An Ethological Framework for Defining Habituation, Sensitisation and Tolerance to Anthropogenic Stimuli

Bejder[1], L.., Samuels[2], A., Whitehead[3], H. and Allen[4], S.

Note: The work presented in this document is being further-developed and will be submitted for publication in a peer-reviewed journal at a later stage.

[1] Dr. Lars Bejder, Research Leadership Fellow, School of Biological Science and Biotechnology, Murdoch University, Perth, Western Australia. E-mail: l.bejder@murdoch.edu.au

[2] Dr. Amy Samuels. Visiting Investigator. Woods Hole Oceanographic Institution, Woods Hole, MA, USA. E-mail: asamuels@whoi.edu

[3] Professor Hal Whitehead. Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada. E-mail: hal.whitehead@dal.ca

[4] Mr. Simon Allen. Research Associate. School of Biological Science and Biotechnology, Murdoch University, Perth, Western Australia. E-mail: s.allen@murdoch.edu.au

ABSTRACT

An important goal of scientific inquiry into effects of anthropogenic activity on wildlife is to provide a sound foundation for wildlife conservation and management efforts. This objective, however, is often jeopardized by misinterpretation of the very science that professes to safeguard wildlife. In particular, imprecise or lax use of the terms, habituation, sensitisation and tolerance can lead to misinterpretation of research findings with unintended and potentially dire consequences for wildlife communities. The most noticeable example is colloquial use of the term behavioural habituation, to refer to any form of moderation in wildlife response to human disturbance. Because habituation is widely assumed to be a positive outcome for wildlife, such a misclassification can lead to inappropriate management decisions including an easing of conservation efforts. Clear definitions of terms, and rigorous methods for distinguishing among them are provided, thereby demonstrating that most cases of presumed habituation or sensitisation actually represent differences in the tolerance levels of wildlife to anthropogenic activity. This distinction is important because there are various mechanisms by which different tolerance levels can arise and by which habituation- and sensitisation-type responses can be explained. By characterizing explanatory mechanisms as learning, physiology, selection or ecology, it is shown that only one mechanism will result in true behavioural habituation (or sensitisation), while others will have detrimental outcomes for targeted animals. A framework is provided for literal and standardized use of terminology, and an empirical technique for discerning among explanatory mechanisms to detect true habituation and sensitisation responses is offered.

INTRODUCTION: INTERPRETING WILDLIFE RESPONSE TO HUMAN DISTURBANCE: THE IMPORTANCE OF SEMANTICS

The ultimate goal of scientific inquiry into effects of anthropogenic activity on wildlife is to provide mitigation from any negative impacts. To this end, investigators endeavour to measure wildlife response and reveal those activities that are threatening to wildlife; to make clear the links between cause and effect and between short-term response and long-term biological significance; and ultimately, to provide practical information that will inform the development of management guidelines specific to the circumstances. But, with regard to wildlife and human activity, the field of impact assessment is a science in the early stages, and accomplishment of these objectives has often been jeopardized by misapplication and misinterpretation of the very science that professes to safeguard wildlife. In reference to wildlife tourism targeting marine mammals, Gales (1999) raised an issue that is pivotal to this problem, stating, "…the demand and growth of this industry has significantly outstripped

the ability of scientists to develop and implement sufficiently sensitive tools that might provide some sound basis for management decisions". Here, this sentiment is built upon to point out that, in impact assessment research and wildlife management, not only are refinements in methodology needed (*e.g.*, Bejder and Samuels, 2003), but an important facet of open channels of communication is careful attention to the translation of research findings into management guidelines. In particular, we caution that imprecise or lax use of terminology can lead to misinterpretation of findings, with unintended and potentially dire consequences for wildlife communities.

These are issues of significant concern for scientists and wildlife managers alike, because the rate at which people and wildlife come into close contact, and the consequent potential for conflict, are on the rise. Spatial overlap between people and wild animals has increased through encroachment of wildlife habitats as a result of urban development and expansion of industry, settlements and infrastructure, as well as direct consumption of natural resources. In addition, human intrusion into wildlife habitat has been promoted by leisure activities, such as camping, snowmobiling, mountain biking, hiking, and diving, that take place in proximity to, but are not focused on, wildlife. Further activities have specifically targeted wildlife to deliberately bring humans into close contact with wild animals. For example, tourism in the form of wildlife viewing and/or wildlife interaction (*e.g.*, feeding, touching), often involves sustained, repeated, close-up encounters with wild animals.

In response to the expansion and intrusion of human activity into natural areas, a number of investigations have been undertaken to try to evaluate what the potential impacts might be. A range of animal attributes has been suggested to influence, either singly or in combination, the responsiveness of animals to human activity. These factors include*:* species (*e.g.*, Gutzwiller *et al.*, 1998), age (*e.g.*, Stalmaster and Newman 1978; Constantine 2001), sex (Williams *et al.* 2002a; Lusseau 2003a) reproductive condition (*e.g.*, Culik and Wilson 1995; Nellemann *et al.* 2000; Parent and Weatherhead 2000), nutritional condition (*e.g.*, Doenier *et al.* 1997; Beale and Monaghan 2004a) and prior experience (*e.g.*, Burger and Gochfeld 1999) (for an overview see: Samuels *et al.* 2003). In addition, wildlife response to human activity has been documented to take many forms, expressed via changes in: home range size and habitat use (*e.g.*, Altmann and Muruthi 1988; McLellan and Shackleton 1989; Albert and Bowyer 1991; Bejder et al., 2006a), foraging behaviour (*e.g.*, Galicia and Baldassarre 1997; Gander and Ingold 1997), reproductive success (*e.g.*, Safina and Burger 1983; Giese 1996; Müllner *et al.* 2004; Bejder 2005), body condition and disease susceptibility (*e.g.*, Altmann *et al.* 1993; Phillips-Conroy *et al.* 1993; Nizeyi *et al.* 1999, Woodford *et al.* 2002; Müllner *et al.* 2004), sex ratio (*e.g.*, Clout *et al.* 2002), daily activity period (*e.g.*, Griffiths and van Schaik 1993), social development (*e.g.*, de la Torre 2000), and mating system and social structure (*e.g.*, Lacy and Martins 2003).

