

Exploiting interspecific olfactory communication to monitor predators

PATRICK M. GARVEY,^{1,2} ALISTAIR S. GLEN,² MICK N. CLOUT,¹ SARAH V. WYSE,^{1,3}
MARGARET NICHOLS,⁴ AND ROGER P. PECH⁵

¹Centre for Biodiversity and Biosecurity, School of Biological Sciences, University of Auckland, Auckland, New Zealand

²Landcare Research, Private Bag 92170, Auckland, 1142 New Zealand

³Royal Botanic Gardens Kew, Wakehurst Place, RH17 6TN United Kingdom

⁴Centre for Wildlife Management and Conservation, Lincoln University, Canterbury, New Zealand

⁵Landcare Research, PO Box 69040, Lincoln, 7640 New Zealand

Abstract. Olfaction is the primary sense of many mammals and subordinate predators use this sense to detect dominant species, thereby reducing the risk of an encounter and facilitating coexistence. Chemical signals can act as repellents or attractants and may therefore have applications for wildlife management. We devised a field experiment to investigate whether dominant predator (ferret *Mustela furo*) body odor would alter the behavior of three common mesopredators: stoats (*Mustela erminea*), hedgehogs (*Erinaceus europaeus*), and ship rats (*Rattus rattus*). We predicted that apex predator odor would lead to increased detections, and our results support this hypothesis as predator kairomones (interspecific olfactory messages that benefit the receiver) provoked “eavesdropping” behavior by mesopredators. Stoats exhibited the most pronounced responses, with kairomones significantly increasing the number of observations and the time spent at a site, so that their occupancy estimates changed from rare to widespread. Behavioral responses to predator odors can therefore be exploited for conservation and this avenue of research has not yet been extensively explored. A long-life lure derived from apex predator kairomones could have practical value, especially when there are plentiful resources that reduce the efficiency of food-based lures. Our results have application for pest management in New Zealand and the technique of using kairomones to monitor predators could have applications for conservation efforts worldwide.

Key words: carnivore; conservation behavior; eavesdropping; interference competition; invasive species; monitoring; olfaction; pest management; pheromone; predator odor.

INTRODUCTION

Apex predators shape and drive community structure, either directly through agonistic encounters or indirectly as mesopredators alter their behavior in response to predation risk (Ritchie and Johnson 2009). Natural selection will encourage the development of mechanisms for subordinate species to recognize dominant predators and avoid confrontations (Kats and Dill 1998, Monclús et al. 2005). Olfaction, the primary foraging sense of most mammals, may mediate trophic interactions by allowing subordinate species to assess the risk of encounter (Roberts and Gosling 2001). Predators deposit odor into the environment, either unintentionally as by-products of metabolic processes or deliberately for communication (Ferrari and Chivers 2009, Wyatt 2010). In this context, communication is deemed to occur when the cues given by one individual influence the behavior of another (Wiley 1983). Odor signals, termed “kairomones” when intercepted by eavesdropping sympatric species, are

primarily produced for intraspecific communication and provide the receiver with information on the depositing species (Peake 2005, Ferrari and Chivers 2009). For example, temporal variation in scent quality can indicate the time elapsed since an odor was deposited (Bytheway et al. 2013) or odor can facilitate predator identification, which may then be related to the risk of encountering this predator (Schoeppner and Relyea 2009). Kairomones may additionally supply information that can help inform the foraging decisions of the eavesdropping species (van Dijk et al. 2008). Unlike visual or auditory cues, odor deposits indicate that a location was risky at some point in the past, but this may not relate to present risk (Kats and Dill 1998). Therefore odors can be ambiguous and require careful inspection to elicit all the information contained in a scent (Hemmi and Pfeil 2010).

Mammalian chemical communication has been exploited for a range of wildlife management applications: to reduce human-wildlife conflicts, improve population monitoring, influence habitat selection, reduce predation, increase the welfare of captive animals, encourage captive breeding, and to improve the success of release programs (Campbell-Palmer and Rosell 2011). Olfactory attractants are primarily food

Manuscript received 19 May 2016; revised 11 September 2016; accepted 8 November 2016. Corresponding Editor: Aaron J. Wirsing.

⁶E-mail: pgar874@aucklanduni.ac.nz

based, but occasionally non-prey pheromone lures such as beaver (*Castor canadensis*) castoreum or muskrat (*Ondatra zibethicus*) scent glands are deployed to attract target species (Long et al. 2012). Intraspecific (pheromone) lures, that stimulate territorial or social responses in conspecifics, have been deployed for wildlife management; for example, lures derived from the scent gland of culled American mink (*Mustela vison*), an alien species in Europe, were used to attract conspecifics to traps and proved as successful as a food based lure during control operations (Roy et al. 2006). Interactions between predators and prey have also been exploited to create deterrents, as predator odor may induce avoidance behaviors, reducing foraging damage by prey species (Apfelbach et al. 2005). Lures have yet to be developed that exploit interspecific olfactory communication between predators.

