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The Behavioral Ecology of Disturbance Responses

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Measuring the impacts of anthropogenic activities on wildlife is crucial for ensuring effective management. Animal behavior is often considered a sensitive index of impact, but its use requires detailed understanding of the context dependent decisions animals make. In this manuscript I identify a number of areas where insights from the field of animal behavior are relevant to studies of human disturbance and activity. In particular, I differentiate between disturbance effects and disturbance impacts and show how context-dependent decision-making often makes animal behavior an unreliable index of impact. I show the areas where animal behavior can be useful in quantifying minimum disturbance impact when additional information is available, and identify a number of areas where further research may help improve the management of anthropogenic activities within wildlife areas.

The effective management of human activities in wildlife areas is an important conservation issue, as the footprint of human influence continues to expand (Green, Cornell, Scharlemann & Balmford, 2005) and incidental impacts of human activities (e.g. noise and disturbance) spread into more areas (Keirle, 2002; Hatch & Wright, this issue; Weilgart, this issue). Such expanding anthropogenic activity is widely perceived to lead to negative consequences for the wildlife beyond habitat loss alone (Frid, 2003; Higham, 1998; Stevens & Boness, 2003; Taylor & Knight, 2003; de la Torre, Snowdon & Bejarano, 2000; Wauters, Somers, & Dhondt, 1997). Understanding how animals respond to noise and more generally, anthropogenic activities is fundamental to resolving potential conflicts between humans and animals (Hatch & Wright, this issue; Weilgart, this issue; Wright et al., this issue, a). There are numerous ways in which it is possible to study animal responses, but changes in an animal's behavior are often the most obvious consequences of anthropogenic activities so it is not surprising that many authors use behavioral observations to understand impacts (Fortin & Andruskiew, 2003; Nettleship, 1972). However, interpretation of the results of animal behavior studies is not always straightforward and while the study of behavior within a conservation context is to be encouraged (Sutherland, 1998) insights from the wider field of animal behavior will have direct relevance to understanding. In this paper I review a number of areas where understanding animal behavior offers insights of management importance in understanding how animals may respond to human activities. This is not an attempt to fully review the impacts of anthropogenic activities on animal behavior, but rather to highlight a few important insights that have sometimes been overlooked in conservation studies (Buchholz, 2007; Sutherland, 1998).

Animal behavior is an eclectic field with a scope that ranges from purely behavioral observation (the assessment of the amount of time an animal

spends doing various activities, for example), through questions relating to resource allocation (how many offspring to have in a litter, how much testosterone to place in an egg, etc.) to more psychological questions of how animals perceive their environment (when in a foraging patch, how long do animals remember recent weather events, etc.) (Alcock, 2003; Buchholz, 2007). Underlying the field is an attempt to understand how animals make decisions and what the consequences of these decisions are. In this paper I will attempt to show how understanding from a number of different areas of animal behavior has implications for understanding how noise and other anthropogenic disturbance is likely to impact animal conservation and welfare, starting with the simplest observations of animal behavior.

Behavioral responses to threatening stimuli

Perhaps the most obvious of the responses an animal makes to a threatening stimulus are simple behavioral responses. It is therefore unsurprising that measuring behavioral responses such the distance at which an animal flees or first responds to human presence have therefore been widely used to address a number of related questions about the impacts of disturbance. Primary among these is the simple question: does human disturbance affect animals (Blumstein, Anthony, Harcourt, & Ross, 2003; Klein, Humphrey, & Percival, 1995; Tuite, Hanson, & Owen, 1984)? Behavioral measures have also been used when human disturbance effects are assumed and the question is more to identify which populations or species are most susceptible to disturbance (Blumstein, Fernández-Juricic, Zollner, & Garity, 2005; Tarlow & Blumstein, 2007). However, behavioral responses involve the animal making a number of different decisions, so a naïve exploration of the simple behavioral response may be inadequate.

For example, on first hearing a noise, a feeding animal may stop foraging and look around for the source. If the noise or its source is threatening enough, the animal's stress response pathways may be activated at this point, the short- and long-term physiological consequences of which are highlighted elsewhere (e.g. Deak, this issue; Romero & Butler, this issue). What an animal decides to do about this threat, however, is not fixed: it may choose to simply keep a wary eye on the threat and resume feeding, or it may flee the area to feed in a safer location. Let us assume the noise is caused by a one-off, short-term stimulus and the animal chooses to abandon the area temporarily but will return when the threat has passed. This is a short-term response to a short-term stimulus and the costs of this response are likely to fall well within the norms the animal is used to (i.e. homeostasis is maintained: Romero, 2004) so this would be an appropriate decision for the animal to make. However, if the stimulus is repeated frequently, the cost of repeated short-term responses (lost foraging time, costs of flight, etc.) may accrue meaning that an animal in the frequently disturbed environment may decide that staying put but maintaining a constant readiness to leave is less costly than fleeing. This may result in increased energetic expenditure and chronic stress with all the physiological consequences associated (Deak, this issue; Romero & Butler, this issue), but is still an appropriate decision if the costs involved in repeatedly leaving the feeding area are greater than the physiological consequences of chronic stress. If we are to accurately interpret behavioral responses to a disturbance event,

therefore, it is crucial that we understand the *context* within which an animal makes decisions.

