a specific stimulus. Despite daily exposure to the tourist boat, and never having been fed, this exploratory approach behaviour persists over time. Due no doubt to a failure to distinguish between tourist vessels and fishing boats, and with so little energy required to complete an investigation, these birds, as an optimal feeding strategy, casually and routinely approach every boat.

3.1.4. Discriminative stimuli

Related to this, approach behaviours may be further differentiated from habituation via an understanding of *discriminative stimuli*. The behaviour of fantails/piwakawaka (*Rhipidura fuliginosa*) is typically misleading. Visitors often encounter the situation where they are walking along a bush track and suddenly numerous fantails appear and flutter tantalisingly close-by. Many may incorrectly assume that it is their presence that has attracted the birds which are attracted to human presence. Rather, the birds are attracted to small flies that have risen from the leaf litter as a result of human disturbance. The attraction to visitors in the bush is indirect. People in this case act as a discriminative stimulus for a likely disturbed forest floor, and consequently available prey. Similarly, Southern Royal albatrosses treat private boats as discriminative stimuli for fish being scaled and gutted and land in their wakes. These examples only serve to further confirm the poor fit between observable behaviour and internal state in terms of understanding animal behaviours in the wild.

3.2. Tolerance

3.2.1. Intrinsic tolerance

Within investigations of human–wildlife interactions the apparent tolerance of wild animals to human approach has remained almost entirely undifferentiated from habituation. The exception is Bejder et al. (2009: p. 181) who define tolerance as the "intensity of disturbance that an individual... tolerates without responding in a defined way". Tolerance may readily be confused with the complete absence of tourist impact. Indeed Higham (1998:529), in reference to viewing Northern Royal albatrosses (*Diomedea epomophora sanfordi*), warned that "tolerance should not disguise the fact that serious impacts may still take place". The manifestations of disturbance in the case of these outwardly tolerant birds have been revealed only by long-term monitoring and

analysis (Higham et al., 2008). A more critical treatment of tolerance allows, in the first instance, for consideration of *intrinsic tolerance*, which varies both between individual animals and species.

Many species of seabirds will demonstrate intrinsic tolerance to boat approach, seemingly oblivious to engine vibration and noise (both mechanical and human). Little penguins (*Eudyptula minor*) demonstrate intrinsic tolerance of boat engine vibration and noise, which indicates that they clearly are able to ignore human presence across settings (i.e. coastal landing zones and open water). Various species of New Zealand shag (cormorant) also demonstrate intrinsic tolerance to human approach (e.g. Spotted shags (*Stictocarbo punctatus*), Stewart Island shags (*Leucocarbo chalconotus*) and Little shags (*Phalacrocorax melanoleucos*)) (Shelton & Higham, 2007). However tolerance inevitably is behaviour (stimulus) specific. Supporting Knight's (2009) treatment of the tourist gaze is the fact that an intense and prolonged stare is sufficient to cause some individual birds (e.g. Spotted shags) to abandon their perches.

3.2.2. Selective tolerance

Tolerance, like habituation, has a spatio-temporal component. Solitary adult male New Zealand sea lions (*Phocartos hookeri*) demonstrate various responses to human approach which may be termed *selective tolerance* (or intolerance). Some adult male New Zealand sea lions will, when in the water in the autumn months, respond intolerantly (e.g. aggressive approach, charging and biting) to the passing kayakers of a commercial operator. Repeated exposure to kayakers, at this time of year, does not decrease the likelihood of aggressive behaviour. At other times of the day when hauled out on a nearby beach the same individual animals will tolerate close approaches by visitors (Shelton & Higham, 2007). The sharp contrasts between agonistic and indifferent responses (which clearly vary on a spatio-diurnal basis) are almost certainly linked to specific spatio-ecological (i.e. territorial dominance) and temporal (i.e. reproduction) elements.

3.2.3. Seasonal tolerance

A variation of selective tolerance is *seasonal tolerance*. The New Zealand wood pigeon/kereru (*Hemiphaga novaseelandiae*) frequents some urban areas in New Zealand and can appear to be indifferent to everyday human activity. Closer analysis reveals seasonal variations in the species' tolerance of human stimuli depending on food availability (Shelton & Higham, 2007). As the season progresses, and food becomes more abundant, kereru increasingly favour branches higher up in trees, and seasonal responses to human activity appear to change.

