Responses of foraging hedgehogs to badger odour

J. F. WARD, D. W. MACDONALD & C. P. DONCASTER
Wildlife Conservation Research Unit, Department of Zoology, University of Oxford

(Received 13 December 1995; initial acceptance 29 January 1996; final acceptance 23 May 1996; MS. number: 51111)

Abstract. Enclosure and field trials were used to investigate the responses of hedgehogs, Erinaceus europaeus, to predator (badger, Meles meles) and non-predator odours. Two hypotheses were tested: (1) hedgehogs are capable of responding to badger odour; and (2) hedgehogs prefer not to forage in areas tainted with badger odour. In enclosure trials, hedgehogs almost exclusively avoided feeding at sites tainted with badger faeces in favour of sites tainted with non-predator faeces, and continued to avoid the previously badger-tainted site after 2 days, but not after 4. Field experiments with free-ranging hedgehogs showed a reduction in foraging effort in response to badger odour over periods of 5 and 30 min, but no evidence of site avoidance over a 24-h period. Lack of persistent avoidance of badger odour in the field was probably due to the costs of predator avoidance, which were negligible in the enclosure owing to the presence of an alternative superabundant food source.

Where predators are a significant cause of mortality, selection will act to favour prey that can recognize and avoid their predators. The prey may use visual or auditory cues to anticipate direct attack, but they may also detect indirect cues to the presence of predators in order to avoid encounters. Amongst nocturnal mammals, odour is an important means of signalling and communication. Its use provides an opportunity for prey species to reduce their probability of being eaten by recognizing the odorous evidence of their predator’s presence (see review by Weldon 1990).

For many prey species, their behavioural responses to this perceived threat of predation are known to influence their local patterns of distribution with respect to the distribution of predators (see review by Lima & Dill 1990), although costs associated with predator avoidance, such as reduced feeding rates and reduced breeding opportunities (e.g. Sih 1988), may well influence the response to the perceived danger.

The local distribution and abundance of hedgehogs in rural Oxfordshire, U.K., correlates inversely with the distribution of badgers (Micol et al. 1994). The result is a patchy distribution of hedgehog populations, and their absence from some areas of their preferred habitat of short-grass fields, hedgerows and copses. Hedgehogs have a well-defined morphological adaptation to the danger of predation, in the form of their dorsal coat of spines. They are not fast-moving animals, and this armoury appears to suffice as a defence against potential predators such as foxes. Foxes, Vulpes vulpes, living in urban Oxford, where hedgehogs are abundant, will occasionally attack hedgehogs and will scavenge from dead hedgehogs, but this species is present at very low frequency in their diet (Doncaster et al. 1990). However, the spines are not adequate defence against badgers, which are able to force access to the hedgehog’s vulnerable underbelly, and are known to prey upon them when the opportunity arises (Doncaster 1993). Risk of predation from badgers is thus a plausible explanatory factor underlying the observed distribution of hedgehogs.

In a study of factors regulating local variation in abundance of hedgehogs, Doncaster (1994) released 50 wild hedgehogs into suitable habitat patches with and without permanent natural populations of hedgehogs. Survival of transplanted hedgehogs was significantly lower at the
site with no naturally occurring population (12 dying compared to three at the control site) and animals introduced at this site dispersed twice as far from the release point as those introduced into the existing control population. The availability of preferred habitat was similar at the two sites, as were hedgehog growth rates. A higher density of badgers at the site with no natural population appeared to be responsible for the higher mortality there, and the high rates of dispersal of released hedgehogs suggested that they were avoiding confronting badgers by moving away from the area.

To test hypotheses such as this, and more generally for a fuller understanding of the dynamics of populations, an understanding of the behaviour of individuals is crucial (Hassell & May 1985). We therefore sought to demonstrate a behavioural mechanism whereby individual hedgehogs could, and would, detect and avoid a potential risk of predation from badgers.

An innate response by a prey species to a predator cue, such as odour, may result if the two species have coexisted over evolutionary time. Gorman (1984) showed that common voles, Microtus arvalis, that have been isolated from mammalian predators for at least 5000 years, strongly avoid stoat, Mustela erminea, odour, suggesting an innate rather than learned response. Similarly, Berdoy & Macdonald (1990) showed that rats, Rattus norvegicus, innately avoid fox urine. Moreover, prey species can be indiscriminate in responding to predator odours (e.g. Dickman & Doncaster 1984; Weldon et al. 1993), and it has been argued that the response-provoking components in one predator’s odour often occur in others with which the prey may not have an evolutionary association (Nolte et al. 1994).