Before continuing further, it is important to note that the *effects* of a disturbance event are not necessarily the same as the *impacts* of that disturbance event. E.G., in the first example above the effect of the one-off disturbance was to make the animal temporarily leave a feeding area, an effect that was not shown by the animal in the second example. Leaving a foraging area might be assumed to be a negative impact (as noted by Gill, Norris, & Sutherland, 2001a), but the impact is likely to be largely negligible compared with the impact on the animal subjected to repeated stimuli in the second example that showed no behavioral effect but may suffer physiological consequences. If we are interested in conservation and welfare, we are clearly much more interested in impacts than simple effects (Gill et al., 2001a; Gill, Sutherland, & Watkins, 1996; Nisbet, 2000). This crucial difference is often ignored when researchers equate effect with impact: certainly human disturbance affects animal behavior, but this does not necessarily mean human disturbance has a (negative) impact on animal conservation or welfare. The previous example illustrates one case where the behavioral measure (whether or not an animal left the area) is clearly not an appropriate index of the impact of the disturbing stimuli. More generally, Gill et al. (2001a) suggested that a lack of behavioral response may not imply a lack of fitness consequence but may instead reflect a lack of choice and Beale & Monaghan (2004a) provided an empirical test showing that such theoretical arguments translate directly to the field and concluded that it is wrong to assume that the most responsive animals are those that are most vulnerable to disturbance.

It seems that context-dependent decision-making behavior therefore limits the practical utility of recording behavioral responses as an index of the impact of stressful stimuli. I therefore consider that ignoring context and using simple behavioral measures as a direct mechanism for assessing either whether animals will suffer impacts of disturbance, or for identifying which populations or species may be most vulnerable to disturbance is seriously flawed. This, however, does not necessarily mean that behavioral measurements cannot be useful for researchers interested in impacts of human disturbance provided the context under which the behavioral decisions are made is understood and no direct link between behavioral effect and disturbance impact is assumed. For example, instead of assuming effect and impact are identical, if behavioral responses are coupled with further information on the costs of the changed behavior itself a *minimum* estimate of the cost of responding can be estimated. In the earlier example an estimate of the energetic costs of lost foraging time and energy spent moving away can be estimated and put in the context of daily energy expenditure. However, for the animal that showed no behavioral response the estimated cost would be zero but as we have already seen this animal is actually much more likely to suffer stress-related impacts than the first animal. Thus estimates of cost based on behavior alone are likely to be underestimates and if the estimated cost is low it does not mean that the impact of the stimulus is necessarily low. It is also clear that this method does not allow comparison between populations or species. If the minimum cost is put in an appropriate context where its importance can be measured against other energetic costs and it can be shown that animals are not compensating for such increased energetic expenditure (e.g. by feeding at night: Lane & Hassall,

1996), the minimum potential for negative impacts can be assessed and may be substantial (Williams, Lusseau, & Hammond, 2006).

Similarly, if the context in which decisions are made is not changed, behavioral measures can be used directly to measure the relative degree to which stressors affect individuals. However, maintaining similarity of context is challenging and variations must be strictly controlled experimentally and/or statistically. If, for example, the degree of impact caused by two different types of boat engine is of interest it may be possible to approach the same individual animals in the same location at the same time of day over a relatively short time span with the two different engines and record the behavioral responses. If one engine type consistently results in greater behavioral responses it is very likely that this engine type is perceived to be a stronger stressor than the alternative. It is crucial, however, that the context is maintained as constant as possible when assessing the impact of the two potential stressors: the individuals must be the same, in the same size group, engaged in the same activity when first approached and in the same location. If any of these variables has changed, the context in which the animals find themselves will also have changed and the results will be highly suspect unless tightly controlled statistically. Statistical control may be appropriate, for example, if the number of individuals within a group is variable and group-size alters behavioral response in a predictable manner: in such cases inclusion of a group-size variable in statistical analysis will go some way to controlling for this aspect of context.

Impacts of avoidance behavior

Perhaps the next stage of assessing the impacts of behavioral responses to threatening stimuli involves asking questions about the redistribution of animals (i.e. avoidance) that is widely observed in areas where frequent disturbances are likely (Tarlow & Blumstein, 2007; Weilgart, this issue). What is the cost to the animals of this avoidance? Does it limit population in some way?

