

Exploiting olfactory learning in alien rats to protect birds' eggs

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Predators must ignore unhelpful background “noise” within information-rich environments and focus on useful cues of prey activity to forage efficiently. Learning to disregard unrewarding cues should happen quickly, weakening future interest in the cue. Prey odor, which is rapidly investigated by predators, may be particularly appropriate for testing whether consistently unrewarded cues are ignored, and whether such behavior can be exploited to benefit prey. Using wild free-ranging populations of black rats, *Rattus rattus*, an alien predator of global concern, we tested whether the application of bird-nesting odors before the introduction of artificial nests (odor preexposure), enhanced the survival of birds eggs (prey) compared with areas where prey and nesting odors were introduced concurrently. In areas where predators had encountered prey odor before prey being available, the subsequently introduced eggs showed 62% greater survival than in areas where prey and odor were introduced together. We suggest that black rats preexposed to prey odor learned to ignore the unrewarding cue, leading to a significant improvement in prey survival that held for the 7-d monitoring period. Exploiting rapid learning that underpins foraging decisions by manipulating sensory contexts offers a nonlethal, but effective approach to reducing undesirable predatory impacts. Techniques based on olfactory preexposure may provide prey with protection during critical periods of vulnerability, such as immediately following a prey reintroduction. These results also highlight the potential benefits to species conservation to be gained from a greater understanding of the cognitive mechanisms driving alien predator behavior within ecological contexts.

predation | sensory learning | habituation | foraging behavior | information use

Efficient predators must identify and then pursue cues of profitable prey while ignoring stimuli that have proved unrewarding (1, 2). Such optimal foraging tactics rely on complex discrimination tasks being made rapidly and accurately within dynamic environments and benefit from attentional mechanisms, such as search images (3, 4), which assist the hunter to focus on useful information. How unrewarding prey cues are ignored remains unexplored in ecological contexts, despite the obvious fitness advantage for generalist predators switching between multiple prey. Being able to deceive predators into ignoring relevant cues may also have practical implications for assisting the survival of vulnerable prey that have ineffective defenses, such as some native prey facing alien predators (5).

Optimal behavior models imply that previous experience influences whether a predator pursues or ignores prey cues (6, 7). In a study examining predatory behavior in wild red squirrels *Tamiasciurus hudsonicus*, Pelech et al. (8) showed that squirrels experienced in finding artificial nests containing food found nests quicker than nonexperienced animals. Successful foraging experience facilitated faster detection of nests and increased prey vulnerability over time. In contrast, repeated unsuccessful foraging experiences should lower a predator's motivation to keep pursuing a particular cue, reducing the risk faced by the donor species. In a process analogous to the development of a positive search image,

we predict that repeated failed foraging attempts “push” the cues into the background of a predator's sensory realm so misleading or irrelevant information can be ignored in the future, a process that efficient predators must use constantly. Although actual sensory perception of the cue may not be affected, decreasing cue salience and responsiveness in this context is a short-term behavioral adaptation likely to arise out of a combination of associative and nonassociative learning processes (9); for example, a predator may initially form an adverse or neutral association with a misleading cue, which fades over time as habituation occurs.

Being able to ignore incoming information is likely to be particularly relevant for olfactory-driven behaviors (10). Olfactory cues are detectable over large temporal and spatial scales (11) and initiate search behavior in a wide variety of predators (12). Mammalian predators live in a rich olfactory world, able to detect and recognize immense numbers of odors and distinguish minute differences in complex mixtures (13, 14). Such capabilities should hinder efficient foraging unless superfluous olfactory information can be quickly disregarded (15, 16).

Bird eggs and nestlings are readily found by scent-hunting predators, and predation by alien mammals, such as black rats, *Rattus rattus*, poses a major threat to the conservation of many avian species globally (17). Inducing populations of wild predators to ignore the cues of vulnerable prey could relax the risk faced by prey during critical times, such as nesting. This study aimed to test whether attack rates on birds' eggs by free-living black rats could be reduced in a natural setting by manipulating the spatial and temporal application of olfactory nesting cues (feathers and feces). Eggs and nesting cues of domestic quails *Coturnix coturnix japonica* were used as the prey, simulating a native ground-nesting species.