New Zealand has one of the highest proportions of threatened taxa in the world, a trend primarily driven by introduced invasive species (Clout 2001, Towns et al. 2006). Island faunas are particularly vulnerable to extinction (McKinney 1997), as many species evolved in the absence of mammals and therefore lack appropriate defensive mechanisms to avoid predation (Terborgh 1974). New Zealand's mammalian carnivores were introduced in the hope that they would act as biological control agents for pests such as rabbits (*Oryctolagus cuniculus*) but, as generalist predators, they attack vulnerable native species as well as introduced mammals (Wodzicki 1950, King and Powell 2007, Wallach et al. 2015). Trophic interactions also occur within this novel invasive predator guild, influencing behavior through interference competition, which will in turn cascade to lower trophic levels (Garvey et al. 2015). Since sympatric predator odor is likely to provoke a response in these mesopredators there may be an opportunity to exploit eavesdropping on olfactory cues to improve wildlife management outcomes.

Laboratory and field experiments on a range of different taxa have predominantly found that predator odor provokes anti-predator responses, often leading to avoidance by the subordinate species (Apfelbach et al. 2005, Monclús et al. 2005). However, the pervasive assumption that predator odor acts as a deterrent to a subordinate species has been recently questioned. Animals coexist in assemblages of closely related species that often use similar communication systems (Hughes et al. 2010), facilitating the possibility of bidirectional olfactory communication. Stoats and polecats (*Mustela putorius*) are naturally sympatric in Europe and display commonalities in gland secretions. These species may have evolved communication networks that allow for information exchange (Brinck et al. 1983, Erlinge and Sandell 1988, King and Powell 2007). Encounters between members of the same predator guild are dangerous, as potential gains are unknown and the risks of a confrontation are great (Hutchings and White 2000). Interspecific olfactory communication may diminish

these risks by providing information on a competitor without requiring a direct interaction.

Recent studies have shown that mesopredators eavesdrop on kairomones; although stoats display subordinate behavior in encounters with larger predators (ferrets *Mustela furo* and cats *Felis catus*; Garvey et al. 2015), the body odor of these dangerous adversaries proved to be a powerful attractant (Garvey et al. 2016). Ferret body odor, which has evolved as a mechanism for communication (Clapperton and Byrom 2005), provoked the strongest attraction, suggesting that coevolution and/or taxonomic relatedness may magnify responses. Further evidence highlighting the role of odor in mediating predator interactions was provided in a study on foxes (*Vulpes vulpes*), where urine from a dominant (dingo, *Canis dingo*) and a subordinate predator (cat) were investigated with greater frequency than conspecific odor or a control (Banks et al. 2016).

We devised a field experiment to test whether ferret body odor would alter the behavior and detection rates of three of New Zealand's most common invasive mesopredators: stoats (*Mustela erminea*), hedgehogs (*Erinaceus europaeus*), and ship rats (*Rattus rattus*). Hedgehogs and rats are important prey for ferrets, while ferrets dominate stoats in interspecific encounters and are known to kill the smaller mustelid (Wodzicki 1950, Smith et al. 1995). Common prey consumed by these four invasive species include: invertebrates, small mammals, reptiles, amphibians, and the eggs of ground nesting birds (Wodzicki 1950, Murphy and Dowding 1994, Smith et al. 1995, Jones et al. 2005). Additionally, stoats compete with ferrets for lagomorph, rodent, and avian prey (King and Powell 2007). Although these species form novel invasive guilds in New Zealand they are sympatric in parts of their native northern hemisphere range, which is important as evolutionary history is thought to influence the intensity of interactions (Connell 1983).

We examined how ferret odor affected detectability and activity of the three mesopredator species. We hypothesized that kairomones from a dominant predator would elicit eavesdropping behavior in mesopredators, based on ecological theory and the results of recent studies. We predicted that ferret kairomones would provoke eavesdropping behavior in mesopredators as measured by (1) increased detections at monitoring sites (i.e., site occupancy), (2) increased total number of observations across all monitoring sites, and (3) increased activity (measured as time spent investigating the odor source). We anticipated that mesopredators (4) would approach the ferret odor before approaching a food-based lure at a monitoring site and that (5) ferret odor would remain attractive for longer than a food-based lure. In the field experiment, deer (*Cervus* spp.) served as a procedural "control," as detections of this large herbivore should be unaffected by ferret odor. We predicted that deer would (6) show no change in occupancy, number of observations, or activity in response to ferret odor.

METHODS

Study location

This study was conducted on Toronui station, a sheep and cattle farm in the Hawke's Bay region of the North Island, New Zealand (39°10' S, 176°46' E). The landscape is dominated by pasture, with patches of forest consisting of mixed broadleaf angiosperm species at lower elevations and mānuka (*Leptospermum scoparium*) and kānuka (*Kunzea robusta*) at higher elevations. There was no recent history of predator control at our study area.

The study ran for 64 days, from January to March 2014. Twenty camera monitoring sites were established within and adjacent to forest patches ≥ 50 ha. Average distance between sites was 2.44 km, with a minimum distance of 900 m, to maintain spatial independence and to ensure that olfactory responses at a monitoring site were unlikely to be biased by other sites. Fourteen sites were established at the forest/pasture margin and a further six sites were placed within a forest patch. Forest margins are used extensively by cryptic predator species (Morris and Davidson 2000), so these areas were selected to maximize the likelihood of detection.

