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Behavioural responses to human disturbance: a matter of choice?

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The strength of an animal's behavioural response to human presence has often been used as an index of an animal's susceptibility to disturbance. However, if behavioural responsiveness is positively related to the animal's condition, this may be an inappropriate index, as individuals showing little or no response may in fact be those with most to lose from changing their behaviour. We tested the link between individual state and responsiveness by manipulating condition via the provision of supplementary food for turnstones, *Arenaria interpres*, on rocky shores. Birds at one site were fed 450 g of mealworms at low tide every day for 3 days while birds at another site acted as a control. On the fourth day, using a standardized disturbance protocol, we recorded flush distances, flight lengths and the amount of time between predator scans for birds in both flocks. After a break of 3 days, the treatments were then swapped between sites and the procedure repeated for a total of six trials. Birds whose condition had been enhanced showed greater responsiveness to standardized human disturbance, flying away at greater distances from the observer, scanning more frequently for predators and flying further when flushed. These findings suggest that our current management of the impact of human disturbance may be based on inaccurate assessments of vulnerability, and we discuss the implications of this for refuge provision.

Behavioural change is often considered the most sensitive measure of the effects of human disturbance on animals, and behavioural responses have frequently been used as an index of disturbance effects (reviewed in Carney & Sydeman 1999). While the use of behavioural indexes in a conservation context is generally welcomed (Sutherland 1996), using behavioural measures as a crude index of disturbance effects has a number of potential limitations. In particular, there are fundamental questions concerning the decisions made by animals responding to humans. The 'state' of an animal represents its position in relation to a number of internal and external variables, thus encompassing its internal condition and environmental circumstances and perceptions of these (McNamara & Houston 1996). If animals make state-dependent decisions whether or not to respond to human presence, then the use of behavioural responsiveness as an index of the fitness consequences of a disturbance event is potentially flawed, since the nature of the response may vary between individuals.

Gill et al. (2001) described how the priorities that animals assign to different activities can affect the behavioural response they show to disturbance. They argued that when animals have many options open to them (as they do when they are well fed and in good condition, or when there are good feeding areas close by), they may be more likely to change their behaviour than when they are more constrained by current requirements. When faced with a disturbance at a good feeding area for example, individuals in good condition may be more capable of bearing the costs associated with suspending feeding or moving to other areas than individuals in poorer condition, for whom continuing feeding is a high priority. Individuals in good condition will therefore show a more marked behavioural response, whereas individuals in poorer condition may have no option but to continue feeding for as long as possible. Similarly, animals feeding in particularly rich habitats may be more able to afford to interrupt feeding during disturbance than those in poor feeding areas where individuals must devote all their available time to feeding. Thus, variation in individual state, both in relation to individual condition and perception of habitat quality, will influence behavioural

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responsiveness to disturbance; individuals appearing least responsive may be those with most at stake. If this is the case, then current measures of sensitivity to disturbance are likely to be inaccurate and, consequently, the management procedures applied may be inappropriate.

We examined experimentally the link between behavioural responsiveness to disturbance and individual state in the turnstone, *Arenaria interpres*. On the southeast coast of Scotland, U.K., the winter population of turnstones is in decline (Dott 1997) and disturbance on feeding areas may be a contributory factor. As turnstones feed on a wide range of prey items (Gill 1986), they are a useful species for such experiments. In winter they show a clear preference for rocky shores and, where rocky outcrops interrupt sandy bays, turnstones flushed from one site will generally move to another area on the same outcrop (Metcalfe 1989). Birds use the same roost throughout the winter period, and will forage in predictable nearby locations. Colour marking has shown that almost all birds roost within 3 km of feeding sites (Metcalfe & Furness 1985; Pearce-Higgins 2001). We manipulated individual state (encompassing both body condition and perceptions of habitat quality) in foraging turnstones by providing supplementary food and examined the response to a standardized human disturbance. If Gill et al. are correct then, when approached, birds in better condition, feeding in the enhanced environments (and therefore with more options available to them), should respond most.

METHODS

We studied turnstones at two sites on rocky areas of the East Lothian coast of Scotland. The sites were 6 km apart, with sandy bays at least 1 km long on both sides of each site. Turnstones were present at these sites at both high and low tide. Site separation and presence of both roosting and foraging birds at both sites made it extremely unlikely that there was any significant turnover or exchange of birds between the sites during the experimental period (Metcalfe & Furness 1985; Pearce-Higgins 2001).