We compared the effects on prey survival of two different factors that altered the olfactory environment and another factor to control for visual cues, using a factorial experiment that resulted in eight distinct treatment combinations (Table 1). The first factor examined two treatments associated with the timing of the prey and odor introduction (see Table 2 for details of each factor). The first treatment was odor preexposure, which involved repeatedly applying prey odor cues into the environment for 7 d before the introduction of prey to temporally decouple the cue from the reward. This process ensured that wild predators had repeated opportunities to experience an unrewarded prey odor without encountering the prey. As predators learn that the cue does not predict a reward, it should become part of the background of their olfactory environment and we expected that the cue would no longer be actively investigated (18). The second treatment simulated a normal situation by introducing the prey and odor concurrently. The second factor examined the effect of

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Table 1. Each of the three experimental factors had two treatments that amalgamated factorially into eight distinct experimental treatments

Experimental treatment	Factor 1: timing of prey and odor introduction	Factor 2: odor distribution	Factor 3: nest layout (visual control)
1	Odor preexposure	Camouflage	Matrix
2	Concurrent	Camouflage	Matrix
3	Odor preexposure	Camouflage	Random
4	Concurrent	Camouflage	Random
5	Odor preexposure	Patchy	Matrix
6	Concurrent	Patchy	Matrix
7	Odor preexposure	Patchy	Random
8	Concurrent	Patchy	Random

odor distribution with two treatments. The first treatment was a form of chemical camouflage, which involved using fresh prey odor to obscure the location of prey by placing odor throughout the environment against which prey are inconspicuous to predators that hunt by smell (19). This technique decouples the cue from the reward spatially and relies on predators recognizing when a disproportionately high level of search effort is required to find prey that are relatively inconspicuous against a background of prey odor. Searching predators only encounter prey intermittently, despite the odor occurring throughout a large area. Such low foraging efficiency should cause an optimal forager to “give up” and search for alternate prey (1, 6). The second treatment replicated a normal, patchy odor distribution with odor only placed with prey items simulating the accumulation of olfactory cues at nests. The visual cue control factor involved placing artificial nests in one of two configurations to account for unavoidable visual cues that rats could use to find prey (factor 3: nest layout); nests were placed either at all grid points in a matrix layout or only at randomly selected grid points where prey were to be located. All nests contained at least one plasticine egg to allow for predator identification (*Materials and Methods*). The prey odor was either placed in artificial nests (if nests were in a matrix layout) or straight onto the ground (when nests were randomly distributed).

Both olfactory techniques, derived from learning and foraging theory, rely on two additional cognitive processes to improve prey survival: (i) predators must generalize the odor of the cue with the prey and not discriminate between them (20); and (ii) predators must learn that investigating the cue is not profitable, either completely, in the case of olfactory preexposure, or economically, in the case of camouflage (9, 21, 22). If these conditions are met, the odor should be ignored if subsequently detected so that the relevant prey remain unnoticed by predators.

We postulated three hypotheses (Table 3): First, that olfactory preexposure would lead to greater survival of prey as rats learned that prey odor was not associated with food and ignored it before

the introduction of the prey. Under this “demotivation” hypothesis, rats should lose interest in the unrewarded prey odor, evident by a marked decline in activity toward the cue during the pre-exposure period, and then continue to lack motivation to investigate the odor cue despite the introduction of prey. Second, that chemical camouflage would lead to greater survival of prey as rats learned that the odor cue is an unreliable indicator of the location of prey. Under this “optimal foraging” hypothesis, inefficient foraging tactics are quickly disregarded and the odor cue ignored despite the occasional presence of prey. Third, a combined hypothesis where the demotivation effect caused by pre-exposure is only evident when the odor is applied as camouflage before prey are introduced, leading to significantly higher prey survival only when both treatments are present.