In this paper we test the hypothesis that hedgehogs can detect and respond to faecal odours of badgers so as to reduce their chances of encountering badgers themselves. Like many carnivores (Macdonald 1985), badgers have specialized scent glands and a highly developed olfactory communication system (Kruuk et al. 1984; Davies et al. 1988). Their odour thus clearly identifies them at a species level, and we assumed that a demonstrable response by hedgehogs to faecal odour would be a response to the associated risk of predation.

By carrying out patch choice experiments on wild-caught hedgehogs in an enclosure, we were able to test their response to predator and non-predator odours in a controlled environment, in which any response could be separated from factors difficult to control for in the wild. In particular, the availability of an alternative food source and the lack of competitors in the enclosure served to reduce the costs of giving up a risky patch, thus making the recorded responses clearer. We followed our enclosure experiments with field experiments to form a more complete picture of how individual hedgehogs’ responses to predator odours might be incorporated into their behaviour and distribution patterns in the wild. Specifically, we aimed to test the hypotheses that: (1) hedgehogs are capable of responding to badger odour; and (2) hedgehogs prefer not to forage in areas tainted with badger odour.

**METHODS**

**Enclosure Experiments**

**Capture and maintenance of hedgehogs**

We located wild hedgehogs on a city golf course and adjoining playing fields in Oxford (Grid Reference SP 543055) by systematic spot light searches and captured them by hand. The collection area was bordered by housing estates and roads. Diurnal and nocturnal surveys and field signs revealed that although foxes were present in the area, badgers were absent.

Hedgehogs were housed in groups of eight in an outdoor enclosure which measured 12 × 6 m. This comprised 2-m-high wooden slat fencing, a wire-mesh roof and a sandy soil floor covered with wire mesh. An adjoining shed, heated by a 250-W infra-red bulb hung approximately 1 m from the floor, contained four wooden nestboxes supplied with hay and dried leaves. The shed roof provided an elevated viewing post from which we could see the whole enclosure without disturbing the hedgehogs, and the enclosure was continuously lit with a low-level red light at each end. Water was freely available.

At the beginning of each night, tinned cat food was provided in two plastic feeding bowls 0.15 m in diameter and supported on each of two portable platforms. The platforms (0.45 × 0.3 m) were raised 0.2 m from the ground; access was via ramps (0.64 × 0.2 m) fitted with wooden slats to prevent the hedgehogs from slipping. They were...
located at the one-third and two-thirds points of the long centreline of the enclosure, with ramps facing each other. We observed hedgehogs as they acclimatized to the enclosure, cat food and feeding platforms over a training period of 1 week. Any individual that did not ascend the platforms was encouraged to do so with pieces of cat food placed at intervals on the ramp.

Following the training period, each hedgehog took part in up to three individual experimental trials, carried out on alternate nights, before being marked with coloured plastic tubing glued over individual spines and released at the site of capture. Previous studies (Doncaster 1993) have shown that such markers cause no ill effects and were lost naturally with the shedding of spines.

Faecal odours

A non-predator control odour unfamiliar to the hedgehogs was provided in the first group of trials by fresh chipmunk, *Eutamias sibiricus*, faeces obtained from a captive pair, and in the second group of trials by fresh fruit bat (Indian fruit bat or flying fox, *Pteropodidae giganteus*) faeces obtained from a captive colony of bats housed at the Cotswold Wildlife Park. Fresh badger faeces were obtained from badger latrines in Wytham Woods (Grid Reference SP 466077 and 471099). Badger and fruit bat faeces were either collected in advance and frozen, or used on the night of collection.

Trial procedure

We conducted experimental trials in the enclosure, with non-participating hedgehogs confined to the shed. In each trial we placed a nestbox containing a hedgehog mid-way between the two feeding platforms, with its entrance perpendicular to the line between them, and allowed the hedgehog 90 min to emerge and forage. Each platform offered approximately 200 g of cat food, more than enough to make up a typical night’s meal of up to 100 g.

We carried out preliminary trials to test the effectiveness of the trial procedures. These were identical to the treatment trials described below, except that no control (non-predator) odour was used, and the hedgehogs had fed the night before. Results suggested that the hedgehogs might be reluctant to feed at all with badger odour present in the enclosure, so for the main experiments they were deprived of food on the night prior to each trial.