Apparent "habituation" is another often-claimed response of wildlife to human activity – an outcome that is sometimes actively sought by humans (e.g, Nisbet 2000). For example, in field studies of animal behaviour, habituation of wildlife to human presence may be desirable when researchers want to study behaviour that is relatively unaffected by their own presence (*e.g.*, Goodall 1986; Tutin and Fernandez 1991; Johns 1996). A common theme in studies of habituation is a stimulus-specific response that weakens after exposure to repeated stimuli in the study subject (but see later for working definition).

The premise to strive for wildlife habituation is based on the general perception that it indicates that the activities have no or little effect on the animal itself – in contrast to the impacts listed above. However, there is considerable disagreement as to whether or not habituation compromises the well being of wildlife (*e.g.*, McLellan and Shackleton 1989; Spradlin *et al.* 1998, 2001; Nisbet 2000; Stone and Yoshinaga 2002; Woodford *et al.* 2002). Here, we make no judgement as to the pros and cons of wildlife habituation, and its counterpart - sensitisation - to human activity, but rather, discuss the unfortunate trend in the mis-identification of wildlife habituation and sensitisation to anthropogenic stimuli in impact studies.

Specifically, in the literature pertaining to effects of anthropogenic activity on wildlife – habituation, sensitisation and tolerance – have come into colloquial use, resulting in applications that are variously loose, inappropriate, and even, interchangeable. This trend is unfortunate because there are management implications of imprecise terminology, in particular, a potential for misinterpretation of the impacts of human activity on wildlife.

Misuse of the term, habituation, is perhaps the most noticeable example because behavioural habituation is widely considered to be a positive outcome for wildlife. Wrongful application of this label with its positive connotations can mislead wildlife managers to conclude that a given human activity had neutral, or even benign, consequences for wildlife, when, in fact, the impacts were negative. With harmful effects going unrecognised, management plans might erroneously call for no corrective action, an easing of conservation efforts, or worse, an

increase in human activity. Inappropriate use of the term, habituation, can, therefore, seriously undermine management plans and may even counteract conservation goals.

Thus, the goal of this paper is to highlight the potentially damaging effects of imprecise language to the formulation of wildlife management plans, and to propose a framework for the literal and standardized use of terminology for categories of behavioural response to human disturbance within the fields of wildlife management and conservation.

CATEGORIES OF BEHAVIOURAL RESPONSE: DEFINING HABITUATION, SENSITISATION AND TOLERANCE

Habituation, and its counterpart, sensitisation, are adaptive behavioural modifications exhibited by animals in response to exposure to human activity that is repetitious or continuous. As these are processes occurring over time, the terms, habituation and sensitisation, do not refer to specific behavioural responses. Behavioural habituation is "the relative persistent waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement" (Thorpe, 1963:61) (Table 1). Habituation is, therefore, a process involving a reduction in response over time as individuals learn that there are neither adverse nor beneficial consequences to occurrence of the stimulus. Conversely, sensitisation is "[i]ncreased behavioural responsiveness over time when animals learn that a repeated or ongoing stimulus has significant consequences for the animal" (Richardson *et al.*, 1995:543) (Table 1). These processes are based on learning and the cumulative experience of individual animals, which will include the number and outcome of exposures to anthropogenic stimuli over the course of each animal's lifetime (Knight and Temple, 1995).

Table 1. Working definitions for categories of behavioural response and requirements for their demonstration.

Term	**Definition**	**Time course of response**	**Requisites to demonstrate response**
Habituation	"the relative persistent waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement" (Thorpe 1963:61)	Longitudinal Process	Sequential measures taken from same individuals over time
Sensitisation	"[i]ncreased behavioural responsiveness over time when animals learn that a repeated or ongoing stimulus has significant consequences for the animal" (Richardson *et al.* 1995:543)		
Tolerance	"the intensity of disturbance that an individual….tolerates without responding in a defined way" (Nisbet 2000:315)	State	Instantaneous measurement

Despite formal definition of habituation and sensitisation as processes, the term, habituation, has come into colloquial use to categorize moderation in wildlife response to human disturbance. In many such cases, however, the moderate responses described were not habituation, but instead, increases in tolerance levels (Nisbet 2000). Tolerance is defined as "the intensity of disturbance that an individual….tolerates without responding in a defined way" (Nisbet 2000:315) (Table 1). Tolerance levels can be measured instantaneously and are, therefore, more readily demonstrated than the longer term processes of habituation or sensitisation. In fact, habituation and sensitisation are identified, and distinguished from each other, by the direction of change indicated by repeated measures of tolerance taken over time. For example, over the course of a habituation process, individual tolerance levels will be on the increase, and conversely, as individuals become sensitised to specific stimuli, their tolerance levels will decrease. Thus, demonstrating, at one point in time, that animals in one group or area are more tolerant than others to disturbance provides one piece of evidence in documenting that habituation may have occurred, but does not rule out other plausible explanations. Confirmation that habituation has occurred would necessarily require longitudinal, sequential measurements of responses of individuals to controlled stimuli (Nisbet 2000), a rigorous assessment technique that has rarely been employed (but see, *e.g.*, Tutin and Fernandez1991; Johns 1996).