In this case, it is clearly necessary to elucidate precisely what role people are playing as discriminative stimuli. People minding their own business, presumably measured by their unmodified patterns of movement, uninterrupted chatter and non-bird-directed gaze, act as discriminative stimuli for approach tolerance. A sudden silence, ceasing walking, or bird-directed gaze act as stimuli for flight. The paradox for the commercial wildlife tourism operator who intends that visitors experience pigeons close-up is that the best advice to be given is to ignore them. Natural settings do not offer the frequency of close contact that would be required to attempt deliberately to manipulate the birds' existing responses. These two examples illustrate a more general concern with how humans can best interact with multiple species of birds in urban areas (Blumstein, Fernandez-Juricic, Zollner, & Garity, 2005).

3.3. Habituation

3.3.1. Approach behaviour

Bejder et al. (2009: p. 181) define habituation as the "relative persistent waning of a response as a result of repeated stimulation

which is not followed by any kind of reinforcement". Shackley (1996) observes that wildlife may habituate to the presence of humans, showing no obvious signs of physiological or behavioural response. If so, such a lack of response may fruitfully be explored within the context of sustainable wildlife tourism and cessation of impact. However, habituation can be assumed to have important spatio-temporal dimensions. New Zealand dabchick (*Poliocephalus rufopectus*) may become habituated to human approach following multiple exposures (Bright, Reynolds, Innes, & Waas, 2003). Similarly diurnal or seasonal habituation may take place in some species of wild animals under certain circumstances. Non-breeding male New Zealand fur seals (*Arctocephalus forsteri*) may be placid on land, where they demonstrate a decreased gross behaviour response to human approach. The same animals may be aggressive to swimmers in the water, which acts against describing any individual animals as being habituated. Nearby breeding colonies of female New Zealand fur seals that are exposed to regular stimuli may become unresponsive to approach.

3.3.2. Socially acquired habituation

Furthermore, there is evidence to suggest that the absence of response behaviours may be socially acquired or *learned* (Bejder et al., 2009) by wild animals. Early exposure, in the presence of an unresponsive mother, may result in seal pups that have never perceived tourist approach as a stimulus for flight. Seal pups do vary in their post-weaning exploratory audacity and some, having moved around the site once in the presence of humans with no ill-effects, begin to include indifference in their behavioural repertoire. Each uneventful visit further reduces the discriminative value of humans. Those adult females who had been born at the colony could conceivably retain their neonate indifference but those recruited from other colonies, where avoidance response to less frequent human approach takes place, may demonstrate *socially acquired habituation* through their peers modelling indifference. Such complexities of seal habituation to human approach, including the confounding effect of probable previous exposure, has been investigated by van Polanen Petel (2005) who suggests a species-specific approach is required in order to manage human–seal interactions optimally.

3.3.3. Reduced physiological arousal

Habituation in the form of complete indifference may be usefully differentiated from *reduced physiological arousal*, in which behavioural responses remain evident, but with reduced energy expenditure and arousal. At Taiaroa Head (Dunedin, New Zealand) Northern Royal albatross (*Diomedea epomophora sanfordi*) are closely monitored (Higham, 1998) and tourists are confined to a soundproof hide glazed with reflective glass. Throughout the breeding season all individual birds in the colony are exposed to close contact and attention from conservation staff, including weekly handling during weighing and measuring. These birds do not abandon their nests but do continue the defensive use of their beaks, as do Northern Royal albatrosses on the remote Campbell Island. Despite having been handled periodically over the years since their hatching these birds did not seem to have habituated to this particular human behaviour. However, although there had been no apparent change in the gross motor component of the birds' defence rituals, there may well have been reductions in human-induced physiological arousal. Thus, the defence behaviour persists, but with reduced determination or persistence.