Although not yet widely applied, resource-use based models have been used as one way of assessing the population consequences of avoidance behavior (Fernández-Juricic, Sallent, Sanz, & Rodríguez-Prieto,, 2003; Gill et al., 1996; Gill, Norris, & Sutherland, 2001b; Percival, Sutherland, & Evans, 1998). Such models develop a behavior-based model to assess the impact of human disturbance, but do not rely on directly measuring the behavioral responses animals show to human presence. Instead, they assume that animals show behavioral responses to humans but suggest that if any significant fitness costs are associated with such responses, a critical, limiting resource will be under-used. Therefore, patterns of resource use are determined instead of measuring behavior directly. If resources are under-utilized in areas where disturbance is high, human disturbance is regarded as having an impact of conservation concern. For example, Gill et al. (2001b) report a study of the effect of disturbance on the Black-tailed Godwit. They showed that, despite this species being perceived as sensitive to human disturbance, no under-use of food resources was detected, presumably either because the birds fed in the most disturbed areas at times when there were few disturbances (e.g. early mornings), or because the birds chose to use the disturbed areas once resources

were used up in undisturbed areas. They therefore conclude that although these animals appear to avoid human presence, this does not reduce the population size supported by the estuaries they studied. Similar issues have been studied using simulation models: Stillman et al. (2000) used an individual based model to show that avoidance behavior may lead to population decline and Blumstein et al. (2005) used a simple model to show that resource use may fall in disturbed areas but neither studies include context-based decision making.

Studies of resource use have so far focused on utilization of food supplies (Fernández-Juricic, Sallent, Sanz, & Rodríguez-Prieto, 2003; Gill et al., 1996; Gill et al., 2001b) and wintering habitat (Percival et al., 1998), but could also be used in relation to other resources, including breeding territories. However, such studies rely heavily on the correct identification of critical resources. If the effect of disturbance was measured on the use of the wrong resource, it would be possible to incorrectly conclude that human disturbance was not an important factor. It is possible, for example, that the utilization of food resources is unaffected by human disturbance, but that resting sites are negatively affected and the population declines because there are insufficient disturbance free areas to rest. Alternatively, it might be possible to wrongly identify human disturbance as limiting populations for similar reasons. For example, if some other external factor holds an animal's population artificially low (e.g. hunting pressure on migration) and these animals show avoidance of humans, they may not make full use of resources in disturbed areas: not all available resources are required to maintain the population so the animals never need to use the resources in more disturbed areas. However, it would be wrong to assume that this pattern of resource use provided evidence that disturbance was implicated in the low population of this species. If the population were to increase (e.g. because hunting pressure is reduced), animals might eventually decide to forage in the more disturbed areas because these previously unexploited resources are now required to maintain the increased population.

On the other hand, if animals do avoid areas with a high frequency of anthropogenic activity and under-use a particular resource or habitat, negative impacts are still not necessary consequences. For example, Mallord, Dolman, Brown, & Sutherland (2007) showed that woodlarks *Lullula arborea* avoided heavily visited habitat. This resulted in fewer individuals breeding in visited areas, but the few birds that did so were freed from competition and enjoyed increased breeding success, with the total number of fledglings from disturbed heaths approximately equal to the number of fledglings from undisturbed heaths where birds were breeding in higher densities. The overall population is therefore determined by a delicate balance between the improvement in breeding success due to density dependent effects and the reduction in habitat availability due to (inappropriate) disturbance avoidance. Whether this balance leads to a stable population or one in decline can only be determined by assessing disturbance impacts across the entire area of suitable habitat and estimating the number of animals that this could support in the absence of human disturbance. This, and especially the effect that might occur when disturbance is seasonal and otherwise perfect habitat becomes poor after animals have settled in the area (e.g. at holiday times) can be seen as forms of an ecological trap (i.e. anthropogenic activities have altered habitat quality

such that the cues an animal uses to select a habitat are no longer appropriate: (Kokko & Sutherland, 2001).

Other measures of impacts of threatening stimuli

Other methods for determining the impacts of anthropogenic stressors have recently been reviewed elsewhere and I shall not attempt this here (Tarlow & Blumstein, 2007). However, methods involving the measurement of physiological and metabolic parameters associated with stress responses are relevant to a discussion of animal behavior because they help explain how impacts may occur even in the absence of behavioral responses.