We used supplementary feeding to manipulate the condition of birds and the environment experienced by them in the experimental site. To examine the effectiveness of the provision of food in doing this, we first measured the effect of provisioning with mealworms on pecking rates. Six 10 × 10 m plots were defined low down on an extensive area of rocks exposed at low tide at a third site in East Lothian, separated from the main sites by at least 15 km. These plots were randomly assigned to three treatment and three control areas. Mealworms weighing a mean ± SE of 0.0935 ± 0.0097 g and containing ca. 63% water, 13% fat, 19% protein and 2% carbohydrates by weight were bought from a specialist live bird food supplier (Wiggly Wigglers Ltd., Lower Blakemore, Herefordshire, U.K.) with overnight delivery from source. Once delivered, mealworms were fed on bran to maintain their condition and all were used in experiments within 48 h. For 3 days we scattered 450 g of mealworms per day in the treatment areas at similar densities to those used in the main experiments described below. On each day, after waiting 15 min for the birds to return, we recorded turnstone feeding rates for 24 birds in the plots from a distance of ca. 50 m, noting the frequency with which individuals pecked at prey items (calculating an average number of pecks/s). Observations continued for 2 h, until the rising tide covered the plots. Throughout this period, observations were alternated between birds in treatment and control plots to eliminate systematic temporal bias. By systematically observing birds from one side of the flock to the other, we tried to ensure that each bird was observed only once to avoid pseudoreplication. We observed each focal bird foraging until hidden from sight and measured the duration of the focal period. Only birds observed for over 1 min were used for analysis, with each bird being treated as an individual datapoint. Each instance of pecking was recorded throughout the observation period, and the frequency (pecks/s) was calculated for each bird. We recorded the identity of every prey item over 2 mm and the frequency with which these were eaten during the observation period. The frequency of pecking was compared between plots to examine the effect of the provision of supplementary food on intake rates. We also recorded the frequency with which other birds fed on the mealworms. To determine further what prey was being taken naturally we visited sites within roosts used only by turnstones after high tide and examined 20 faecal samples for prey remains.

In each round of the main experiments, the two sites were randomly assigned to either experimental or control treatment. For 3 consecutive days we visited experimental sites at low tide, located the foraging turnstones and scattered around 450 g of mealworms on the nearby rocks, such that both density and total mass were the same as in the preliminary trials. As in the preliminary trials, supplemented areas were covered by the rising tide after approximately 2 h. During the same low tide we visited the control site and disturbed the birds there by locating and approaching the flocks in the same way as was done when spreading mealworms. On the fourth day no food was given, and on the rising tide a standard disturbance stimulus was used, consisting of one observer walking along the shore to the main flock of foraging birds. Experimental disturbance and response measurement were carried out sequentially at the two sites, the order of testing being determined at random.

We recorded three behavioural measures of disturbance typically used in other studies (e.g. Burger & Gochfeld 1983; Rodgers & Smith 1995; Fowler 1999). We first noted the distance from the observer at which birds flew off (flush distance, e.g. Lord et al. 2001) and the distance of the flight undertaken (e.g. Madsen 1998a). Flush distance was determined after the birds had flown by pacing from the point that the observer had reached when the birds flew to the location where the nearest flushed bird had been. Flight distance was determined by pacing from this point to the site where the flock first landed, once the birds moved away from the area of their own accord. Each datapoint was therefore the value for that site for the flock as a whole. For each bird present we then measured the length of two interscan intervals (the length of time the bird spends with its head down feeding between scans for predators e.g. Bélanger & Bédard 1989), and calculated the average for each bird. As with the feeding rate observations, the vigilance observations were made by studying birds systematically from one side of the flock to the other to ensure each bird was observed only once. We also recorded the number of birds present, as this may affect the behavioural measures taken (Metcalfe 1989; Burger & Gochfeld 1991).

After a break of 3 or 4 days during which no food was provided, we switched treatments so the control site became the experimental site and vice versa. A complete round of experiments consisted of both sites being used for both treatments. After another break of 3 or 4 days, the cycle was repeated with treatment sequence assigned at random. Three treatment rounds were carried out in February and March 2002 resulting in six trials at each site, three being controls and three being experimental. While weather conditions on test days were effectively controlled by the paired nature of the experimental procedures, the number of birds found at each site on each day varied from 10 to 25. There was, however, no consistent difference in the number in relation to either site or treatment (site: $F_{1,8} = 1.066$, $P = 0.332$; treatment: $F_{1,8} = 1.066$, $P = 0.332$).

Data analysis was carried out in R v1.6.1 and follows Crawley (2002). For each of the three main behavioural parameters we built Generalized Linear Models (GLM) including the site, treatment and their interaction. All other tests are two tailed, and, unless stated otherwise, means are given ± SD.