Results

Prey introduced to grids that had been preexposed to odor had 62% higher survival after 7 d than prey in grids, where prey and odor were introduced concurrently (Fig. 1A). The higher rate of survival was a result of rats attacking fewer nests on preexposed grids by the time prey were introduced (Fig. 2A). Following the introduction of prey, nest visitation (a proxy for foraging activity) was significantly lower on preexposed grids than on grids where the prey and odor were introduced concurrently (repeated-measures ANOVA postprey introduction – timing of odor introduction: $F_{1,32} = 15.58, P = 0.0004$; time: $F_{6,27} = 6.52, P = 0.0002$). Odor preexposure (factor 1) was the only experimental factor that influenced prey survival (Cox proportional hazards effect likelihood ratio tests $df = 1, \chi^2 = 14.81, P = 0.0001$), with no difference in prey survival attributed to odor distribution (factor 2) or nest layout (factor 3) (Fig. 1B and C). Microhabitat factors did not affect prey survival, nor were there any significant interactions between experimental factors. Similarly, apart from a general drop in rat attacks on nests over time across all treatments, the odor preexposure treatment was the only factor

Table 2. Descriptions of the two treatments within each of the three experimental factors

Experimental factor	Treatment A	Treatment B
1. Timing of prey and odor introduction	Odor preexposure: Odor applied for 7 d before the introduction of prey. Odor refreshed daily until prey attacked.	Concurrent prey and odor introduction: Prey and odor introduced on same day at same time. Odor applied daily until prey attacked.
2. Odor distribution	Camouflage: Odor applied at 36 evenly spaced points within 1 hectare. Prey only placed at nine randomly selected points.	Patchy: Odor and prey only placed at nine randomly selected points within 1 hectare.
3. Nest layout (visual control)	Matrix: Artificial nests containing plasticine eggs placed at 36 evenly spaced points within 1 hectare.	Random: Artificial nests only placed at nine randomly selected points within 1 hectare.

Table 3. Descriptions of the techniques tested by each factor and the associated hypotheses predicted to reduce attacks on prey

Factor	Treatment	Description	Predicted behavioral response	Hypothetical mechanism
1. Timing of prey and odor introduction	Odor preexposure	Odor placed in environment repeatedly before introduction of prey	Decline in predator activity at odor points before introduction of prey. Activity remains low following prey introduction resulting in high prey survival.	Demotivation possibly as a result of learning to disregard odor and filtering into olfactory background.
2. Odor distribution	Chemical camouflage	Odor spread in a grid pattern over a wide area at same time as prey introduced	Decline in predator activity throughout odor grid over time. Only random attacks on prey that decline over time resulting in high prey survival.	Optimal foraging: Odor is not a strong enough predictor of prey location to outweigh costs of investigating it.
Combined factor 1 and 2	Combination	Area has odor applied in a grid pattern for a period before introduction of prey.	Decline in predator activity at odor points before introduction of prey. Activity remains low following prey introduction resulting in high prey survival.	Demotivation possibly as a result of learning to disregard odor and filtering into olfactory background. Concentrated odor distribution reinforces the response.

that influenced foraging activity following the introduction of prey (repeated-measures ANOVA post prey introduction – timing of odor introduction: $F_{1,32} = 15.58, P = 0.0004$; time: $F_{6,27} = 6.52, P = 0.0002$) (Fig. 3).

Discussion

Prey survival was significantly better when predators were exposed to prey odor for a period before prey were introduced, supporting our demotivation hypothesis. Rats learned to ignore a non-rewarding cue, allowing the introduction of prey to occur without attracting attention and reigniting interest. Once the expectation of finding food dissipated, rats lost motivation to continue investigating the odor, enabling subsequently introduced prey to survive compared with those introduced at the same time as the conspicuous and attractive odor cue. Contrary to our optimal foraging hypothesis, chemical camouflage did not result in improved prey survival and rats rapidly found birds' eggs camouflaged among a similar olfactory background.

When prey and odors were introduced simultaneously, the rat's neophilic behavior toward new odors led to rapid predation of quail eggs regardless of other factors within the treatment, such as the layout of artificial nests or distribution of odor cues. The

initial interest of rats in the prey odor placed prey under intense pressure. The rat's motivation to investigate the odor cue waned after ~3 d, by which time approximately half the prey had been eaten in grids where prey and odor were introduced concurrently. As prey density declined and eggs became harder to find, rats probably lost motivation to keep investigating the odor and switched back to searching for familiar food. In grids without prey for the first 7 d, rats lost interest before the introduction of prey.