Study species

Ferrets are the second largest terrestrial predator in New Zealand, after feral cats, and are the largest of three introduced mustelid species (Wodzicki 1950). Ferrets predominantly use olfaction to communicate, depositing enduring odors that proclaim territorial boundaries or signal reproductive receptiveness (Clapperton 1989). Chemicals secreted from glands on the chin and neck are deliberately rubbed onto surfaces, often when caching food or after a new den site has been established (Clapperton 1989). Ferrets, as with all mustelids, possess ventral glands (Macdonald 1985) and scent marks have evolved to convey detailed information to conspecifics on the social, reproductive, and health status of the depositing individual (King and Powell 2007, Hughes et al. 2010).

Stoats are a highly successful alien predator, designated as one of the world's 100 worst invasive species (Lowe et al. 2000). They occur predominantly in forests, but also in grassland, and are one of the primary agents of decline for over half of all forest birds currently threatened in New Zealand (King and Powell 2007, Innes et al. 2010). Stoat populations can fluctuate due to resource pulses of prey, making them elusive when at low densities in certain environments, seasons, or in particular years (King and Powell 2007). They have keen olfactory senses that are employed to track prey, and for intraspecific communication (Erlinge and Sandell 1988). Our study was conducted in January–March, when the stoat breeding season has completed and sub-adults are actively searching for new territories (King and Powell 2007).

Hedgehogs were introduced primarily to help reduce garden pests, but have become major pests themselves, preying on native insects, reptiles, and the eggs/fledglings of ground-nesting birds. Introduced onto offshore islands in the UK, hedgehog predation resulted in dramatic declines in wading birds (Jackson and Green 2000). Hedgehogs are found across a range of habitats and primarily employ olfaction while foraging for food (Wodzicki 1950, King 2005).

Ship rats arrived as stowaways on ships and have successfully invaded many islands worldwide, including those of New Zealand (Russell and Clout 2005). They are generalist foragers and are associated with extinctions or declines of numerous indigenous species including reptiles, flightless invertebrates, burrowing seabirds, and passerines (Towns et al. 2006).

Ferret odor

Body odor from captive ferrets was collected by placing a clean towel in their bedding area, where it would be in direct contact with the donor animal. Predator body odor has stronger endocrine and behavioral effects on prey than other odors such as urine or feces, as it may indicate a high likelihood that the predator is nearby (Apfelbach et al. 2005). Male ferrets were selected as donor animals as male body odor is more pungent due to greater concentrations of an aromatic compound (indole), and males are a greater threat to mesopredators by virtue of their size (Clapperton et al. 1988). Towels were placed in the bedding area of individual ferrets for 1 month to ensure the material was thoroughly impregnated with odor. Towels were inspected to remove any excreta before being cut into 15-cm² segments and stored in a freezer (−80°C) until required, up to a maximum duration of 2 months.

Ferret odor was tested alongside rabbit meat, which is the standard lure used to trap carnivores in New Zealand (Wodzicki 1950, Pierce et al. 2007), to assess whether it could improve the detection rate of mesopredators. A previous pen trial had tested stoats' response to three odor treatments: rabbit meat, ferret odor, and rabbit meat + ferret odor combined (G. Morriss, *unpublished data*). The grouping of both odors together provoked the greatest attraction for stoats and therefore our field trial compared the rabbit + ferret treatment against the rabbit treatment. Comparing various bait types for stoats, Pierce et al. (2007) found that fresh rabbit meat was the most effective. Rabbit meat typically remains in traps for periods ranging from 1 to 3 weeks, but this can be extended to several months where site access is constrained (McMurtrie et al. 2011).

Perforated plastic vials were used to allow odor volatiles to disperse while preventing removal of the lure. Each vial (9 × 3 cm) was drilled with ~50 holes that were 5 mm in diameter. Two vials were used at each monitoring site, one placed at the base of a steel post, with the second placed 20 cm from the base, enabling us to

distinguish between approaches to a specific container. Vials were secured to the ground using pegs to ensure that the camera remained trained on the container. The standard size of a vial was used as a reference to estimate the head-body-tail length of *Rattus* spp., which facilitates identification. We randomly deployed one of two possible treatments at each site. For the first treatment one vial received a portion of rabbit meat (3 g), while the second vial remained empty. For the second treatment, rabbit meat was again added to one vial, but the second vial contained 15 cm of towel that had been impregnated with ferret body odor. Each treatment was deployed at one-half of the sites for the first 32 days, and rotated across sites for the second 32-day period, which ensured all sites received each treatment over the study.

Camera trapping

A total of 40 infrared cameras, triggered by heat and/or motion, were deployed for the study. Cameras were placed in pairs (matched by model type) at each monitoring site, one mounted horizontally and one vertically. Four types of cameras were used: Reconyx Hyperfire PC 900 (26) (Reconyx, Holmen, Wisconsin, USA), LTL Acorn Ltl 5210A (10) (Shenzen LTL Acorn Eletronics, Sanzao Town, Jinwan District, China), Moultrie M990i (2) (Moultrie, New Zealand) and Bushnell (2) (Bushnell Outdoor products, Overland Park, Kansas, USA). Detection efficiency may vary between models (Glen et al. 2013), but cameras were assigned to a monitoring site for the entire study, to ensure consistency across treatments.