Each trial was either a treatment or a follow-up trial. In a treatment trial, we tainted one platform with badger odour and the other with non-predator odour, by placing an odorous specimen tube on each platform, behind and approximately 2 cm from the feeding bowls. We alternated the locations of the platforms tainted with badger and non-predator odour between treatment trials to control for any effect due to site within the enclosure. Concentrated odours were presented in the form of specimen tubes containing badger or non-predator faeces. Dilute odours were presented in the form of specimen tubes from an immediately preceding concentrated odour trial which had been emptied, washed out and wiped over, leaving no visible trace of faeces and an odour barely detectable to humans. Follow-up trials, using subjects from previous treatment trials, were identical to the treatment trials except that no experimental odours were present. We thoroughly washed platforms, ramps and bowls using detergent, and discarded used specimen tubes after each night’s set of trials.

The ‘safe’ site for a treatment trial was the site with a platform tainted with non-predator odour, and for a follow-up trial was the site that had been safe in the original treatment trial for that hedgehog. After each trial we weighed the amount of food left, to calculate the amount eaten from the safe site as a proportion of the total amount eaten. Subjects that did not eat from either site were assigned a proportion of 0.5 (no preference). The standard arcsine-square root transformation was applied to these results when used in parametric statistical tests, as this helps to correct for non-normality and non-homogeneity of variance found in proportional data.

Experimental groups and trial sequences

The preliminary trial group consisted of five male and three female adult hedgehogs weighing $821 \pm 40 \text{ g (X \pm se)}$, each taking part in a single treatment trial without a non-predator control odour.

The two main experimental groups, referred to as the concentration/persistence and persistence-only groups, were tested in late April 1992 and late June 1993, respectively. Weather conditions
were dry and temperatures were typical of the time of year. Each group comprised six male and two female adult hedgehogs. Mean weights of the hedgehogs at the time of their first trial were 868 ± 50 g for the concentration/persistence group and 807 ± 45 g for the persistence-only group, and did not differ significantly between the two groups (independent samples t-test: t_{14} = 0.904, P > 0.38).

To test for variation in intensity and persistence of the hedgehogs’ response to odour depending on its concentration, the concentration/persistence group was split into two sub-groups of four animals, subjected to either a concentrated treatment trial (two males and two females) or a dilute treatment trial (four males). Each hedgehog took part in a single treatment trial and two follow-up trials, on the second and fourth nights after the first trial.

The concentration/persistence group was tested using the same platforms for all trials. Although both of the platforms were used for all four treatments, and were thoroughly cleaned, imperceptible residual odour might have acted as a confounding effect on persistence in site preference. To ascertain whether any persistent preference for a safe site was due to residual odour on the platform or to memory of the odour position, the persistence-only group was tested using a concentrated treatment trial and two follow-up trials, in the same order, on the second and fourth nights after the first trial.

Preparation of odours

Two different control odours were used. For the short-term experiments at Oxford, Abingdon and Frilford, where the hedgehogs were not likely to be familiar with badgers, we used fruit bat odour so that both badger and control odours would be unfamiliar to the hedgehogs. At Eynsham, hedgehogs were likely to be familiar with badger odour and so we used a familiar odour (sheep) as the control (sheep were present in the fields in Eynsham Park).

We obtained fresh fruit bat faeces from the captive colony at the Cotswold Wildlife Park. We collected fresh badger faeces from latrines found in or around Wytham Woods, and fresh sheep faeces from fields adjoining Wytham Woods. Faeces were either used on the night of collection or frozen for future use.

We made odour missiles from blown, oven-dried quail eggs refilled with dissolved (1 part faeces to 1 part water) badger, fruit bat or sheep faeces. Once filled with a faecal solution the shell was sealed with plastic tape. To prevent observer bias, we labelled shells with arbitrary numbers which corresponded to a record of the odour with which they were filled.