3.3.4. Reduced avoidance behaviour

A fourth manifestation of habituation may be termed *reduced avoidance behaviour*. This arises in cases where approach/avoidance is at the discretion of individual animals. While it is conceivable

that approach behaviour may be habituated the more likely case in wild animal populations is that avoidance behaviour may decrease over time. This appears to be the case in Yellow-eyed penguin (*Megadyptes antipodes*) colonies that are exposed to increasing tourist interactions, where established members of the colony may become less timid over time, but there may be a simultaneous reduction in the recruitment of prospecting birds. The impact of humans on this most phlegmatic but inquisitive of penguins is the subject of ongoing study (Seddon, Smith, Dunlop, & Mathieu, 2004). This work is predicated on the fact that measuring penguin habituation using only approach/avoidance behaviour is inappropriate since physiological arousal fluctuates independently of observable behaviour (Ellenberg & Mattern, 2004) and the relationship varies both between individual penguins of the same species and different penguin species (Ellenberg et al., 2006).

3.4. Sensitisation

Finally, it is important to attempt to differentiate between sensitisation and habituation. Usually, sensitisation refers to an increase in the strength of a response upon repeated or ongoing exposure to a stimulus that has significant consequences (Bejder et al., 2009). However, it is noteworthy that repeated exposure to tourists appeared to lower the production of corticosterone, commonly a stress hormone, in Galapagos marine iguana (Romero & Wikelsi, 2002). Lower corticosterone production in response to human interaction, compared with animals who have no human interaction, seems to demonstrate *sensitisation*, the opposite of habituation, but in this case the *lowering* of corticosterone production, although demonstrating sensitisation, may legitimately be labelled *paradoxical sensitisation*. Of course one study is inconclusive

but it does raise an intriguing possibility. If robust, this finding implies that chronic sub-optimal physiological processes may be a naturally-occurring phenomenon in some species of wild animals.

4. Wildlife habituation and sustainable nature-based tourism: a management model

This discussion addresses the proposition that ecotourism operators who are committed to providing a sustainable nature-based product will be interested to know how their activities may be influencing the environments in which they do business. The inherent tensions between business practice and sustainability in nature-based tourism have been well described (Fennell, 2003; McKercher, 1993a, 1993b, 1998; Newsome et al., 2005). The preceding discussions allow for the development of a management model for sustainable wildlife tourism interactions (Fig. 1) based on a critical behavioural formulation of *habituation*.

Following Duffus and Dearden (1990) Fig. 1 is constituted principally by three key elements; site users, focal animals (individuals or local populations) and the wider ecology of the wild animals engaged with human approach and observation. Such a representation recognises that any human–wildlife interactions are spatially bound; that is, human interactions with individual wild animals can take place in a variety of settings that vary across a range of habitats where different behaviours (e.g. migration, feeding, resting, socialising, breeding, raising neonates etc.) take place. Animal responses to human approach and interaction inevitably vary between settings.

The model recognises also the temporal variation that exists in terms both of site users (e.g. timing and duration of visit, and seasonal context), and focal animals (e.g. diurnal, seasonal and life