The design of our study was influenced by the attributes of our focal species (stoat/hedgehog/rat). In habitat (pasture and native bush) similar to our study area, the average home ranges (male–female) are: stoats, 145–75 ha; hedgehogs, 9.6–4.2 ha; and ship rats, 3.76–1.06 ha (King 2005). These home ranges informed our decision on camera spacing so that we reduced the risk of detecting the same individual at multiple monitoring sites (Rovero and Marshall 2009). Smith et al. (2015) recommended a spacing of <700 m to ensure a control device is encountered by a female stoat. As stoats have the largest home ranges of the targeted mesopredators, we set the spacing of monitoring sites at a minimum of 1 km to minimize multiple recordings of the same individuals, although two sites were 900 m apart due to logistical constraints.

The optimum camera orientation when photographing small mammals depends on the target species, although the most suitable orientation has even been shown to vary between studies on the same species (Smith and Coulson 2012, Taylor et al. 2014). We therefore evaluated two orientations and decided a posteriori on the optimum configuration for our target mesopredators. Vertical cameras were mounted on a steel post, facing downwards from 1.5 m above the ground, with the vials placed in the center of the field of view. Horizontal cameras were mounted on timber stakes 1.5 m away from the base of the steel post. These cameras were mounted

5 cm above ground level, which is approximately the shoulder height of the target mesopredators. All cameras had identical settings or as close as possible where slight variations existed between models: high sensitivity, three photographs per trigger, and no delay between triggers. Vegetation was removed to allow for an unobstructed field of view and to minimize false triggers. Camera batteries and memory cards were replaced after the first month. Metadata (date, time, location) were extracted from the images using R v. 2.14.1 (R Development Core Team 2015); the function designed for this process, and associated information is provided in supporting material (Data S1: Metadata S1).

Data recording and analysis

Cameras that were orientated horizontally documented the greatest number of species, both in terms of observations (independent record of an individual) and total number of photographs. We therefore chose the horizontal orientation at all sites, with the vertical orientation only selected when the horizontal camera was out of commission. We considered the selected camera at each monitoring site to be an independent sampling unit.

Data were analysed for differences in observations or behavior of the target mesopredators, following the addition of ferret odor. To distinguish photographs of separate animals from repeated photographs of the same individual, we plotted histograms of the time elapsed between consecutive photographs for each species (Brook et al. 2012). Most consecutive photographs of the same species occurred <5 minutes apart, suggesting that these were repeated detections of an individual during one visit to the monitoring site. We considered records of a species to be independent at a monitoring site if detections were separated by more than 30 minutes, unless individuals could be distinguished. The following variables were calculated (1) observation rate, (2) triggers per observation, (3) site occupancy, (4) observations per period, and (5) mesopredator behavior. A summary of the response variables and related predictions are included in Table 1. *Observation rate* was defined as the number of observations per 100 trap days (1 trap day = 1 camera trap set for 24 h; Rovero and Marshall 2009, Glen et al. 2014). Cameras were set to record in bursts of three photographs each time they detected motion; we refer to each burst with at least one image of an animal as a trigger. The *observation rate* of mesopredators is a consequence of an individual's detection of the odor and subsequent behavioral response. These factors will change as a scent attenuates or the perceived value of investigating an odor changes. *Triggers per observation*, an index of a species activity within the camera's field of view, were calculated at each monitoring site: number of camera triggers divided by number of independent observations. A mesopredator's behavioral responses and engagement with an odor will directly influence the time spent in front of a camera and the variable *triggers per observation* captures this information.

TABLE 1. Predictions and associated response variables.

Prediction	Response variable
(1) Kairomone (ferret odor) will increase detections at a monitoring sites	(a) independent observation, (b) observation rate, (c) site occupancy
(2) Kairomone will increase total observations across all sites	observation rate, site occupancy
(3) Kairomone will increase activity at a site	(d) triggers per observation, (e) mesopredator behaviors
(4) Kairomone will be initially approached in preference to rabbit odor	mesopredator behaviors
(5) Kairomone will sustain attraction over time	(f) observations per period: triggers per observation
(6) Kairomone will not influence deer behavior	observation rate, site occupancy, triggers per observation

Notes: (a) A species record was defined as an *independent observation* if detections were separated by more than 30 minutes (unless individuals could be distinguished). (b) *Observation rate* was the number of observations per 100 trap days (1 trap day = 1 camera trap set for 24 h). (c) *Site occupancy* is a binary response variable with 1 indicating a species was detected at the monitoring site and 0 indicating non-detection. (d) *Triggers per observation* is the number of camera triggers divided by number of *independent observations*. (e) *Mesopredator behaviors* were a group of behaviors including cautious approach, scent marking, contact sniffing, self-anointing, and biting of the odor vial. (f) *Observations per period* are independent observations in each period of 8 days.