Neophilic behavior may hasten the transition of an initially conspicuous and attractive cue to part of the olfactory background. However, until this transition is complete, prey remain at risk. By temporally decoupling the cue from the prey, we exploited the normal perceptual filtering that occurs to sensory information gathered during foraging (i.e., we placed prey into the environment after predators' attention to it waned). The initial level of activity at nests suggests that black rats recognized cues associated with domestic quail odor and artificial nests as potential prey despite not having encountered the species previously (23), which may be a result of their generalist habits and a causal factor in their detrimental impacts on native bird populations globally (24). Motivation to investigate new, unrecognized food cues and disregard unrewarded odors are likely to be adaptive for alien predators and

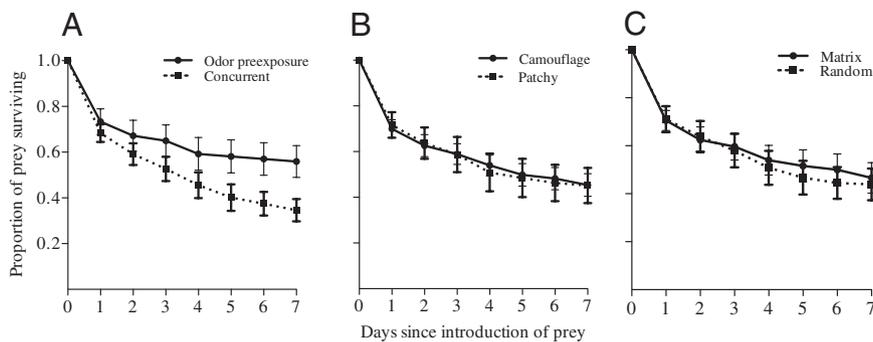


Fig. 1. Effect of the three experimental factors on the proportion of prey surviving following their introduction to the grid (\pm SEM). Grids where prey odor was preexposed (A) showed ~62% higher survival after 7 d than grids where prey and odor introduced concurrently (Cox proportional hazards effect likelihood ratio tests $df = 1, \chi^2 = 14.81, P = 0.0001$) ($n = 40$ grids), but there is no effect of chemical camouflage ($n = 40$ grids) (B), or the visual control for the artificial nests ($n = 40$ grids) (C), on prey survival time.

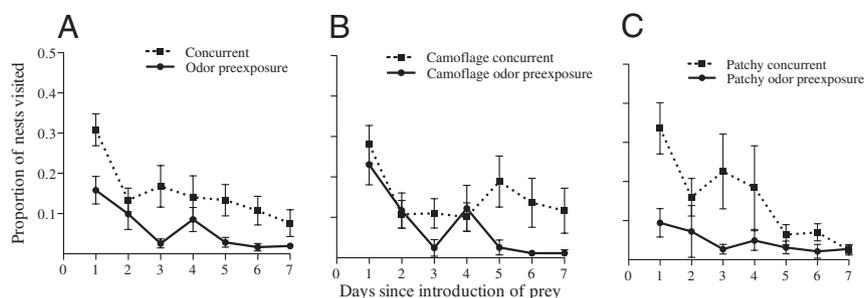


Fig. 2. By the time prey were introduced, grids where odor was preexposed had less rat activity than grids where prey and odor were introduced concurrently. The effect is most obvious when odor is patchily distributed at target nests only than when odor is throughout the grid (camouflage). Graphs show the proportion of artificial nests visited by rats during the days when prey was present (i.e., days 1 to 7 in grids where prey and odor were introduced concurrently and days 8 to 14 in grids that had odor preapplied). (A) The proportion of artificial nests visited by rats following the introduction of prey on all grids with and without odor preexposure (\pm SEM) ($n = 40$ grids); (B) grids with and without odor preexposure that also had camouflage applied ($n = 20$ grids); (C) grids with and without odor preexposure where odor was only applied to nine random points (patchy) ($n = 20$ grids).

promote optimal foraging behavior. The conditions needed to bring a previously disregarded odor cue back into the olfactory foreground remain unclear but most probably relate to both the amount and type of reinforcement experienced and the reward value of the subsequent prey. In this study, odor preexposure inhibited a reignition of rats' strong interest in the cue following the introduction of prey. After a brief rise, interest in the cue declined rapidly and remained extremely low for the following 6 d.