IMPACT ASSESSMENT RESEARCH TYPICALLY DOCUMENTS DIFFERENCES IN LEVELS OF TOLERANCE – NOT HABITUATION OR SENSITISATION

Due to practical and financial constraints, the vast majority of impact assessment studies are constrained to the evaluation of a limited number of points in time – constraints that necessarily restrict opportunities to document

long-term processes such as habituation and sensitisation. As a result of these limitations, assessment of the impacts of human disturbance typically follows one of two study designs: (1) instantaneous comparison at one point in time of responses between communities that have different histories of exposure (*e.g.*, duration, frequency, intensity) (Figure 1a); or (2) sequential comparison at two points in time of responses within one community (Figure 1b). For example, in Figure 1a, the goal would be to evaluate effects of anthropogenic activity on animals that have been exposed to a given stimulus ("impact" group; Figure 1a-1), by comparing them with animals having little or no history of exposure ("control" group; Figure 1a-2). In Figure 1b, members of the same community would be sampled at different exposures to the anthropogenic disturbance. In both designs, documenting differing levels of tolerance within or between communities of animals is readily achieved, but this is not the case with respect to habituation or sensitisation. Proof of behavioural habituation or sensitisation is feasible only by employing the latter design, and then, only when the *same* individual animals are sampled through time. This second criterion, in particular, is one that is seldom met. Animal identities are rarely taken into account in impact assessment research, and as a result, even when sequential observations are taken within a community, it is not possible to detect behavioural change in individuals. Thus, without longitudinal monitoring, sequential measures of the same individuals, and/or pre-exposure observations, it is difficult to meet the conditions required to detect behavioural habituation or sensitisation.

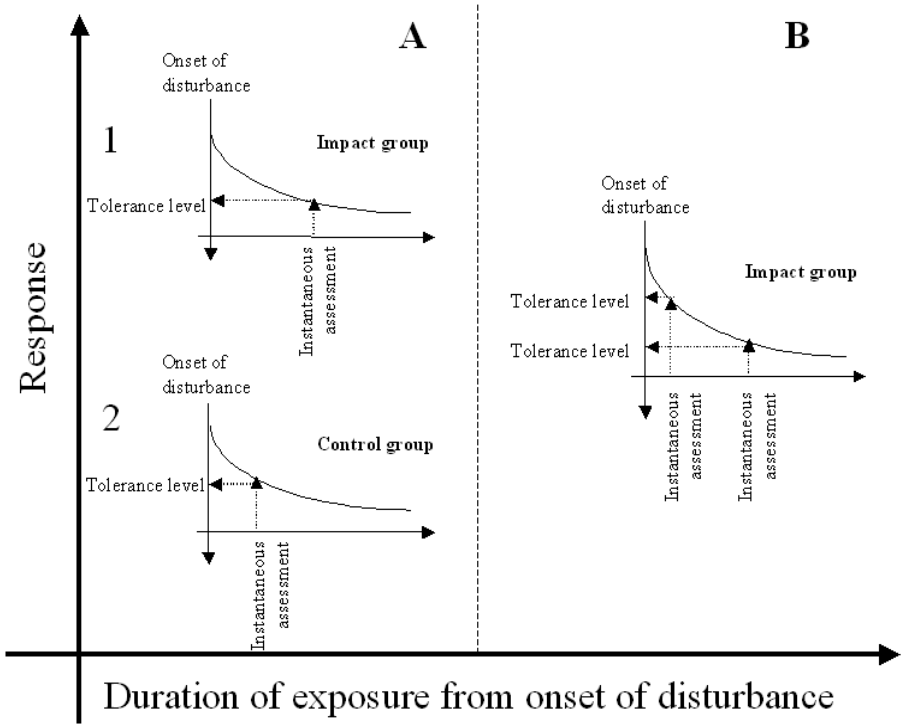

Figure 1. Examples depicting two study designs typically used for assessment of anthropogenic impact on wildlife. The origin represents the time of onset of the disturbance factor and, hence, the x-axis denotes duration of exposure to the stimulus, and the y-axis represents corresponding levels of response to the stimulus. Figure 1a depicts an instantaneous comparison at one point in time of responses between an "impact" (1a-1) and a "control" (1b-2) group that have different durations of exposure. Figure 1b depicts a sequential comparison at two points in time of responses measured within one community at different exposure levels. Note direction of y-axis in small insert figures: tolerance levels increase as response levels decrease (large y-axis).

If it is levels of tolerance that are typically detected in impact assessment studies, how are these findings to be interpreted? Further inspection of Figure 1a, shows that there are several ways in which the differences in observed tolerance levels between impact and control groups can occur. In one scenario, members of the impact group have truly become more tolerant to disturbance through a gradual process of behavioural habituation, *i.e.* learned habituation. In this case, additional, temporally spaced observations are needed to confirm that true waning of responsiveness has occurred. In a second scenario, a segregation of the less tolerant members of the

impact group occurred prior to onset of the assessment, resulting in biased sampling of constituents of the impact group. In such a case, an assessment would not reflect the avoidance responses of the less tolerant group members that moved away from the area of disturbance; instead, only responses of more tolerant individuals remaining in the area would be measured (*e.g.*, Griffiths and van Schaik 1993; Fowler 1999; Bejder et al., 2006b). In a third scenario, a response resembling habituation occurred through physiological or ecological means rather than through learning. For example, animals may exhibit reduced responsiveness to a given stimulus because of physiological impairment, *e.g.*, deafening due to repeated or prolonged exposure to loud acoustic stimulus. Or, animals may exhibit reduced responsiveness to an element in their ecosystem other than the given stimulus. For example, the focal species may respond to the habituation of prey species or displacement of predators in response to the human disturbance, rather than to the disturbance directly. And, in a fourth scenario, a habituation-type response was the result of habitat differences between impact and control sites, that is, with no suitable habitat elsewhere to which animals at the impact site could move, they were compelled to remain in proximity to the disturbance (Gill *et al.* 2001). In this case, criteria for habitat suitability might include abundance of predators, prey or shelter, social factors, etc. In only one of the four scenarios presented above could behavioural habituation be invoked, and in that case, confirmation would require additional sampling. Analogous explanations can give rise to differences in tolerance levels within one population or community measured at two different times (Figure 1b).