Experimental procedure: short-term observations

We located individual free-ranging hedgehogs using a red flashlight. Once found, we observed a hedgehog for 5 min, using a dimly lit torch, for two consecutive 5-min periods during which its behaviour was recorded. After the first observation period an egg was selected at random and thrown to within approximately 0.3 m of the hedgehog. On impact, the eggs nearly always smashed open liberating the odour, but if they remained intact then the trial ceased and the hedgehog was marked, with three colour-coded plastic tubes glued over individual spines, so that it would not be reused. If the egg smashed, the hedgehog’s behaviour was observed for the

Field Experiments

Field sites

We conducted field experiments to investigate short-term reactions to odour treatment mainly on the Oxford golf course, and also at playing fields in Abingdon (Grid Reference SU 491974) and Frilford (Grid Reference SU 441971), although only one hedgehog was tested at each of the latter two sites. Experiments to investigate longer-term responses were carried out at Eynsham Park (Grid Reference SP 395124/9), Oxfordshire. All had large, well-mown grassy areas with resident hedgehogs. The Oxford and Abingdon sites were surrounded by urban residential areas, whilst the sites at Frilford and Eynsham were surrounded by farmland and villages. There was no evidence that badgers were present in Oxford, Abingdon or Frilford, although foxes were seen at the first two sites. Small numbers of badgers were present, however, at Eynsham. None of the hedgehogs tested had previously undergone any experimental manipulation.
second period. At the end of this period the egg was inspected to determine the type of odour, and the hedgehog caught and marked as described above.

During the observation periods, we scored feeding rate, movement pattern, sniffing of the air and average speed before and after odour input, and used the difference between the scores as a measure of disturbance. We scored feeding rate as the number of prey items taken during the observation period, movement pattern as the number of times a hedgehog crossed its own tracks, and sniffing as the number of times a hedgehog made a distinct sniff at the air. For these three behaviour patterns we calculated the treatment score as the difference between the before and after scores, with the difference taken in the sense that gives a higher score for greater disturbance (reduced intake, straighter movement, increased sniffing). We calculated average speed (m/s) using the straight-line distance between a hedgehog's position at the start of an observation period and its position at the end of the observation period. Scores from 1 to 5 were allocated to speed classes: <0.15 m/s, <0.35 m/s, <0.55 m/s, <0.75 m/s and >0.75 m/s. For this behaviour, the treatment score was the absolute magnitude of the difference between the before and after scores (as hedgehogs can react to disturbance either by freezing or by flight).

We carried out 19 observations with each of fruit bat and badger odour over two experimental periods within the same season, with treatments allocated equally to each period. The fruit bat group comprised eight males and 11 females with a mean weight ± SE of 762 ± 37 g and the badger group comprised 10 males and nine females with a mean weight of 716 ± 59 g (no significant difference in weight).

The experimental protocol for investigating the longer-term effects of odour was similar to that for short-term effects, but was intended to be less intrusive and used 30-min instead of 5-min observation periods. Using radiotracking for location and beta lights for observation we could observe a free-ranging hedgehog from a distance of 15–20 m, approaching to 5 m only to project the missile at the end of the first 30-min period. We recorded the number of turns it made through 90° or more, its initial response to the odour, and the distance it travelled during different stages of the trial. We counted the numbers of turns through 90° or more over two 5-min periods during a 30-min observation period (5–10 and 20–25 min) and took the average value. The treatment score was taken to be the percentage decrease in the number of turns (turning being a searching behaviour expected to decrease in response to disturbance). A proportional score was used because of the high variance in the initial turning rate (owing to random individual and environmental factors). A hedgehog's initial response to egg impact was usually to cover its face by pulling down a fringe of spines, partially rolling up, and we recorded the length of time that it held this position. We placed four pegs in the ground to mark the hedgehogs’ positions at different stages. The first was placed when the hedgehog was initially located, the second at odour input, the third at the end of the observation period, and the fourth 24 h later. Three distances were calculated: between pegs 1 and 2, 2 and 3, and 2 and 4.

RESULTS

Enclosure Experiments

In the preliminary trials, three hedgehogs failed to eat and the remainder ate a mean ± SE of 20 ± 5 g exclusively from the safe (untainted) site, demonstrating a significant preference for this site (one-tailed sign test: $k=0$, $N=5$, $P=0.031$).
The combined results of the two main experimental groups show clearly the effects of odour type (predator versus non-predator) and of time since exposure to odour (trial number). Hedgehogs ate a significantly greater proportion from the safe site than from the unsafe site in the treatment trial (one-tailed Wilcoxon matched-pairs signed-ranks test: \( T^+ = 111, N=15, P=0.001 \)) and first follow-up trial (\( T^+ = 84.5, N=14, P<0.025 \)) but not in the second follow-up trial (\( T^+ = 48, N=14, \text{ns} \)). The decrease in preference for the safe site over the three trials is also demonstrated by the Page test for ordered alternatives (\( k=3, L=209.5, N=16, P<0.01 \)).