Site occupancy is a binary response variable with 1 indicating a species was detected at the monitoring site at least once during the study, and 0 indicating non-detection. Mesopredator *site occupancy* will be determined by a species' abundance and range, but occupancy will also be a function of the detection probability, which may be influenced by the odor treatment. Occupancy models that explicitly account for imperfect detection provide an index of abundance for species without identifiable markings (Meek et al. 2014). *Site occupancy* was used as the binomial presence/absence measure of a species at a site (MacKenzie 2006). Accurate estimation of species occupancy should account for imperfect detection, i.e., a species may be present at a site but not detected (MacKenzie 2006). This requires sufficient data to estimate detection probability. When detections were too few to estimate detection probability, naïve occupancy estimates were calculated. These ignore detection probabilities and will therefore be biased low. Monitoring periods were divided into intervals of 5 days and we ran a single species single season model framework to estimate occupancy in the software package PRESENCE 9.0 (Hines 2006). We also divided the 32-day treatment period into four intervals of 8 days. An 8-day interval is comparable to the weekly re-baiting protocol used for most trapping operations (e.g., McMurtrie et al. 2011) and this enabled us to analyze change over an operational time scale. *Observations per period* are the *independent observations* in each period of 8 days for each species, and cameras active for shorter durations were excluded from the analysis. *Observations per period* will reveal changes in mesopredator behavioral responses over time, as a scent attenuates or the value of investigating the potential resource diminishes.

Mesopredator behaviors were recorded that may help to explain responses to dominant predator odor. These included cautious approach, scent marking, contact sniffing, self-anointing, and biting of a lure vial. We were able to categorize *mesopredator behaviors* from images as they each had distinct, recognizable, body movements. Cautious approach was assessed by the mesopredator's body posture on its initial approach and also by the time taken for the individual to reach the vial after triggering

the camera. Contact sniffing was defined as touching a vial with the nose or tongue and we recorded which odor vial was first contacted on a visit. Self-anointing behavior is defined as an animal spreading its odor through its pelage by licking, which may act as a deterrent to predators (Weldon 2004).

We analysed the effect of the ferret odor using generalized linear mixed models (GLMM), from the MASS package in R (Venables and Ripley 2002), which enabled us to assess the influence of fixed and random effects. The response variables for the analysis were *observation rate* and *triggers per observation*. A Poisson error distribution was selected as we had continuous count data (Venables and Ripley 2002). The fixed effect included in the model was "treatment" (rabbit or rabbit + ferret) and "order" (first or second), while "site" was entered as a random effect, to account for the non-independence of errors associated with repeated measures on the same monitoring site. The fixed effect "order" was included in the model to test whether the deployment of a treatment at a site influenced mesopredator detections in the following period. Models were assessed by plotting the residuals and testing for overdispersion. Where results of the GLMM revealed significant treatment effects, we constructed additional species models for the four 8-day time periods, with the response variables *observations per period* and *triggers per observation*, to assess each period's contribution to the significant result. Differences in mesopredator *site occupancy* and additional *mesopredator behaviors* were assessed using Fisher's exact test. To reduce the risk of experiencing a Type I error as a result of conducting multiple comparisons, we used the Benjamini-Hochberg method to control for the false discovery rate (FDR; Benjamini and Hochberg 1995). This approach provides greater power than conventional Bonferroni-based methods, balancing the risk between Type I and Type II errors by describing the proportion of significant tests that are actually null (Verhoeven et al. 2005, Waite and Campbell 2006). We interpret $P \leq 0.05$ as significant if the FDR equivalent of a P value was also ≤ 0.05 . All statistical analyses were performed in the R environment (version 2.14.1, R Development Core Team 2015).

TABLE 2. Summary of sampling effort and camera trapping results for the response of mesopredators (stoat, hedgehog, and ship rat) to the body odor of a dominant predator (ferret).

Species	Cameras set (functioning)	Camera days (mean)	Cameras with at least one detection	Total no. triggers	Total no. observations	Observation rate
Rabbit treatment						
Stoat	20 (19)	566 (29.78)	4	26	7	1.41
Hedgehog	20 (19)	566 (29.78)	17	318	95	16.78
Rat	20 (19)	566 (29.78)	13	258	74	13.07
Deer	20 (19)	566 (29.78)	6	86	26	4.59
Rabbit + ferret treatment						
Stoat	20 (19)	524 (27.57)	11	155	28	5.34
Hedgehog	20 (19)	524 (27.57)	16	856	162	30.92
Rat	20 (19)	524 (27.57)	13	281	98	18.70
Deer	20 (19)	524 (27.57)	7	97	28	5.34

Note: The definitions of *trigger*, *observation*, and *observation rate* are given in Table 1.

RESULTS

Camera trapping effort

Sampling effort totaled 1834 trap days for the 20 paired cameras, when both orientations were included. Two monitoring sites were removed from the analysis, one due to cattle disturbance and a second due to flooding. With the horizontal camera preferentially selected, there were 1090 trap days for analysis.

Observation rate and observations per period

Collectively across all sites, there were 465 independent observations of the three mesopredators: 288 with the ferret odor and 177 without, a 63% overall increase with the addition of the kairomone (Table 2). There was a corresponding increase in the overall *observation rate* for all three mesopredators. Also the number of mesopredator *observations per period* was greater with the addition of the ferret odor, and these differences were significant in periods 3 and 4 (Fig. 1).