Thus, interpreting the findings of impact assessment research for management purposes is not entirely straightforward. What is clear, though, is that common presumptions do not hold up. When results indicate that responses of the impact group are more moderate than those of the control group, it is often assumed that behavioural habituation has occurred. When results indicate that the impact group has greater tolerance than the control group, it is often assumed that there are no detrimental impacts on members of the impact group. Are either of these interpretations correct? As the analysis of Figure 1a, above, shows, other explanations are equally plausible and more information is needed.

DISCERNING BETWEEN EXPLANATORY MECHANISMS: WOULD THE REAL 'HABITUATION' PLEASE STAND UP?

In an ideal world, impact assessment research would be initiated prior to the onset of anthropogenic activity, would feature sequential monitoring of responses, and would focus on the same individual animals over time. In this model, a waning or waxing of wildlife response to human activity could be readily identified. Unfortunately, such ideal monitoring conditions rarely exist. Even under the best of circumstances, confirming that the documented response is truly behavioural habituation or sensitisation is problematic, given the various mechanisms that can explain observed decreases or increases in responsiveness over time.

As an example, consider Figure 2a, which depicts a "habituation-type" response. With the introduction of a given stimulus, behaviour, as measured by some response variable, changes (y-axis). With repeated occurrence of the stimulus over time (x-axis), the cumulative exposure grows with a concomitant decline in the response variable, which ultimately approaches the pre-stimulus level. The observed pattern conforms to Thorpe's (1963) ethological definition of habituation: with increased exposure, an animal learns that the stimulus has neither adverse nor beneficial effects, and the animal's responsiveness to that stimulus wanes.

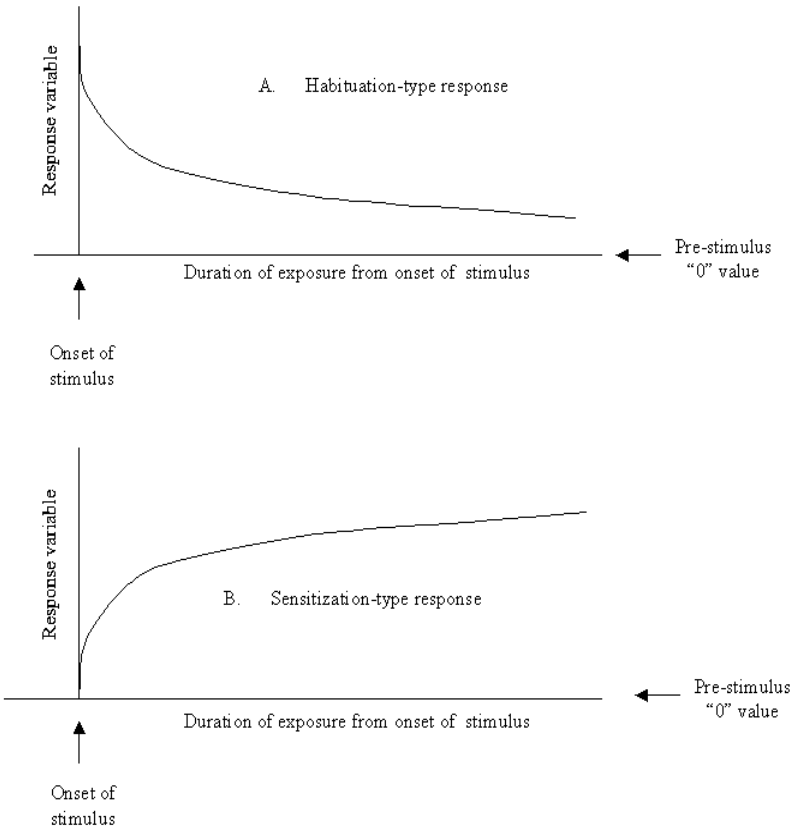

Figure 2. Illustration of 'habituation-type' response (A), and 'sensitisation-type' response (B). As in Figure 1, the origin represents the time of onset of the stimulus and, hence, the x-axis denotes duration of exposure to the stimulus, and the y-axis represents corresponding levels of response to the stimulus.

Still looking at Figure 2a, now consider that, as is common in studies of anthropogenic effects on wildlife, the response variable (y-axis) is actually a measure of the mean population response. In the ideal monitoring scenario, the behaviour of randomly-chosen members of the population would be measured at intervals following the introduction of the stimulus, and a curve, the same as that shown in Figure 2a, would be drawn from the resulting data set. From these two examples, it is clear that a number of different mechanisms can produce the curve shown in Figure 2a. Explanatory mechanisms include:

> *learning*: individual animals learn with repeated exposure not to respond to a given stimulus, *i.e.* true behavioural habituation;
> *physiology*: animals exhibit reduced responsiveness to a given stimulus because repeated or prolonged exposure results in physiological impairment, *e.g.* deafening in the case of a loud acoustic stimulus;
> *selection*: animals exhibit individual variation in responsiveness to a given stimulus such that the most responsive individuals are disproportionately vulnerable and are removed from the study population through death, morbidity, spatial displacement, or reduced reproductive success. For example, if the less tolerant individuals move out of a region in response to human activity, a reduction in the average density of animals, and therefore, a more moderate average response among animals within the disturbed area would be observed (Fowler 1999; Bejder et al., 2006a,b).
> *ecology*: animals exhibit reduced responsiveness to an element in their ecosystem other than the given stimulus, *e.g.*, habituation of prey species, or displacement of predatory species.