Within the concentration/persistence group, one hedgehog in the concentrated treatment sub-group ate only during its first trial, one in the dilute treatment sub-group ate only during its third trial, and another in the dilute treatment sub-group did not eat during its third trial. All seven hedgehogs that ate during their treatment trial approached the safe site first and ate exclusively from it. In the first follow-up trial four ate exclusively from the safe site, whilst in the second, two ate exclusively from the safe and one exclusively from the unsafe site. An ANOVA on the transformed proportions eaten from the safe site by this group (model \( S_4(C_2)T_3 \): four subjects in each of two concentration sub-groups, with repeated measures over three trials; concentration and trial number as fixed effects) showed no significant effect of concentration (\( F_{1,6}=0.097, \text{ns} \)) but a significant effect of trial number (\( F_{2,12}=7.24, P<0.01; \text{Fig. 1} \)).

Hedgehogs in the persistence-only group ate during every trial, with five out of eight in the treatment trial approaching the safe site first and eating exclusively from it. Of the three eating from the ‘unsafe’ site in this trial, all ate at this site first. Two of these hedgehogs ate, respectively, 7 and 38% from the unsafe site; the individual that took 38% ate only 16 g in total, compared with the group mean \( \pm \text{se} \) for this trial of 73 \( \pm 14 \) g. Both left the platform within a few minutes of ascending it, one taking up a flat/frozen defence stance before departure. The third hedgehog to eat from the unsafe site did so exclusively in all three trials, but also demonstrated abnormal and persistent running behaviour when not eating, possibly as a result of parasitic infection. In the first follow-up trial two hedgehogs ate exclusively from the safe site, whilst in the second, one ate exclusively from the safe and three exclusively from the unsafe site.

The transformed proportions eaten from the safe site by the concentration/persistence and persistence-only groups were compared using an ANOVA on group and trial number (model \( S_8(G_2)T_3 \)) which showed no significant effect of the different treatment of the two groups (\( F_{1,14}=0.389, \text{ns} \)) and, again, a significant effect of trial number (\( F_{2,28}=13.14, P<0.001; \text{Fig. 2} \)). However, the total amount eaten in a trial did vary significantly between groups (ANOVA as above: \( F_{1,14}=7.62, P<0.025 \)) but there was no effect of trial number (\( F_{2,28}=2.15, \text{ns} \)) or group–trial number interaction (\( F_{2,28}=0.24, \text{ns} \)). Concentration/persistence group hedgehogs ate an average \( \pm \text{se} \) of 42 \( \pm 12 \) g in each trial compared with 85 \( \pm 14 \) g for the persistence-only group.

**Field Experiments**

*Short-term effects of odour*

Hedgehog intake rate over a 5-min period dropped from an average \( \pm \text{se} \) of 4.2 \( \pm 0.6 \) to
items when exposed to badger odour and from 3.5 ± 0.6 to 1.7 ± 0.4 items when exposed to fruit bat odour. This represents a 97% reduction in feeding rate in response to badger and a 50% reduction in response to control odour input (i.e. to the experimental procedure, and egg impact in particular).

One-tailed Wilcoxon two-sample tests (independent groups) show the response to badger odour was significantly greater than to bat odour for all behaviour patterns: intake ($W=474$, $N_1=N_2=19$, $P<0.002$), movement pattern ($W=442$, $N_1=N_2=19$, $P<0.02$), sniffing ($W=440$, $N_1=N_2=19$, $P<0.025$) and average speed ($W=130.5$, $N_1=N_2=19$, $P<0.001$; Fig. 3). One-tailed sign tests show that both treatments caused a significant reduction in the number of items taken (badger: $k=0$, $N=19$, $P<0.001$; bat: $k=0$, $N=14$, $P<0.001$), but only badger odour significantly straightened movement pattern ($k=5$, $N=19$, $P=0.032$) or increased sniffing ($k=4$, $N=17$, $P=0.025$). Of the nine hedgehogs in the badger group, five increased speed by at least two speed classes, and three decreased speed by at least two classes. In contrast, the speed class of five of the 10 hedgehogs in the bat group was unchanged, with four increasing speed by one class, and one decreasing by two classes.