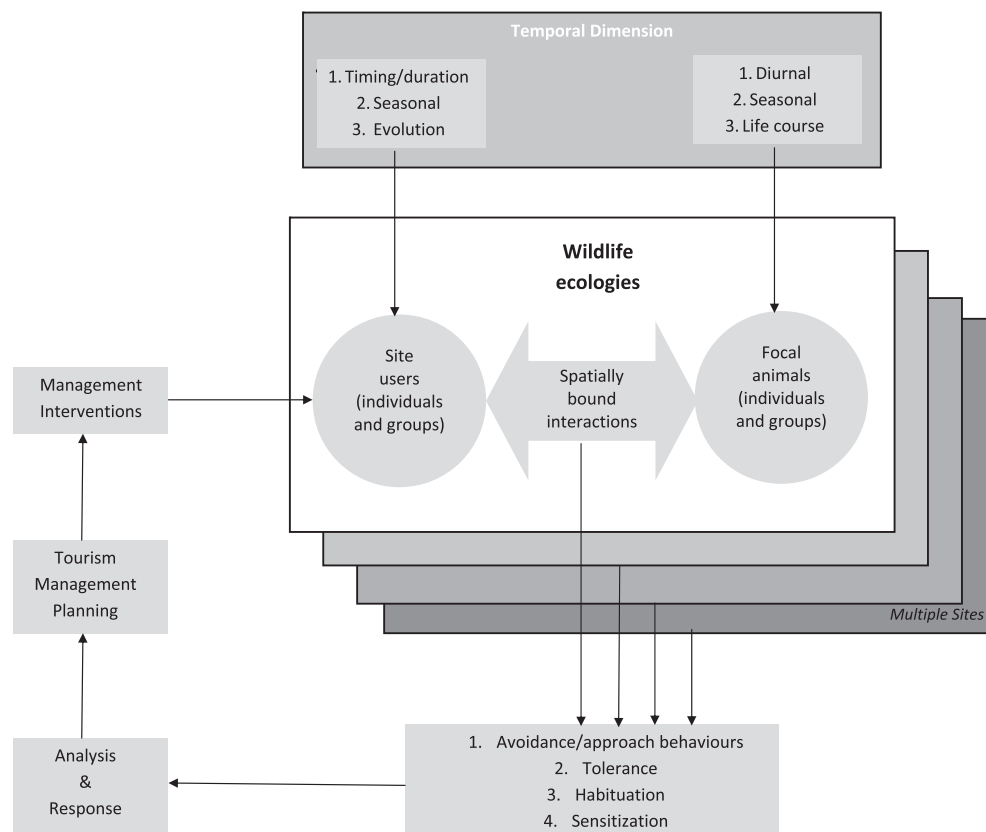


Fig. 1. Management model for sustainable wildlife tourism interactions based on a critical behavioural formulation of the term *habituation*.

course), which influence the outcomes of human–animal interactions. Avoidance/approach behaviours, tolerance, habituation and sensitisation can fruitfully be considered within this context. A critical understanding of spatio-temporal ecology and the interactions of tourists and focal animals can then be applied in terms of tourism management planning and consideration of conscious management interventions (Fig. 1). This would require a critical understanding of the unitary term habituation, which is attempted in this article. It would also necessitate a mixed (biological and social) science platform of research to inform an integrated and adaptive management approach (Higham, Bejder, & Lusseau, 2009).

5. Discussion

As nature-based products are offered in more and more remote places (i.e. previously unexploited ecosystems) it becomes increasingly likely that any given individual animal will encounter humans, engaged in particular behaviours, at some stage of its life. The animal may approach the human, as neonates and juveniles of many species do. If, on repeated exposure to these particular human behaviours, this approach behaviour decreases, and is not replaced by escape/avoidance behaviour, then the animal may accurately be described as being habituated to the human behaviours to which it has been exposed, in a particular spatio-temporal setting.

Any habituation/sensitisation process is dynamic, and may reflect the hormonal state of the individual animal at the time of exposure to the particular human behaviour. If the individual animal demonstrated indifference to the human behaviour right from the start then habituation is not the best term to use to describe the situation; tolerance or resilience may be more useful. Similarly, animals may respond to human activity through increases in physiological processes, commonly grouped under the term *arousal*. Decreasing physiological arousal upon repeated exposure indicates habituation, increased arousal indicates sensitisation. The unusual situation where an initially high level of arousal may be reduced by exposure to human activity may be tentatively labelled *paradoxical sensitisation*. It is possible also for wildlife to decrease one response to human presence, for example fleeing, but to increase another response. Chimpanzees' activity rates in Kibale Forest, Uganda, habituate to the presence of increasing numbers of observers but vocalisation increases (Johns, 1996).

It is useful at this point to address two issues. Firstly, why is it important to specify to what human behaviours, in what settings and at what times do individual animals habituate, and to avoid the simpler descriptor; habituation to humans? Habituation to humans, by definition, involves decreased vigilance in response to human presence, decreased communication of alarm upon coming across humans and/or decreased avoidance of, or fleeing from, humans. The argument then is that habituated animals are made vulnerable in that habituation to one potential predator, *Homo sapiens* will induce a generalised reduction of predator-preparedness (Beale & Monaghan, 2004).

We argue that this concern evaporates when habituation is more usefully formulated. If habituation is related to spatially and temporally constrained specific human behaviours, rather than simply to human presence, then it is reasonable to hypothesise that individual animals will retain predator-preparedness outside of these parameters. Discriminating between human behaviours is consistent with laboratory-based enquiry that has demonstrated that many species have the ability to discriminate even between individual human beings performing the same behaviours (Davis, 2002). Predator-preparedness training in birds, in common with exploratory behaviours (Huber, Rechberger, & Taborsky, 2001), can

occur through social learning. For example adult Sandhill cranes teach predator-preparedness by modelling vigilance and predator-response even to unrelated captive-reared conspecific chicks (Heatley, 1995). There is debate about how possible habituation to human activity acquired while in captivity, for example in a rehabilitation facility, should be managed. A fine-grained analysis is available addressing the issue of how much deliberate training-for-release should take place, what such training should comprise, and exactly how humans should be involved in its delivery (Bauer, 2005).