Some penguins are noted for their lack of behavioral responses to visitors, especially in areas where visitors are frequent (e.g. Nimon, Schroter, & Stonehouse, 1995; Fowler, 1999). This lack of response led to the suggestion that these birds are "habituated", a claim also made for other species (Nisbet, 2000) but, if a real phenomenon, it is more likely to refer to learned non-response as physiological acclimation seems unlikely (Wright et al., this issue). For example, Fowler (1999) studied the hormonal and behavioral responses of penguins in areas of differing disturbance. Fowler showed no difference in physiological responses between birds in medium and low disturbance plots, but found a significantly decreased hormonal response in the high disturbance areas, indicative of acclimation. However, as variation was large in the control plots but small in the disturbed plots the results suggest that, rather than birds acclimating, birds that showed high responses left the area. This is further suggested by the lower nesting density in the high disturbance plot (Fowler, 1999). Fowler also showed that average strength of the behavioral responses in each plot decreased with visitor levels, but did not examine the relationship between an individual's hormonal and behavioral responses.

Additional work on the heart-rate of kittiwakes *Rissa tridactyla* and European shag *Phalacrocorax aristotelis* with a long history of exposure to human visitors also highlighted extreme individual variation in heart-rate responses to disturbance (Beale, 2004). These studies found that even when negligible changes in behavior were observed in response to a potentially threatening stimulus, heart rate of those birds that do respond could increase by 50%. This clearly indicates that these birds are likely to be experiencing physiological stress responses which must be considered chronic in areas with frequent disturbance events. However, a raised heart-rate may itself have conservation consequences, as maintaining raised heart-rates requires increased metabolic costs which may, in turn, affect demographic parameters. I estimated an increase of 7.5 – 10% in daily energy expenditure for some individual Kittiwakes in Scotland (Beale, 2004), an increase likely to result in eventual abandonment of nesting attempts once energy reserves drop below a critical level: this is indeed the proposed mechanism linking anthropogenic activity to nesting failure in this species (Beale & Monaghan, 2004b). It is also worth noting that individualistic heart-rate responses to human disturbance again indicate the importance of understanding animal behavior, where some individuals choose to respond, and others not. Only by understanding that there are susceptible and unsusceptible individuals can the observed change in breeding success be comprehended, not by simply considering the mean response of the population.

It is, of course, important to question whether even declines in breeding success reflect an impact of genuine conservation concern. Indeed, breeding success is not necessarily a good surrogate of fitness thanks in part to density dependent effects (Frederiksen, Lebreton, & Bregnballe, 2001; Olijnyk & Brown, 1999). Moreover, breeding success is often far less important in determining populations of relatively long-lived animals than winter mortality (Russell, 1999; Weimerskirsch, Brothers, & Jouventin, 1996), a distinction likely to hold for many long-lived species. A decrease in breeding success of 9%, as observed for Kittiwakes in Scotland is, in fact, unlikely to have a major impact on the population as a whole.

Conclusions

Understanding that animals are individuals that make context-dependent decisions about how to respond to their environment results is an important insight with practical application to understanding how animals respond to anthropogenic stimuli. It is also crucial to differentiate between disturbance effect and disturbance impact. I have shown how this context-dependent decision making means the use of simple behavioral indices as a direct measure of disturbance impact is unsound, and have pointed out areas where incorporating further information can make behavior measures potentially useful. I have shown how the decisions animals make about where to feed and breed can be influenced by human activities and the consequences or otherwise this might have for the population. I have shown that in birds at least, it is clear that disturbance from anthropogenic activity can reduce breeding success even in the absence of behavioral effects. I have also shown how even physiological responses to anthropogenic activity can be individualistic, indicating that a more profound understanding of these responses also required understanding decision making behavior. Throughout, I have attempted to stress the distinction between effects and impacts, a distinction that is crucially important when making management decisions. Research on the effects of human disturbance is slowly taking account of the need to understand behavior (Fernández-Juricic et al., 2003; Gill et al., 2001b; Stillman et al., 2000), though papers continue to be published that overlook context-dependant decision-making behavior (Frid, 2003; Fortin & Andreskiew, 2003; Fernández-Juricic, Vaca, & Schroeder, 2004; Blumstein et al., 2005).

Future work on disturbance impacts is likely to be valuable and the impact of recreation on biodiversity has been identified as one of the 100 ecological questions of high policy relevance in the UK (Sutherland et al., 2006). Future efforts must distinguish between effect and impact and must adequately incorporate context-dependent decision making behavior. Although behavioral measures are inappropriate for assessing the comparative impact of disturbance on multiple species (even at the same location different species will experience the environment differently and will find themselves in different contexts), there is clearly a need to identify methods to protect multiple species (Blumstein et al., 2005). It is likely that further advances may be made through the use of individual based models that allow individuals to make truly context-dependent decisions. Further studies that identify disturbance effects at multiple levels – behavioral, physiological and metabolic

– are likely to improve understanding of disturbance impacts. Finally, I believe that more study of the behavior of people in wildlife areas is likely to offer new insights into how to manage conflicts between humans and wildlife. This aspect of human disturbance research is currently largely neglected, but must be considered a crucial part of the equation.

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