**Long-term effects of odour**

The difference in the percentage reduction in turning rate between the badger and sheep treatment groups was tested using a one-tailed Wilcoxon two-sample test, which showed significantly greater response (reduced turning) to badger odour ($W=37$, $N_1=N_2=5$, $P=0.028$). Both treatments caused a significant reduction in turning rate (one-tailed sign test: $k=0$, $N=5$, $P=0.031$) with badger odour giving a reduction of 69 ± 9%, and bat odour a reduction of 40 ± 9%.
Differences between the distances moved by hedgehogs before and after odour input (Fig. 4) were tested using a two-tailed Wilcoxon two-sample test. There was no significant difference between badger and sheep odour groups for any of the three distances ($W = 29$, $N_1 = N_2 = 5$, NS), although there appeared to be a tendency (not significant) for hedgehogs exposed to badger odour to be further from the odour input site on the following night. Moreover, there was no significant difference between the distances covered in each of the three periods (Kruskal–Wallis one-way analysis of variance by ranks: $k = 3$, $H = 1.03$, $N = 10$, $P > 0.3$).

The lack of a significant difference between the distances covered in the 30 min after odour input may be, at least in part, a consequence of the wide variation in behaviour over the course of this period. The hedgehogs' initial response to odour input was usually to adopt the 'fringe down' posture, and then move away, in some cases bolting towards the nearest cover. By the end of the 30 min, however, movement away from the site had slowed, and in many cases the hedgehog had started to forage again.

Hedgehogs exposed to badger odour spent less time in the initial 'fringe down' posture ($T \pm \text{SE} = 3.6 \pm 0.5 \text{ min}$) than hedgehogs exposed to sheep odour ($4.6 \pm 1.1 \text{ min}$) but the difference was not significant (two-tailed Wilcoxon two-sample test: $W = 24.5$, $N_1 = N_2 = 5$, NS).

**DISCUSSION**

We have shown that hedgehogs given a choice between two superabundant food sources in an enclosure, when exposed to a single treatment with badger odour, avoided feeding at the treated site (in favour of an untreated or non-predator odour treated site) and continued to avoid that site after 2 days, but not after 4. Free-ranging hedgehogs, without artificial food sources, reacted more strongly to a single treatment with badger odour than to one with a non-predator control odour over short time-scales (5 min) but this immediate reaction did not appear to be reflected in any greater dispersal from the treatment site over longer time-scales (30 min and 24 h).

The greater total amount eaten by the persistence-only group than by the concentration/persistence group in the enclosure trials does not appear to be a result of experimental factors (different non-predator odours in the treatment trial, different platforms in the follow-up trials) as these would be expected also to give a significant interaction between group and trial number (the same argument applies to a difference in potency of the badger odour). Since the groups were well matched for sex and weight, seasonal or year-to-year differences in hedgehog appetite and condition provide a likely explanation, particularly in view of the fact that the persistence-only group were no heavier than the concentration/persistence group, despite being 2 months advanced in the season. Greater appetite in the persistence-only group may explain why three hedgehogs were willing to feed at the badger-tainted site; observations suggest that they rushed up the first platform they encountered and, given the abundant food supply, were for some time either tolerant of, or simply oblivious to, the presence of badger odour. Nevertheless, site preference, as measured by proportion eaten, was...
independent of individual or group variability in appetite and did not differ between the two groups.

The responses of hedgehogs in the longer-term field experiments exhibited two curious features which require explanation. First, the initial ‘fringe-down’ reaction to the odour missile was relatively short-lived for hedgehogs in the short-term experiments (not recorded, but typically no more than 30 s) but lasted for several minutes in the long-term experiments. This is probably due to a combination of differences in experimental procedure and hedgehog populations: hedgehogs in the short-term experiments were, to some extent, disturbed by the observer being within 5 m during the 5 min before delivery of the odour, whereas those in the long-term experiments were undisturbed until the sudden arrival of the odour missile and (as a rural rather than urban population) might also be expected to react more strongly to human presence. Second, the distance measurements, as well as showing no significant difference due to odour, were remarkably similar over all three periods of observation. These distances correspond to the typical size of the lawn areas in which the hedgehogs were observed, and indicate that 30 min was sufficient for the hedgehogs to make wide use of a particular area. The cumulative home range areas of hedgehogs vary widely between individuals, sexes, populations and habitats (values between 5.5 and 102.5 ha are quoted in the review by Reeve 1994) but are considerably larger than these individual lawns, suggesting that the reason hedgehogs were invariably found in the same area 24 h later is that they had a pattern of home range usage that did not vary greatly from night to night. Nightly ranges outside the breeding season are typically a few hundred metres (Reeve 1994) and hedgehogs will often use the same nest site for several days (Reeve & Morris 1985), or return to the same garden on consecutive nights (Morris 1985).