RESULTS

In the preliminary trials, turnstones in areas with supplementary feeding had peck rates around 30% higher than birds in the control areas (control: 0.389 ± 0.081 pecks/s; experimental: 0.299 ± 0.083 pecks/s; $F_{1,24} = 5.61$, $P = 0.027$). During the observations, the only large items of prey observed being eaten were mealworms with an average of 0.012 ± 0.009 mealworms/s in the supplemented areas. Birds fed in both control and treatment plots from the start of the experiments until the tide covered the areas approximately 2 h later. In the control areas, prey items were too small to be identified and were never larger than 2 mm in length. A few redshanks, *Tringa totanus*, present in the area also fed on mealworms during the observations, and a single curlew, *Numenius arquata*, fed for a brief period on one day. Other wader species present (mainly oystercatchers, *Haematopus ostralegus*) were not observed feeding on mealworms. Analysis of prey remains suggested that prey taken in unprovisioned areas were mainly barnacles, mostly *Semibalanus balanoides*, and other small crustaceans.

In all six trials in the main experiment, experimentally 'enhanced' birds flushed at a greater distance from the disturbance than control birds ($F_{1,8} = 6.182$, $P = 0.038$) and scanned for predators more frequently than control birds ($F_{1,8} = 10.87$, $P = 0.011$; Figs 1a, 2). The treatment effect was therefore significant, and there was no site effect or interaction between site and treatment (Table 1).

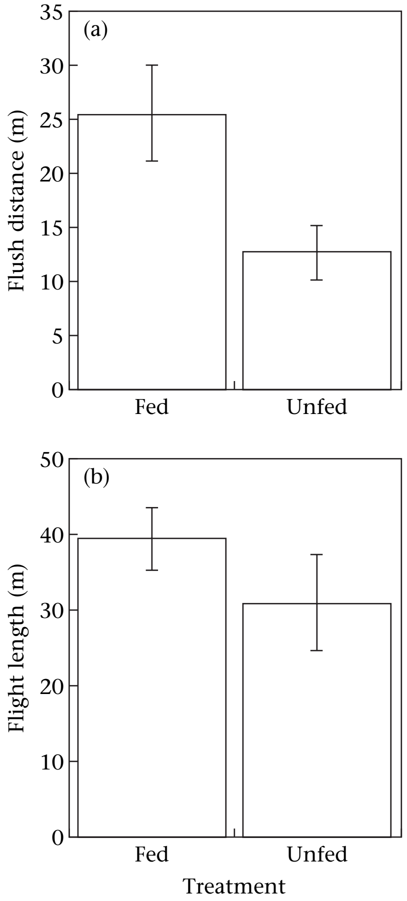

Figure 1. Behavioural responses to a standardized disturbance regime by turnstones subject or not subject to supplementary feeding: (a) flock flush distance; (b) flock flight length. The data are combined for all trials in the same feeding treatment for illustrative purposes; the statistical analysis accounted for other sources of variation (see text and Table 1 for details). Means are shown ± SE.

Thus, the birds in better condition in the rich feeding areas responded sooner to disturbance and searched for predators more frequently. On five of six trials, the distances flown by experimental birds were greater than those of control birds (Fig. 1b). There was a significant interaction between treatment and site with respect to distance flown ($F_{1,8} = 10.26$, $P = 0.013$), suggesting that the effect of the treatment varied with site, being stronger at one site than at the other.

DISCUSSION

The provision of supplementary food had a clear effect on the pecking rates of foraging turnstones for the period supplementary food was available. With average intake rates of 0.011 mealworms/s, and the manipulation lasting around 120 min, this represents an intake of 77.8 mealworms, or 7.3 g, per bird, per day. From the nutritional value of the supplied mealworms, this gives an approximate energy intake of 65.2 kJ per bird per day. Average daily energy requirements are estimated for wintering

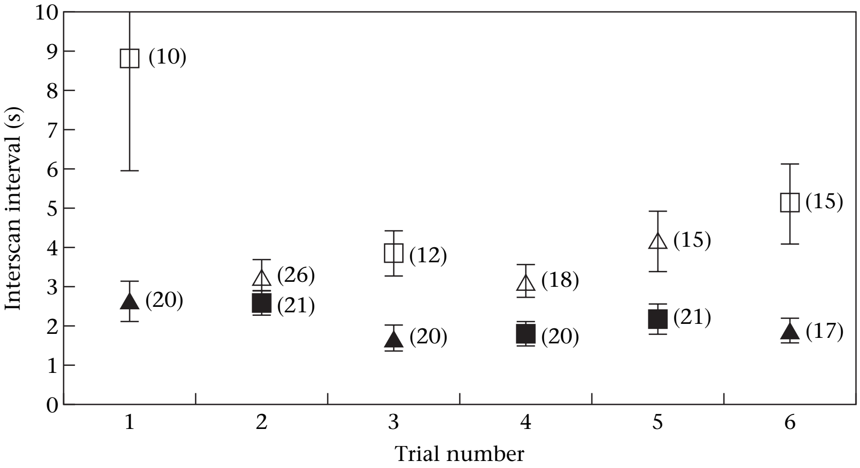

Figure 2. Changes in interscan interval in response to a standardized disturbance regime by turnstones at two sites subject or not subject to supplementary feeding. Number of individual birds measured is given in parentheses. Filled symbols indicate the site with supplementary feeding in each trial; shapes identify the individual site. Means are shown ± SE.