The response of rats to the different odor distribution treatments appears to explain the brief rise in foraging activity following the introduction of prey in odor preexposed grids (Fig. 2A). When odor preexposure occurred at only nine random grid points in the patchy treatment there was less evidence of a postprey introduction spike in foraging activity compared with when odor was preapplied to the entire grid in the camouflage treatment (Fig. 2B and C). It may be that following fewer encounters with the odor the rats learned to ignore a more general quail odor, reducing the likelihood of the eggs attracting attention after their introduction. Black rats should have the olfactory capability to distinguish between quail odor and egg odor (25), but generalizing may be less cognitively costly and adequate for normal foraging activities (16, 26). That rats required little spatial reinforcement to filter an unrewarding odor into their olfactory background suggests their cognitive processes are adapted for optimizing foraging efficiency in situations where encountering novel food is common.

By curtailing predator motivation to investigate prey odor cues, odor preexposure has the potential to protect vulnerable prey against wild predators for biologically meaningful periods of time (27). Reintroduced animals placed into new environments are conspicuous to predators (27), suffering rapid and high rates of predation that undermine attempts to reestablish populations (28). Applying odor cues across release sites before reintroductions should reduce risks to vulnerable individuals and reduce the likelihood they become "sitting ducks" to savvy predators. Knowledge of predator hunting behavior should inform the appropriate temporal and spatial scale at which to apply the relevant olfactory cues. The technique is likely to be particularly useful when native predators pose a threat to prey but are themselves of conservation concern, limiting options for predator control. Affecting events at the start of the predation sequence (29) is likely to be more successful than alternate approaches to reducing prey vulnerability, such as training prey to recognize and evade predators (30), which do not deter a predators' motivation to pursue the prey individual. Inducing predators to disregard prey cues taps into normal foraging behaviors to protect prey at risk from alien predators, moving information about prey location into a predator's olfactory background during critical periods. Our findings expand the relevance of predator learning and sensory perception as selective forces within olfactory systems, revealing

that subtle changes in predator motivation to pursue cues can benefit prey survival.

Materials and Methods

Artificial nests with domestic quail, *C. coturnix japonica*, eggs as the "prey" were used to simulate ground-nesting birds, with quail feathers and feces as the odor cue. A locally unfamiliar prey type and odor cue were used to ensure that learning of the prey:cue association by resident rats commenced with the experiment. Although several authors have criticized the use of artificial nests as a means of determining predation rates (31, 32), we used artificial nests to compare relative rates of predation between treatments rather than to infer actual rates of predation (ref. 8). This study was conducted in accordance with University of New South Wales Animal Ethics Approval 05/97A and Department of Environment and Climate Change Scientific License s11700.

Procedure. Field sites. Forty-one hectare grids were established between January and August, each consisting of a 6×6 square array of points ~ 16 -m apart, within natural bushland of Sydney Harbor and Lane Cove National Parks in Sydney (Australia). Grids were at least 500-m apart for independence and supported similar native eucalypt woodland, with a shrubby understorey and some areas of weed invasion. Previous studies had confirmed the presence of black rats throughout the study area, and rats were detected in all grids. Subsequent trapping studies in Sydney Harbor National Park found average rat densities of ~ 25 individuals per hectare (± 7.8) (33).

Prey and prey cue. Small artificial nests made of half a tennis ball covered in coconut husks were placed on the ground at grid points. Nests were either

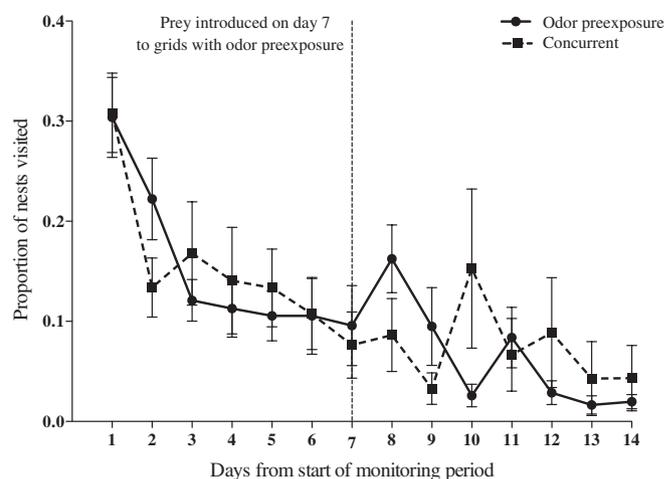


Fig. 3. Foraging activity of rats in all grids with and without odor preexposure over the entire 14-d monitoring period (\pm SEM) ($n = 40$ grids). Dotted line shows timing of prey introduction to grids where odor had been applied for the previous 7 d.