All of these mechanisms can result in the habituation-type curve depicted in Figure 2a, but only the one that invokes learning by individual animals – true behavioural habituation – is likely to have no direct detrimental consequences for the long-term fitness of the community and/or population. However, it is important to note that some scientists believe that behavioural habituation can result in harmful outcomes for wildlife, for example,

through increased exposure to disease or loss of wariness to vehicular activity (*e.g.*, Spradlin *et al.* 1998; Stone and Yoshinaga 2000; Woodford *et al.* 2002).

The three other mechanisms that produce habituation-type curves are unlikely to denote good news for targeted animals. Ecological factors may sometimes have benign or neutral effects, as when target animals respond to the habituation of their prey to a given stimulus, rather than to the stimulus itself. But outcomes of physiological damage and selection are likely negative.

For sensitisation, a parallel but opposite schema can be generated, with a "sensitisation-type" response that increases with cumulative exposure (Figure 2b). The same range of mechanisms can be called upon to explain this type of curve:

> *learning*: individual animals learn with repeated exposure to respond to a given stimulus, *i.e.*, true behavioural sensitisation;
> *physiology*: animals exhibit increased responsiveness to a given stimulus because repeated or prolonged exposure results in physiological sensitisation (*e.g.* chemical sensitisation);
> *selection*: animals exhibit individual variation in responsiveness to a given stimulus such that the least responsive individuals are disproportionately vulnerable to dire consequences, *e.g.*, those that take the least evasive action suffer the greatest mortality, morbidity, etc;
> *ecology*: animals exhibit increased responsiveness to an element in their ecosystem other than the given stimulus, *e.g.*, an increase in the abundance of predatory species.

Now consider the variety of ways in which the habituation- and sensitisation-type curves depicted in Figure 2 could have been produced. Various units of analyses could have been used. These include sequential measures of the same individuals, communities or populations over time; or comparisons at one point in time between individuals, communities or populations with differing cumulative exposure. Depending on the unit of analysis used, and which of the four mechanisms is in operation (learning, physiology, selection, or ecology), the observed response may or may not be depicted as a habituation- (or sensitisation-) type curve. So, assume a habituation-type response (as in Figure 2a), and consider different possibilities for the response variable measured on the y-axis and the response curve shown:

1. *The response curve is the trajectory of the mean response of a population measured over time:* This could result from any of the four mechanisms.
2. *The response curve is the mean trajectory of the responses of known individuals measured over time:* This could be caused by learning, physiology, or ecology, but not selection because the trajectory is based on measurements at the level of the individual, not the population.
3. *The response curve is fitted through points calculated for several different populations with different cumulative exposure:* This could result from any of the four mechanisms.
4. *The response curve is fitted through points calculated for subsets of one population from different areas within its range, each area having differing cumulative exposure, with all measurements made at the nearly the same time. In this scenario, movement of individuals between subpopulations is assumed*: This could result from an ecological effect, or possibly a type of selection in which the animals exhibiting the greatest response avoid the areas of greatest impact. This could not result from learning or physiological damage because variation in response by area depends on each area's exposure history rather than the exposure history of the entire population.
5. *The response curve is fitted by comparing the responses of a set of known individuals in different areas with differing cumulative exposure within their range, with all measurements made at the nearly the same time and with the same instantaneous level of exposure (i.e., same individuals being examined in different areas within their home range – the different areas having different levels of exposure)*: This could only result from an ecological effect because variation in responses of individual animals depends on each area's exposure history, not the exposure history of the individual animals.

Table 2. Combinations of units of analysis and explanatory mechanisms that produce habituation- or sensitisation-type response curves, *i.e.*, curves depicting decreasing or increasing response with increased cumulative exposure.

Timeframe of Comparison	Unit of analysis	Explanatory Mechanism			
		Learning	Physiology	Selection	Ecology
Over time	1. Population mean	Y	Y	Y	Y
	2. Same individual(s)	Y	Y		Y
At one point in time	3. Separate populations with differing cumulative impacts	Y	Y	Y	Y
	4. Subsets of same population from areas with differing cumulative impacts			Y?	Y
	5. Same individual(s) but from areas with differing cumulative impacts				Y

These scenarios are summarised in Table 2. The converses also hold true. For instance, if animals do not change their behaviour as they enter different parts of their range that have different cumulative exposure, then an ecological mechanism can be ruled out as a cause of a habituation-type response of the mean population trajectory over time.

This analysis suggests ways in which the underlying mechanism for a habituation- or sensitisation-type response can be identified. Take, for example, a situation in which the population mean shows a habituation-type response when plotted over time (first scenario, above), but the trajectories of individual animals do not (converse of second scenario, above), then selection becomes the most plausible mechanism.

As another example, consider a case in which individuals exhibit a habituation-type response to a given stimulus over time, ruling out selection as a mechanism (second scenario, above). Additionally, if the response of each individual is similar in different areas that have different levels of cumulative exposure (converse of fifth scenario, above), then an ecological factor can also be ruled out, leaving learning and physiological damage as plausible mechanisms for the habituation-type response.