Hedgehogs (55%) were the most frequently detected species based on *observation rate*, followed by rats (37%) and stoats (8%). The order of the treatments did not

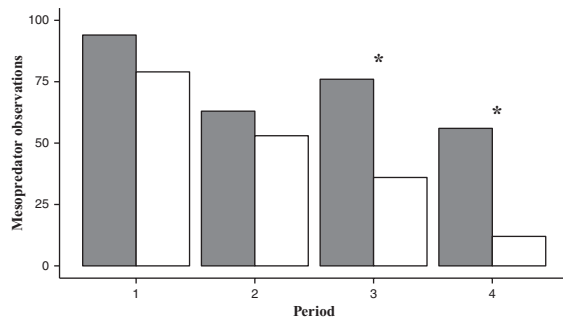


FIG. 1. Mesopredator (stoat/hedgehog/rat) *observations per period* for each of the four 8-day time periods. Treatments are represented by grey bar (rabbit + ferret) and white bar (rabbit). Asterisks denote a significant difference between treatments at ($P < 0.05$). [Color figure can be viewed at wileyonlinelibrary.com]

influence mesopredator *observation rate* (GLMM; $P = 0.74$). There was a significant increase in stoat *observation rate* with the addition of ferret odor (Fig. 2, Table 3). Stoats made up 10% of observations with rabbit + ferret odor and 5% with rabbit only. In addition to stoats, one ferret was detected at the rabbit treatment and a ferret and weasel (*Mustela nivalis*) were detected at the kairomone treatment. Treatment type did not significantly influence the number of observations or the *observation rates* for rats or deer (Fig. 2, Table 2) and there was some evidence of increased *observation rate* for hedgehogs. Stoat *observations per period* were higher at sites with ferret odor than those without, and there was a particularly marked difference after the first period (Table 4). Increases were also recorded for the hedgehog *observation rate*, with the deviation most pronounced in the third and fourth period (Table 4).

Triggers per observation

There were 6861 photographs taken of the target mesopredators, 4744 with the ferret and rabbit combination and 2117 with rabbit only, an overall increase of 124% with the addition of the ferret odor. The most photographed mesopredators were hedgehogs (71%), followed by rats (22%), and then stoats (7%). Treatment order did not influence *triggers per observation* for mesopredators (GLMM; $P = 0.37$). For hedgehogs, *triggers per observation* were significantly higher with the addition of the ferret odor, particularly in the first and second period (Table 4, Fig. 3). There was some evidence that *triggers per observation* for stoats were different for the entire month and significant differences were recorded in three of the four monitoring periods (Table 4, Fig. 3). Rats had fewer *triggers per observation* with the addition of ferret odor in period 1, but there were no differences in subsequent periods (Fig. 3).

Site occupancy

Fisher's exact test showed a significant increase ($P = 0.04$) in the number of sites where stoats were

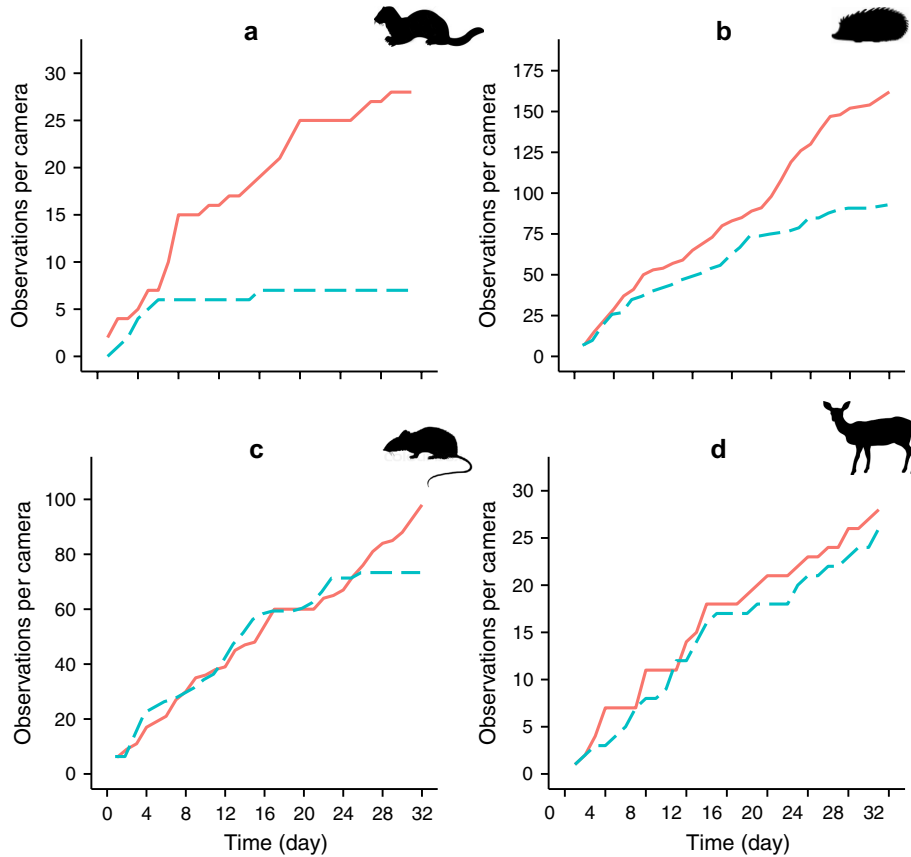


FIG. 2. Cumulative observations per active camera, recorded over the 32-day treatment period for (a) stoat, (b) hedgehog, (c) rat, and (d) deer. Treatments are represented by solid red line (rabbit + ferret) and dashed blue line (rabbit). [Color figure can be viewed at wileyonlinelibrary.com]