"target" nests, containing prey (a domestic quail egg) and a smaller plasticine egg, or "nontarget" nests containing two plasticine eggs of the same size as those in target nests. Target nests were located at nine randomly selected points and nontarget nests placed at other locations in the grid. Plasticine eggs allowed for predator identification at both target and nontarget nests (see *Predator* below for more details). Nonsulfurous plasticine (Rainbow modeling clay, Newbound P/L) was used to reduce the olfactory attractiveness of plasticine to predators. Prey odor (feathers, feces) was collected fresh from local domestic quail farms and frozen immediately to -20°C . Ten grams of quail odor was applied each day to each grid point or nest, approximating the natural rate of deposition from a pair of nesting birds and simulating the accumulation of odor at areas of concentrated activity. At the same time the odor was refreshed, nests were visually inspected for signs of attack, providing data on prey survival and nest visitation by predators. Inspections were conducted daily until all nests containing prey had been attacked, or up to 14 d.

Predator. The alien black rat is the only *Rattus* species recorded in the area (34) and has a home range of ~ 0.8 hectare (35). Therefore, predator identity could be determined from characteristic tooth imprints in plasticine eggs and compared with voucher skulls (36, 37). This commonly used method was considered reliable, as all other potential nest predators within the study area left distinctively different imprints to rats: that is, large birds, such as Australian Ravens, *Corvus coronoides*, Pied Currawongs, *Strepera graculina*, and Laughing Kookaburras, *Dacelo novaeguineae*; reptiles, such as Eastern Blue Tongue Lizards, *Tiliqua scincoides scincoides*; as well as other mammals, such as Common Brushtail Possums, *Trichosurus vulpecula*, Common Ringtail Possums, *Pseudocheirus peregrinus*, foxes, *Vulpes vulpes*, and domestic dogs, *Canis familiaris*. Any attack on a nest, regardless of whether the quail egg was completely taken or not, was recorded as a predation event and the nest considered "dead," but only attacks by rats were included in the analysis. Although we could only assume that the predator leaving marks on the plasticine egg also attacked the quail egg, rat teeth marks were often observed on the remains of quail eggs opened in a characteristic manner and left close to the artificial nest. Predation by other native and introduced species was censored so that survival up to the time of death was included in the survival analysis but the predation event was not (38).

Experimental Design. Three factors were tested in a multifactorial design: the two experimental techniques (olfactory preexposure and chemical camouflage) and a procedural control for visual cues associated with the artificial nests (nest layout). Each factor had two states (e.g., preexposure with odor or not) (Table 2) which, when combined factorially, resulted in eight distinct treatments (Table 1) that were applied randomly to grids ($n = 5$ per treatment, 40 grids in total). Each of the eight treatments consisted of a different combination of the states of three factors combined, with each state of each factor applied to half the grids (Table 3). To test for the effects of olfactory preexposure on prey survival (factor 1), half of all of the experimental grids

(20 grids) had prey odor added at grid points for 7 d before prey being introduced and when prey was introduced on day 8. The other 20 grids had both prey and odor placed at the relevant grid points from day 1 (i.e., no odor preexposure). In grids with olfactory preexposure, the target nests containing quail eggs were placed 1–2 m from the original odor point to mitigate location-specific learning that may interfere with responses to the treatment. To test the effect of chemical camouflage (factor 2) on prey survival, half of all of the grids were camouflaged and had prey odor placed at all 36 points to create a uniform odor background throughout the grid; the other noncamouflaged grids had odor placed at the nine target prey nests only and were referred to as "patchy." Because artificial nests were used to determine foraging activity and to hold prey odor and prey, the third factor controlled for these. To test if rats were using other visual and olfactory cues associated with the artificial nests to find them, rather than the prey odor, half of all of the grids (20 grids) were set out with artificial nests containing a plasticine egg at all 36 points (matrix layout); the other half had nests at the nine randomly selected prey points only (random layout).