Using this method of analysis, responses caused by physiology and learning cannot be distinguished by behavioural investigation, as these columns are identical in 4.2. To discriminate between physiology and learning, psychological or physiological investigations would be needed, and/or examination of multiple response variables. For instance, a habituation-type response based on auditory, but not visual, response variables would point to physiological damage (hearing impairment) rather than learning as the causative mechanism. Thus, by focusing on the responses of individual animals, and comparing their behaviour in different areas, it is possible to eliminate confounding selection and ecological explanations, but a multifaceted approach may be needed to distinguish between physiological and learning as explanatory mechanisms.

PROCEED WITH CAUTION: BEHAVIOURAL HABITUATION CAN BE INFERRED ONLY FOR THE TYPE OF RESPONSE THAT HAS BEEN MONITORED

Practical and financial constraints not only reduce the number of points typically measured in impact assessment research, but also restrict such monitoring to observable, behavioural responses, rather than, for example, physiological responses that typically have no visible, external sign and are not as readily detectable as behaviour in free-ranging animals. Such an emphasis on one modality of response effectively limits the scope of conclusions that can be drawn from the investigation. Thus, even after other explanatory mechanisms have been ruled out and true behavioural habituation has been confirmed, findings must still be handled with caution because the conclusion is likely to be specific only to the response variable(s) that have been monitored.

Accordingly, the most effective course of action would be to complement behavioural assessment by monitoring an animals' physical condition and such physiological measures as heart rate, body temperature, and/or hormonal levels. The strength of this course of action is affirmed by studies in which both behavioural and physiological responses were monitored simultaneously. These have produced the disconcerting result that, although typically easier to document, behaviour, in and of itself, may not always be a sufficiently sensitive or timely indicator of the effects of disturbance (Beale and Monaghan 2004a,b). For example, several studies have shown that, at the same time that animals exhibited little or no behavioural sign of disturbance, physiological evidence of their distress could be detected (*e.g.*, Moen *et al.* 1982; Culik *et al.* 1990; Wilson *et al.* 1991; Nimon *et al.* 1995; Regel and Putz 1997; Ratz and Thompson 1999; Müllner *et al.* 2004). Thus, it is clear that animals

can respond in one modality but not another, and therefore, likely that animals may become habituated in one modality but not another.

Research on killer whales and human disturbance further highlights the complexities involved in interpreting wildlife responses and demonstrating behavioural habituation. Williams *et al.* (2001) documented a decline from the 1980s to the 1990s in the overt avoidance of vessels by resident killer whales (*Orcinus orca*). The data, however, were insufficient to discriminate among explanatory mechanisms. Plausible explanations include: the whales became habituated to boat traffic through individual experience (learning), or became less responsive through hearing impairment inflicted by vessel noise (physiology). Additionally, the result may be related to ecological change, such as salmon abundance, that may or may not be related to vessel activity (ecology). Or, the result may be a product of sampling biases, *e.g.*, whales having differing tolerance levels or experiencing vessel operators of differing abilities were sampled in the two time periods. Thus, despite long-term monitoring, the case for behavioural habituation to vessels by killer whales is equivocal.

The situation is further confounded by additional experimental evidence obtained in 1998 showing that killer whales at that time still responded with avoidance to vessels both in compliance or in violation of local whale watch guidelines (Williams *et al.* 2002a,b). One plausible explanation of the apparently contradictory findings is that animals can show signs of habituation to one aspect of human disturbance, while at the same time responding negatively to a different feature of the same activity. The overall waning in avoidance to vessels does not rule out the possibility of detrimental acoustic impacts of the same activity. For example, apparent behavioural habituation, expressed as a reduction in physical avoidance, would not necessarily mitigate effects of acoustic masking by boat noise on the whales' acoustic sensitivity and/or their detection of prey and conspecifics (*e.g.*, Bain and Dahlheim 1994; Erbe 2002; Foote *et al.* 2004). Thus, documented behavioural changes in one response variable over time do not, in and of themselves, confirm that other responses (*e.g.* physiological ones) or impacts (*e.g.* acoustic masking) are not occurring.

Clearly, if research findings are to be effective in forming management plans for killer whales, it is important to discriminate among competing mechanisms in order to explain the observed effect. Without rigorous analysis, an apparent waning in response would likely be interpreted to show that habituation had occurred, and the subsequent management plan might specify that no whale-watch guidelines or protected areas were needed (a conclusion that might also have been drawn from this study without access to the long-term datasets – Bejder et al., 2006a,b). Instead, a more informed synthesis of several studies, looking at a number of response variables, indicated that guidelines and boat exclusion zones can, and should, play a beneficial role in recovery plans for threatened killer whale populations (Baird 2001). In the killer whale example, changes in whale behaviour were noted on a scale of tens of years, but longitudinal replication of studies on known individuals would be required to determine the root cause of the behavioural change.

CONCLUSION

In the realm of scientific inquiry into effects of human activity on wildlife, managers and scientists alike tend to operate under the assumptions that: (1) it is relatively easy to demonstrate behavioural habituation of wildlife to anthropogenic stimuli, and (2) habituation-type responses imply that there is an absence of detrimental consequences for targeted animals. This paper endeavours to show that neither assumption is entirely correct, and that the misinterpretation of scientific findings resulting from reliance on these false premises can have detrimental consequences for wildlife. Thus, to classify wildlife response as habituation should not be done without considerable scrutiny, as this classification is likely to have serious management ramifications, even an easing or cessation of conservation efforts. Therefore, we urge conservation biologists, ethologists and wildlife managers to use care in assigning the label, habituation, without fulfilling the stringent requirements of carrying out sequential monitoring over time of the responses of individuals to a given stimulus. we further caution against extrapolating from habituation demonstrated for specific response variable(s) to variables or modalities that have not been assessed.