turnstones as a maximum of 290 kJ/day (Smart & Gill 2003), so our supplementary feeding can be expected to have provided 22% of the daily energy requirements for wintering turnstones. Gudmundsson et al. (1991) showed that turnstone condition can vary significantly over periods as short as 24 h. Thus, particularly, given that the birds in the study area are in decline and apparently short of undisturbed feeding areas (Dott 1997), after 3 days of manipulation the condition of birds foraging in the enriched treatment plots is likely to have been substantially enhanced relative to those in control areas. It is also clear that our manipulations increased the quality of the feeding areas in the experimental sites.

Birds in experimental sites were likely to have had more options open to them than control birds when faced with a disturbance: they were in better condition and probably also perceived their immediate environment to be richer, so could afford to respond by flying away or stopping feeding sooner than birds in poorer condition. In line with Gill et al.'s hypothesis, we found that birds with more options open to them responded more to human presence; they scanned for predators more frequently, took flight sooner and flew further away from an approaching human. Their behavioural responses to disturbance were changed such that those responding most were actually the least likely to suffer any fitness consequences associated with such disturbance: the opposite result from what is assumed when behaviour is used as an index of disturbance effects. These state-dependent behavioural responses to a standard disturbance are strong evidence in support of Gill et al.'s (2001) hypothesis, and further suggest that behavioural indexes of disturbance suffer from a fundamental flaw. We expect that the differing effect of the treatment on flight distance at the different sites was due to local topography, as the area of suitable rocky shore differed between sites.

Currently, flush distance is frequently used as a currency for measuring susceptibility to disturbance (e.g. Madsen 1985; Anderson 1988) and its species-specific properties are a key assumption of wildlife buffer zones (Blumstein et al. 2003). However, as demonstrated in this experiment, birds may change their response according to their individual state and the state of the environment in which they find themselves, independently of the strength of the disturbance event. In fact, in our experiments individuals that had most to lose from a reduction in feeding time showed the least behavioural response. Such effects may also apply among species. As we predicted, birds in manipulated areas were consistently more risk averse than control birds, acting as though they had more response options open to them. These findings are consistent with behavioural models developed and tested in predator–prey systems such as the condition-dependent use of feeding areas with varying predation risks of redshanks (Hilton et al. 1999).

Our results suggest that a reserve manager relying only on behavioural measures of disturbance (such as flush distance) to determine which birds are at higher risk is likely to make inappropriate decisions. For example, in dividing a nature reserve into zones with minimal human activity and areas where visitors are encouraged, we need to know where disturbance effects are greatest. Current practice involves measuring flush distances at various sites and determining in which areas responses are greatest.

Table 1. Results of Generalized Linear Models explaining the three measured disturbance activities: interscan interval, flush distance and flight length

Measure	Parameter	$F_{1,8}$	*P*
Interscan interval	Site	2.408	0.159
	Treatment	10.870	0.011
	Site × treatment interaction	2.166	0.179
Flush distance	Site	0.235	0.641
	Treatment	6.182	0.038
	Site × treatment interaction	1.586	0.243
Flight length	Site	2.564	0.148
	Treatment	2.564	0.148
	Site × treatment interaction	10.260	0.013

Areas where responsiveness is high are considered more sensitive sites in need of greater protection (e.g. Madsen 1998b; Evans & Day 2001). By contrast, our results indicate that the high level of responsiveness at the site of greatest response may be caused by the presence of birds in good condition or in particularly rich feeding areas, which do not necessarily need extra protection. If this is the case in the nature reserve in question, the designated zones would give inappropriate levels of protection to vulnerable groups.

Other factors may of course also influence the options animals have available to them. Animals that feed on a widespread and common resource, for example, may also have more options open to them than animals feeding on scarcer, localized resources, regardless of their condition. We would therefore expect that such generalists would also show greater behavioural responses to disturbance than those relying on scarce resources would. If this were so, then again protection levels based on the speed of response would be inappropriate.

Our experiment shows that responses to human disturbance vary with the animal's state and context, in a way that differs from the assumptions that underpin current management practices. It cannot be assumed that the most responsive animals are the most vulnerable. Alternative measures such as measurement of stress levels (e.g. Nimon et al. 1996; Fowler 1999) or methods involving measurements of resource use (e.g. Goss Custard et al. 1995; Gill et al. 1996) are needed to allow more fundamental assessment of disturbance effects.

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