It is reasonable to suppose that habituation can be socially learnt also in natural settings, and be passed on in a sophisticated rather than generalised way. Different species teach their offspring different sensitivities. For cliff-dwelling birds visited by tourists, size-of-party has been reported to have species-specific effects (Beale & Monaghan, 2005). It is not unreasonable to suggest that certain species may teach their young not to respond to a particular wildlife guide, acting within certain behavioural limits. In such cases it is critical that individual animals are the unit of analysis in rigorous longitudinal studies (Bejder et al., 2009).

The second issue that needs to be addressed is one of management. If, as suggested here, some or all of the behaviours of many wild species can be brought under stimulus control, then what happens to the *wild* in *wildlife*? The application of stimulus control techniques to the management of human behaviour is widely reported in the Applied Behaviour Analysis literature. Using the nuanced approach to habituation outlined here it is conceivable that wildlife managers and visitor managers could co-operate to apply behavioural technologies to structure almost completely the nature of human–wildlife interactions site-by-site, species-by-species, and in some cases to the level of individual animals, taking into account time of day and time of year. This level of management, although common in zoos and other captive settings, if applied to natural settings would challenge directly the motivation for visiting such sites in the first place. Nonetheless, in certain cases the conservation outcomes available using such an approach may be justified.

6. Conclusion

This article highlights the wide variability of wild animal responses to human approach and interaction. In doing so, it begs the question; which individual animals or groups of animals respond in what fashion to what kind of tourist behaviour in what contexts? Clearly individual (or groups of) animals that respond passively in one setting, may in other settings not be so sanguine. For example, where a particular set of contingencies operate to induce decreasing gross behavioural responsiveness, on land, to a fairly narrow set of visitor behaviours, in a group of seals who shared non-breeding status, evidence of spatially and temporally bounded habituation may exist. The responsiveness of physiological processes within individual seals, the role of developmental maturation and the influence of vicarious or social learning through the observation of calm conspecifics remain largely unexamined, although available for formulation.

Clearly, a fine-grained behavioural approach is required to overcome the poor fit between observable wildlife behaviour in the presence of humans and individuals' internal states, and to accommodate the fact that habituation is spatially and temporally bounded. Given that such a poor fit is unhelpful to individual, species or whole-of-ecosystem management, it seems desirable that ecotourism operators actively address likely habituation or other conditioning to humans as part of their business plan or concession application. As such, wildlife managers and visitor managers could co-operate to apply behavioural technologies

to structure almost completely the nature of human–wildlife interactions. A tourism management model that accommodates a nuanced understanding of wildlife habituation is presented, building upon a formulative framework for human–wildlife interactions. The development of empirical case studies to inform and monitor tour operator best practices is a valuable avenue of future research.

Knight (2009) presents three approaches to making wildlife viewable; capture and confinement, habituation, and attraction. While of the three, habituation is the least likely to be associated with diminished behaviours, the question of diminished wildness remains unanswered. Exploring this question will, no doubt, reveal a trade off between using habituation as a tourism management tool and the potential evolutionary costs to focal animal populations, not only in terms of physiological and behavioural responses, but also in terms of exposure to disease (Bejder et al., 2009). One provocative approach, integrated with the field of neurobiology, will be designer wild species, specifically habituated for viewing. Alternatively, Knight (2009) observes that learnt animal behaviours can be unlearnt, giving rise to the notion of the reversal of habituation. As Knight (2009: p. 180) comments, “In an age when our visual appetite for wildlife has never been greater, there may be good reasons for keeping this appetite in check and acting to make viewable wild animals unviewable again”. Before further contemplating the reversal of habituation, a more critical understanding of habituation itself is required. This amplifies the need for “studies (that) adopt a long-term experimental design involving sequential sampling of the same individuals at different levels of exposure to a disturbance” (Bejder et al., 2009: p. 181). In the meantime, these thoughts pose intriguing questions that are available for scholars to debate and research.

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