The egg-throwing method of odour delivery permitted detailed behavioural observation of the response to badger odour of a relatively large number of free-ranging hedgehogs. Drawbacks of the method include the sudden impact, variation in distance from the subject on landing, and the need for a fairly close human approach. Indeed, the treatment has much in common with an actual encounter with a predator, rather than the more gradual process of encountering a natural dropping, although it is difficult to see how the latter might be adequately simulated and controlled in field trials.

Nature of the Response to Odour

The preferences demonstrated in the enclosure experiments cannot be explained either as a generalized avoidance of faecal odour (controlled for by non-predator odour in the main trials) or even as an ‘attractive’ quality of non-predator odour (unlikely since the badger/no odour choice in the preliminary trials resulted in maximum possible preference for the no odour platform, whilst the preference for a non-predator odour was less strong overall). Insofar as hedgehogs that were unlikely to have had previous exposure to badgers (in Oxford and Abingdon) none the less displayed a strong response to their odour, our results suggest an innate rather than a learned avoidance of badger odour by foraging hedgehogs. However, avoidance of a predator odour can be either species-specific (Swihart 1991; Nolte et al. 1993) or a general response to a carnivore (Stoddart 1982; Weldon et al. 1993; Nolte et al. 1994) and, furthermore, some prey learn to respond only to predators that are actively dangerous (Dickman 1992). Since the hedgehogs were likely to be familiar with foxes, if they had learned to avoid fox odour, subsequent avoidance of badger odour may have been a response to a chemical component shared by the two predators. A similar ambiguity was found by Dickman & Doncaster (1984) in a study of the response of small mammals to fox and badger odour. Although our data cannot distinguish between a response to badger odour in particular, and to predator odour in general, the discussion below does not rely on any such distinction.

Predation Risk and Cost of Avoidance

There is extensive empirical evidence to demonstrate that animals are capable of adjusting their food quality and altering their behaviour to lessen the risk of predation and maximize their probability of survival (McNamara & Houston 1987, 1990), and trade-offs between foraging and predation avoidance by nocturnal mammals are frequently observed (Kotler 1984; Lima 1985; Lima & Valone 1986; Brown et al. 1988; Brown &
In evaluating these trade-offs, we need to consider the magnitudes both of the potential risks and of the costs of avoidance.

In the enclosure, hedgehogs were presented with an alternative, profitable food source, such that choosing not to feed at one platform incurred little or no extra cost in terms of lost feeding opportunities. The perceived risk of predation at the site tainted with badger odour, together with possible energetic costs and inefficiency due to heightened vigilance, appear to have been sufficient to tip the balance firmly in favour of the safe site both on the night of odour treatment, and in the follow-up trial 2 days later. Limitations of memory, lack of reinforcement of the original odour stimulus, and the possibility of missed opportunities at the risky site may all contribute to the disappearance of a preference by the night of the final trial.

In contrast, we found that free-ranging hedgehogs’ responses to badger odour were relatively short lived. Despite an initial departure from the immediate site of odour input, the hedgehogs did not appear to change their longer term use of local food resources in response to this single exposure to predator odour (the tendency for hedgehogs exposed to badger odour to forage further from the site of odour input on the following night, although not significant in this small sample, may warrant further investigation).

For these free-ranging hedgehogs, choices made solely on the basis of predation risk might be expensive in terms of travel costs, lower profitability of alternative food sources and reduced breeding opportunities. Under natural conditions, such costs may discourage continued avoidance of a previously tainted site over an extended period of time. Habitat quality, in particular, is an important factor, as Merkims et al. (1991) concluded in recommending that managers intending to use predator-based repellants should ensure that alternative sites available to pests are of better habitat quality than areas to be protected.

Differences between the responses of enclosed and free-ranging hedgehogs may also be due to differences in perceived risk, as well as in the costs of predator avoidance. Thus it may be that enclosed hedgehogs, with a restricted range of options for escape, may perceive a greater risk from the presence of predator odour than do those in the field.