detected using rabbit + ferret odor, as compared to rabbit only. There was no difference in the number of sites with detections of hedgehogs ($P = 0.65$), rats ($P = 0.95$), or deer ($P = 0.93$). Stoats were detected at only 4 of 19 sites (21%) with the rabbit treatment, but were recorded at 11 of 19 sites (58%) with the addition of the ferret kairomone (Fig. 4; Appendix S1; Fig. S1). Average distances between pairs of cameras that detected stoats were 1.5 km (maximum = 2.1 km, minimum = 0.9 km). Estimates of

occupancy and distribution for rats and hedgehogs were similar with both treatments (Appendix S1; Fig. S1).

Mesopredator behaviors

In instances where the treatment employed was ferret odor and rabbit, we recorded 20 occasions where a stoat made contact with a lure vial on its first approach. The vial containing ferret odor was contacted on 15 of these

TABLE 3. General linear mixed models (GLMM) results for responses by mesopredators to ferret odor based on *observation rate* and *triggers per observation*.

Source of variation	Value	SE	df	<i>t</i>	<i>P</i>
Observation rate (model: GLMM, Poisson distribution)					
Stoat	1.46	0.27	18	5.34	<0.0001 †
Hedgehog	0.57	0.21	18	2.7	0.0158
Rat	0.22	0.2	18	0.83	0.29
Deer	0.15	0.35	18	0.44	0.66
Triggers per observation (model: GLMM, Poisson distribution)					
Stoat	1.1	0.49	18	2.23	0.0397
Hedgehog	0.81	0.28	18	2.94	0.0091 **
Rat	0.32	0.26	18	0.51	0.62
Deer	0.37	0.24	18	1.53	0.14

Notes: GLMM tested for difference between treatments: rabbit vs. rabbit + ferret odor. *P* values are in boldface type if they remained significant (≤ 0.05) after controlling for a false-discovery rate (FDR) of 5%. ** $P < 0.01$; † $P < 0.0001$.

TABLE 4. GLMM results for *observation rate*, *observations per period*, and *triggers per observation* for stoats and hedgehogs in each period.

Source of variation	Value	SE	df	<i>t</i>	<i>P</i>
Total mesopredator observation rate (Poisson)					
Period 1	0.17	0.2	17	0.85	0.41
Period 2	0.2	0.32	16	0.65	0.52
Period 3	0.82	0.23	15	3.61	0.0025**
Period 4	1.67	0.41	8	4.06	0.0036**
Stoat observation per period (Poisson)					
Period 1	0.61	0.49	17	2.05	0.06
Period 2	20.07	0.28	16	411.98	<0.0001†
Period 3	1.86	0.8	15	2.32	0.0348
Period 4	26.07	0.151	8	171.52	<0.0001†
Hedgehog observation per period (Poisson)					
Period 1	0.18	0.26	17	0.68	0.5
Period 2	0.33	0.28	16	1.17	0.26
Period 3	0.95	0.34	15	2.74	0.015
Period 4	1.1	0.048	8	2.22	0.056
Stoat triggers per observation (Poisson)					
Period 1	0.88	0.48	17	2.42	0.027
Period 2	21.24	0.37	16	450.38	<0.0001†
Period 3	2.19	0.41	15	2.48	0.026
Period 4	27.49	0.98	8	3475	<0.0001†
Hedgehog triggers per observation (Poisson)					
Period 1	0.94	0.34	17	2.74	0.015
Period 2	2	0.43	16	4.66	0.0003***
Period 3	0.47	0.34	15	1.38	0.18
Period 4	0.43	0.43	8	1	0.34

Notes: These two species displayed evidence of a treatment effects (Table 3). GLMM tested for difference between treatments: rabbit vs. rabbit + ferret odor. *P* values are in boldface type if they remained significant (≤ 0.05) after controlling for a false-discovery rate (FDR) of 5%. ***P* < 0.01, ****P* < 0.001, and †*P* < 0.0001.

occasions, whereas the rabbit meat lure was contacted on 5 occasions. There were 5 instances where stoats cautiously approached the ferret odor vial, yet similar slow deliberate movements were never recorded when rabbit meat was the sole lure. Scent marking by stoats, when the treatment included ferret odor, was observed on 6 occasions, once by body rubbing with the head/neck and otherwise by anal drag (Appendix S1: Fig. S2). Scent marking by stoats was not recorded when rabbit meat was the treatment and no scent marking was recorded by other mesopredators.

Hedgehogs engaged with the ferret lure for greater durations than any other mesopredator, repeatedly circling the vial. Self-anointing was recorded on 33 occasions at monitoring sites with ferret odor, but never with the rabbit meat treatment. This behavior appears not to be age specific, as it was recorded for hedgehogs of all sizes (Appendix S1: Fig. S3).