Environmental Influences. To account for habitat influences on nest vulnerability, eight microhabitat variables were measured around each target nest (35). Within a 1-m^2 area around the nest, the percent area covered by bare ground, rock, leaf litter, woody debris, woody stems, and green vegetation was visually estimated. The density of vegetation up to 20-cm high was estimated using a $50\text{ cm} \times 20\text{ cm}$ coverboard at the four compass points of the 1-m^2 area, with the highest and lowest points used in the analysis. We used principal components analysis to remove correlation between the microhabitat variables and summarize the information within. Four distinct factors (or components) were chosen to include in further analysis (see *Analysis* below) based on the contribution of each factor to explaining the overall variance between sites (percent variance explained: 27.64, 15.90, 15.90, 13.85). A total of 73.3% of the variance between sites was accounted for by these four factors.

Analysis. We compared the effect of the treatment and microhabitat factors on prey survival using Cox's proportional hazards modeling (39). Repeated-measures ANOVAs examined the effect of treatment factors on foraging activity (nests attacked per day/total nests available) from the time of prey introduction and from day 1. Multivariate tests were used when sphericity assumptions were not met and the univariate Greenhouse–Geisser ϵ was less than 0.75 (postprey introduction: Mauchly's criterion = 0.21, $\chi^2 = 45.85$, $df = 20$, $P = 0.0008$) and univariate Greenhouse–Geisser ϵ -adjusted values were used when sphericity assumptions were met (whole experiment: Mauchly's criterion = 0.36, $\chi^2 = 29.10$, $df = 20$, $P = 0.09$) (40). Results were analyzed in JMP 8 (41).

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- MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. *Am Nat* 100 (916):603–609.
- Dall SRX, Cuthill IC (1997) The information costs of generalism. *Oikos* 80(1): 197–202.
- Tinbergen L (1960) The control of insects on pinewoods. I. Factors influencing the intensity of predation by songbirds. *Arch Neerl Zool* 13:265–343.
- Gendron RP (1986) Searching for cryptic prey: Evidence for optimal search rates and the formation of search images in quail. *Anim Behav* 34(3):898–912.
- Banks PB, Dickman CR (2007) Alien predation and the effects of multiple levels of prey naiveté. *Trends Ecol Evol* 22(5):229–230, author reply 230–231.
- Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theor Popul Biol* 9(2):129–136.
- Stephens DW, Krebs JR (1986) *Foraging Theory* (Princeton Univ Press, Princeton, NJ).
- Peled SA, Smith JNM, Boutin S (2010) A predator's perspective of nest predation: Predation by red squirrels is learned, not incidental. *Oikos* 119(5):841–851.
- Shettleworth SJ (2010) *Cognition, Evolution and Behaviour* (Oxford Univ Press, New York), 2nd Ed.
- Wilson DA (2009) Olfaction as a model system for the neurobiology of mammalian short-term habituation. *Neurobiol Learn Mem* 92(2):199–205.
- Hughes NK, Banks PB (2010) Interacting effects of predation risk and signal patchiness on activity and communication in house mice. *J Anim Ecol* 79(1):88–97.
- Burghardt GM (1990) Chemically mediated predation in vertebrates: Diversity, ontogeny, and information. *Chemical Signals in Vertebrates*, eds Macdonald DW, Muller-Schwarze D, Natynczuk SE (Oxford Univ Press, New York), pp 475–499.
- Linster C, Smith BH (1999) Generalization between binary odor mixtures and their components in the rat. *Physiol Behav* 66(4):701–707.
- Dreumont-Boudreau SE, Dingle RN, Alcolado GM, LoLordo VM (2006) An olfactory bidirectional discrimination in the mouse. *Physiol Behav* 87(3):634–640.
- Hudson R (1999) From molecule to mind: The role of experience in shaping olfactory function. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 185(4):297–304.
- Gottfried JA (2009) Function follows form: Ecological constraints on odor codes and olfactory percepts. *Curr Opin Neurobiol* 19(4):422–429.
- Blackburn TM, Cassey P, Duncan RP, Evans KL, Gaston KJ (2004) Avian extinction and mammalian introductions on oceanic islands. *Science* 305(5692):1955–1958.
- Mackintosh NJ (1975) Theory of attention—Variations in associability of stimuli with reinforcement. *Psychol Rev* 82(4):276–298.
- Ruxton GD (2009) Non-visual crypsis: A review of the empirical evidence for camouflage to senses other than vision. *Philos Trans R Soc Lond B Biol Sci* 364(1516):549–557.
- Cleland TA, Naria VA, Boudadi K (2009) Multiple learning parameters differentially regulate olfactory generalization. *Behav Neurosci* 123(1):26–35.
- Stephens DW (2007) Models of information use. *Foraging: Behavior and Ecology*, eds Stephens DW, Brown JS, Ydenberg RC (Univ of Chicago Press, Chicago), pp 31–58.
- Adams-Hunt MM, Jacobs LF (2007) Cognition for foraging. *Foraging: Behavior and Ecology*, eds Stephens DW, Brown JS, Ydenberg RC (Univ of Chicago Press, Chicago, London), pp 105–140.
- Dangles O, Irschick D, Chittka L, Casas J (2009) Variability in sensory ecology: Expanding the bridge between physiology and evolutionary biology. *Q Rev Biol* 84(1):51–74.
- Harris D (2009) Review of negative effects of introduced rodents on small mammals on islands. *Biol Invasions* 11(7):1611–1630.
- Uchida N, Mainen ZF (2003) Speed and accuracy of olfactory discrimination in the rat. *Nat Neurosci* 6(11):1224–1229.
- Wilson DA, Stevenson RJ (2003) Olfactory perceptual learning: The critical role of memory in odor discrimination. *Neurosci Biobehav Rev* 27(4):307–328.
- Banks PB, Norrdahl K, Korpimäki E (2002) Mobility decisions and the predation risks of reintroduction. *Biol Conserv* 103(2):133–138.
- Fischer J, Lindenmayer DB (2000) An assessment of the published results of animal relocations. *Biol Conserv* 96(1):1–11.
- Endler JA (1991) Interactions between predators and prey. *Behavioural Ecology: An Evolutionary Approach*, eds Krebs J, Davies N (Blackwell, Oxford), pp 169–196.