More generally, it is possible that the actual risk of predation is low or negligible. Hedgehogs are well adapted to avoid predation: as well as their nocturnal habits, which safeguard them from potential diurnal predators such as raptors (Cramp & Simmons 1980), they make the morphological investment of a protective coat of spines, together with the underlying muscular system which enables them to roll up. Spines provide a level of security from the threat of predation that may reduce the need for a rapid behavioural response, or allow additional foraging opportunities in areas with high predation pressure (Sweitzer & Berger 1992). Other morphologically protected species, however, display rigorous behavioural traits in response to predation pressure. For example, both African bush-tailed, Atherus africanus, and Indian crested, Hystrix indica, porcupines avoid moonlight (Emmons 1983; Alkon & Salz 1988). Indian crested porcupines prefer to forage in areas providing cover, and presumably protection from predators (Brown & Alkon 1990). Quills, then, are not the only means by which porcupines avoid potential predation. Similarly, spines alone are insufficient to protect hedgehogs against badgers, although they might provide protection from other predators, allowing hedgehogs to use rich food resources in open areas safely where badgers are absent.

Finally, because the longer-term experiments were conducted in an area (Eynsham Park) that has only a small badger population, it is possible that the hedgehogs in this area have learned that occasional encounters with badger odour do not indicate any significant threat of predation.

The Nature of Predation Risk and Cues from Badgers

Land use by a foraging badger is similar to that of a foraging hedgehog, as both have invertebrates, and earthworms in particular, as principal items in their diets (Kruuk 1989; Reeve 1994). This adds the dimension of competition for (possibly) limited food resources to the interaction between hedgehogs and badgers. The intricacies of intra-guild predation (Polis et al. 1989) are not explored here, other than to note that attempts to avoid badgers by a shift in micro-habitat are likely to prove unprofitable (since badgers will tend to occupy profitable micro-habitats) and thus
larger-scale dispersion from areas of high badger density is likely to be favoured, as observed by Doncaster (1994).

The adaptiveness of persistent avoidance of the area around an individual odour cue will depend strongly on the likelihood of the predator (or others in its social group) returning to that area, over different time-scales. Badgers defecate chiefly at communal latrines, so whilst their faeces might not be distributed widely around their territories, they might indicate a high risk of encounter. Foraging badgers frequently mark by ‘squatting’, depositing a mixture of faecal matter and sub-caudal and anal gland secretions (Kruuk et al. 1984); odour deposited in this way might convey a different risk to hedgehogs than that indicated by faeces alone, and we might therefore expect a different level and persistence of response to it. For example, Dickman (1992) found that house mice, Mus domesticus, avoid cat, Felis catus, and fox faeces more strongly than the faeces of western quoll, Dasyurus geoffroii, a carnivorous marsupial. He suggested that this was due to the correlation between predator and faecal presence for cat and fox, whereas quoll foraging and defecation areas may not coincide because, like badgers, they use latrines (Serena & Soderquist 1989). Dickman suggested that if mice encounter quoll faeces infrequently because of their clumped or inaccessible distribution, little benefit may be derived from avoiding them (note that this is the opposite of the ‘high risk’ argument above, yet is based on the same distribution; frequency of use will determine the true risk). This may also be true of hedgehogs and badger faeces. Nevertheless, badger faeces contain anal gland secretions (Davies et al. 1988), and latrines are also used for territory marking (Roper et al. 1986), so it seems likely that faeces would provide a clear cue of predation risk to hedgehogs.

As well as composition, freshness of odour might be detected and interpreted by hedgehogs: fresh odour might indicate a nearby predator, stale odour, an infrequently used area. Faeces in these experiments were collected from regularly used latrines, yet would have been at least 2–3 h old at time of use. Although Kruuk (1989) reported that badgers often forage in the same area (usually less than 1 ha) for up to 2 h, it seems unlikely that the experimental odour would have been fresh enough to convey such an immediate risk.

Conclusion

In conclusion, we found that hedgehogs respond to a single treatment with badger faecal odour both in an enclosure and in the wild, but alter their foraging behaviour substantially only in the enclosure, where the costs of avoidance are presumed to be smaller in relation to the perceived risk than they are in the wild. We have demonstrated that this response to badger odour provides a feasible mechanism, or partial mechanism, by which hedgehogs can perceive risk and disperse from areas of high badger density, but it seems likely that substantial reinforcement of the odour stimulus used in these experiments would be necessary to convey a level of risk sufficient to outweigh the costs of dispersion. Such reinforcement might be temporal (through repeated encounters with fresh odour), spatial (through encounters over significant areas of the home range), or arise from other cues (different odours, sightings, or actual encounters).

ACKNOWLEDGMENTS

John Krebs and Roger Austin made helpful suggestions throughout the planning and execution of these experiments, which were supported by a SERC grant to J.F.W.

REFERENCES