Instead, in many instances, a designation of varying levels of tolerance, which carries no a priori stigma, is more appropriate and correct than using the labels, habituation or sensitisation. We have shown that demonstrating, at one point in time, that animals in one group or area are more or less tolerant than others to anthropogenic stimuli provides one piece of evidence to suggest that behavioural habituation or sensitisation has occurred, but does not rule out other plausible explanations. Similar habituation- and sensitisation-type response curves can occur through other mechanisms, such as physiology, selection and ecology, none of which are likely to signify positive outcomes for targeted animals.

In the present paper, a methodological framework for distinguishing among explanatory mechanisms for given habituation- or sensitisation-type responses is provided. This method will help to clarify appropriate designation of behavioural habituation and sensitisation, and conversely, to prevent inappropriate designation thereof. This empirical technique is offered in the hope that it will enhance conservation attempts by promoting sound scientific evidence as the basis for informed management policies.

REFERENCES

Albert, D.M. & Bowyer, R.T. (1991) Factors related to grizzly bear-human interactions in Denali National Park. Wildlife Society Bulletin, 19, 339-349.

Altmann, J. & Muruthi, P. (1988) Differences in daily life between semiprovisioned and wild-feeding baboons. American Journal of Primatology, 15, 213-221.

Altmann, J., Schoeller, D., Altmann, S.A., Muruthi, P., & Sapolsky, R.M. (1993) Body size and fatness of free-living baboons reflect food availability and activity levels. American Journal of Primatology, 30, 149-161.

Bain, D.E. & Dahlheim, M.E. (1994). Effects of masking noise on detection thresholds of killer whales. In Marine Mammals and the Exxon Valdez (ed R.R. Loughlin), pp. 243-256. Academic Press, San Diego.

Baird, R.W. (2001) Status of Killer Whales, Orcinus orca, in Canada. Canadian Field-Naturalist, 115, 676-701.

Bejder, L. 2005. Linking short and long term effects of nature-based tourism on cetaceans. Ph.D. thesis, Dalhousie University.

Bejder, L. & Samuels, A. (2003). Evaluating impacts of nature-based tourism on cetaceans. In Marine Mammals: Fisheries, Tourism and Management Issues (eds N. Gales, M. Hindell & R. Kirkwood), pp. 229-256. CSIRO Publishing.

Bejder, L., Samuels, A., Whitehead, H., Gales, N., Mann, J., Connor, R., Heithaus, M., Watson-Capps, J., Flaherty, C and Kruetzen, M. 2006a. Decline in relative abundance of bottlenose dolphins (Tursiops sp) exposed to long-term disturbance. Conservation Biology 20 (6): 1791–1798

Bejder, L., Samuels, A., Whitehead, H. and Gales, N. 2006b. Interpreting short-term behavioural responses within a longitudinal perspective. Animal Behaviour. 72, 1149-1158

Burger, J. & Gochfeld, M. (1999) Role of human disturbance in response behavior of Laysan albatrosses (*Diomedea immutabilis*). Bird Behavior, 13, 23-30.

Clout, M.N., Elliott, G.P., & Robertson, B.C. (2002) Effects of supplementary feeding on the offspring sex ratio of kakapo: a dilemma for the conservation of a polygynous parrot. Biological Conservation, 107, 13-18.

Culik, B., Adelung, D., & Woakes, A.J. (1990). The effect of disturbance on the heart rate and behaviour of Adelie Penguins (*Pygoscelis adeliae*) during the breeding season. In Antarctic ecosystems: Ecological change and conservation (eds K.R. Kerry & G. Hempel), pp. 177-182. Springer-Verlag, Berlin.

Culik, B.M. & Wilson, R.P. (1995) Penguins disturbed by tourists. Nature, 376, 301-302.

de la Torre, S., Snowdon, C.T., & Bejarano, M. (2000) Effects of human activities on wild pygmy marmosets in Ecuadorian Amazonia. Biological Conservation, 94, 153-163.

Doenier, P.B., DelGiudice, G.D., & Riggs, M.R. (1997) Effects of winter supplemental feeding on browse consumption by white-tailed deer. Wildlife Society Bulletin, 25, 235-243.

Erbe, C. (2002) Underwater noise of whale-watching boats and potential effects on killer whales (Orcinus orca), based on an acoustic impact model. Marine Mammal Science, 18, 394-418.

Foote, A.D., Osborne, R.W., & Hoelzel, A.R. (2004) Whale-call response to masking boat noise. Nature, 428, 910.

Fowler, G.S. (1999) Behavioral and hormonal responses of Magellanic penguins (*Spheniscus magellanicus*) to tourism and nest site visitation. Biological Conservation, 90, 143-149.

Gales, N. (1999) An overview of the management of commercial swim-with-dolphin programs in Australia. In Abstracts: Wild Dolphin Swim Program Workshop (eds K.M. Dudzinski, T.G. Frohoff & T.R. Spradlin), 28 November, 1999. Maui, Hawaii.

Galicia, E. & Baldassarre, G.A. (1997) Effects of motorized tourboats on the behavior of nonbreeding American flamingos in Yucatan, Mexico. Conservation Biology, 11, 1159-1165.

Gander, H. & Ingold, P. (1997) Reactions of male alpine chamois (*Rupicapra r. rupicapra*) to hikers, joggers and mountainbikers. Biological Conservation, 79, 107-109.

Giese, M. (1996) Effects of human activity on Adélie penguin *Pygoscelis adeliae* breeding success. Biological Conservation, 75, 157-164.

Gill, J.A., Norris, K., & Sutherland, W.J. (2001) Why behavioural responses may not reflect the population consequences of human disturbance. Biological Conservation, 97, 265-268.