30. Griffin AS, Evans CS, Blumstein DT (2001) Learning specificity in acquired predator recognition. *Anim Behav* 62:577–589.
31. Moore RP, Robinson WD (2004) Artificial bird nests, external validity, and bias in ecological field studies. *Ecology* 85(6):1562–1567.
32. Thompson FR, Burhans DE (2004) Differences in predators of artificial and real songbird nests: Evidence of bias in artificial nest studies. *Conserv Biol* 18(2):373–380.
33. Hanson N (2011) Rats in the ranks—Demographic responses of an invasive species *Rattus rattus* to pest control in urban bushland remnants. *Masters of Philosophy (Research)* (University of NSW, Sydney).
34. Banks PB, Cleary GP, Dickman CR (2011) Sydney's plague outbreak 1900–1910: A disaster for foreshore wildlife? *Wildlife Responses to Disasters, Australian Zoologist*, eds Lunney D, Law B, Predavec M (Royal Zoological Society of NSW, Mosman, Australia), Vol 35, pp 1033–1039.
35. Cox MPG, Dickman CR, Cox WG (2000) Use of habitat by the black rat (*Rattus rattus*) at North Head, New South Wales: An observational and experimental study. *Austral Ecol* 25(4):375–385.
36. Moller AP (1989) Nest site selection across field-woodland ecotones: The effect of nest predation. *Oikos* 56(2):240–246.
37. Roos S (2002) Functional response, seasonal decline and landscape differences in nest predation risk. *Oecologia* 133(4):608–615.
38. Klein JP, Moeschberger ML (2003) *Survival Analysis: Techniques for Censored and Truncated Data* (Springer, New York), 2nd Ed.
39. Cox DR (1972) Regression models and life-tables. *J R Stat Soc, B* 34(2):187–220.
40. Lehman A, O'Rourke N, Hatcher L, Stepanski EJ (2005) *JMP for Basic Univariate and Multivariate Statistics—A Step-by-Step Guide* (SAS Institute, Cary, NC).
41. SAS Institute (2009) *JMP version 8.0* (SAS Institute, Cary, NC).