Griffiths, M. & van Schaik, C.P. (1993) The impact of human traffic on the abundance and activity periods of Sumatran rain forest wildlife. Conservation Biology, 7, 623-626.

Gutzwiller, K.J., Marcum, H.A., Harvey, H.B., Roth, J.D., & Anderson, S.H. (1998) Bird tolerance to human intrusion in Wyoming montane forests. The Condor, 100, 519-527.

Johns, B.G. (1996) Responses of chimpanzees to habituation and tourism in the Kibale Forest, Uganda. Biological Conservation, 78, 257-262.

Knight, R.L. & Temple, S.A. (1995). Origin of wildlife responses to recreationists. In Wildlife and recreationists: coexistence through management and research (eds R.L. Knight & K.J. Gutzwiller), pp. 81-91. Island Press, Washington D.C.

Lacy, K.E. & Martins, E.P. (2003) The effect of anthropogenic habitat usage on the social behaviour of a vulnerable species, *Cyclura nubila*. Animal Conservation, 6, 3-9.

McLellan, B.N. & Shackleton, D.M. (1989) Immediate reactions of grizzly bears to human activities. Wildlife Society Bulletin, 17, 269-274.

Moen, A.N., Whittemore, S., & Buxton, B. (1982) Effects of disturbance by snowmobiles on heart rate of captive white-tailed deer. New York Fish and Game Journal, 29, 177-183.

Müllner, A., Linsenmair, K.E., & Wilkelski, M. (2004) Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). Biological Conservation, 118, 549-558.

Nellemann, C., Jordhoy, P., Stoen, O., & Strand, O. (2000) Cumulative impacts of tourist resorts on wild reindeer (*Rangifer tarandus tarandus*) during winter. Arctic, 53, 9-17.

Nimon, A.J., Schroter, R.C., & Stonehouse, B. (1995) Heart rate of disturbed penguins. Nature, 374, 415.

Nisbet, I.C.T. (2000) Disturbance, habituation, and management of waterbird colonies. Waterbirds, 23, 312-332.

Nizeyi, J.B., Mwebe, R., Nanteza, A., Cranfield, M.R., Kalema, G.R.N.N., & Graczyk, T.K. (1999) Cryptosporidium sp. and Giardia sp. infections in mountain gorillas (Gorilla gorilla beringei) of the Bwindi Impenetrable National Park, Uganda. Journal of Parasitology, 85, 1084-1088.

Parent, C. & Weatherhead, P.J. (2000) Behavioral and life history responses of eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*) to human disturbance. Oecologia, 125, 170-178.

Phillips-Conroy, J.E., Hildebolt, C.F., Altmann, J., Jolly, C.J., & Muruthi, P. (1993) Periodontal health in free-ranging baboons of Ethiopia and Kenya. American Journal of Physical Anthropology, 90, 359-371.

Ratz, H. & Thompson, C. (1999) Who is watching whom? Checks for impacts of tourists on Yellow-eyed Penguins, *Megadyptes antipodes*. Marine Ornithology, 27, 205-210.

Regel, J. & Putz, K. (1997) Effect of human disturbance on body temperature and energy expenditure in penguins. Polar Biology, 18, 246-253.

Richardson, W.J., Greene, J.C.R., Malme, C.I., & Thomson, D.H., eds. (1995) Marine mammals and noise, pp 576. Academic Press, San Diego.

Safina, C. & Burger, J. (1983) Effects of human disturbance on reproductive success in the black skimmer. Condor, 85, 164-171.

Samuels, A., Bejder, L., Chicoski, B., Engleby, L., & Mehta, A. (2003). An annotated bibliography pertaining to human interaction with terrestrial wildlife. Report to the Marine Mammal Commission #T74463123, Bethesda, 20814 Maryland, USA.

Spradlin, T.R., Terbush, A.D., & Smullen, W.S. (1998) NMFS update on human/dolphin interactions in the wild. Soundings: Magazine of the International Marine Animal Trainers Association, 23, 25-27.

Stalmaster, M.V. & Newman, J.R. (1978) Behavioral responses of wintering bald eagles to human activity. Journal of Wildlife Management, 42, 506-513.

Stone, G.S. & Yoshinaga, A. (2000) Hector's dolphin *Cephalorhynchus hectori* calf mortalities may indicate new risks from boat traffic and habituation. Pacific Conservation Biology, 6, 162-170.

Thorpe, W.H. (1963) Learning and instinct in animals, 2 edn. Methuen and Co Ltd, London.

Tutin, C.E.G. & Fernandez, M. (1991). Responses of wild chimpanzees and gorillas to the arrival of primatologists: Behaviour observed during habituation. In *Primate Responses to Environmental Change* (ed H.O. Box), pp. Pages 187-197. Chapman and Hall, London.

Williams, R., Bain, D.E., Ford, J.K.B., & Trites, A.W. (2002a) Behavioral responses of male killer whales to a "leapfrogging" vessel. Journal of Cetacean Reserach and Management, 4, 305-310.

Williams, R., Trites, A., & Bain, D.E. (2001). Are killer whales habituating to boat traffic? In. Report to the Scientific Committee of the International Whaling Commission. SC/53/WW3.

Williams, R.M., Trites, A.W., & Bain, D.E. (2002b) Behavioural responses of killer whales (*Orcinus orca)* to whale-watching boats: opportunistic observations and experimental approaches. Journal of Zoology (London), 256, 255-270.

Wilson, R.P., Culik, B., Danfeld, R., & Adelung, D. (1991) People in Antarctica - How much do Adélie penguins *Pygoscelis adeliae* care? Polar Biology, 11, 363-370.

Woodford, M.H., Butynski, T.M., & Karesh, W.B. (2002) Habituating the great ages: The disease risks. Oryx, 36, 153-160.