Rats attempted to bite into the kairomone vial on nine occasions, with most instances occurring (7/9) in the latter half of the trial; this behavior was only recorded for vials with ferret odor (Appendix S1: Fig. S4).

DISCUSSION

Our results support the prediction that kairomones from an apex predator should provoke eavesdropping by mesopredators, significantly increasing detections for stoats. Ferret body odor remained attractive for the

duration of the experiment whereas detections with rabbit meat decline steadily with time. Apex predator kairomone was engaged by hedgehogs for shorter durations as its freshness diminished, while stoats continued to maintain their interest in the latter stages of the trial. Inspection of aged predator cues is a relatively low-cost activity, but the quality of information available in a scent recedes as the freshness declines (Bytheway et al. 2013). The most marked responses to ferret odor were discerned for stoats. Stoat observations increased four-fold, their estimated *site occupancy* changed from rare to widespread, and stoats engaged with the rabbit + ferret treatment for substantially longer than the rabbit treatment. Hedgehogs also approached lures containing ferret odor more frequently and for significantly longer periods than lures with rabbit meat. Rat observation rates at the end of the first period were slightly greater with the addition of the kairomone, yet *triggers per observation* for a detected individual were 50% lower. Other studies have demonstrated rat avoidance of fresh kairomones (e.g., Burwash et al. 1998), with these responses diminishing as the predator cue aged (e.g., Apfelbach et al. 2005, Bytheway et al. 2013). Over the entire length of the trial, our results suggest that wild rats were not significantly attracted or repelled by ferret odor. These results concur with studies that have demonstrated no evidence that predator odor reduced (e.g., Bramley and Waas 2001) or increased (Banks 1998) rat detections over longer durations.

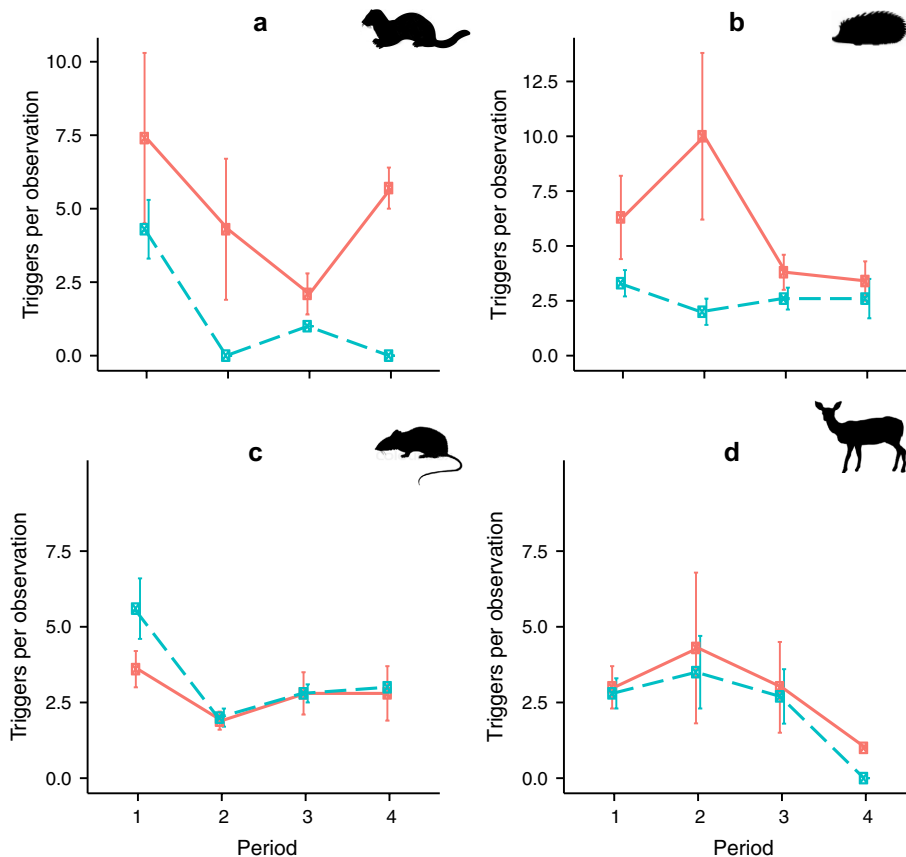


FIG. 3. *Triggers per observation* (mean \pm SE) for the four time periods for (a) stoat, (b) hedgehog, (c) rat, and (d) deer. Treatments are represented by solid red line (rabbit + ferret) and dashed blue line (rabbit). [Color figure can be viewed at wileyonlinelibrary.com]

Chemical cues make an uncertain world more predictable and olfaction is particularly important for species that are solitary, inhabit complex habitats, or are nocturnal (Kats and Dill 1998). When prey encounter predator scent, avoidance may be the optimum defense, and prey frequently avoid a detected kairomone (e.g., Dickman and Doncaster 1984, Jędrzejewski et al. 1993). However, mesopredators, particularly highly mobile species, encounter a myriad of chemical cues that potentially provide a rich source of information (Bytheway et al. 2013). Careful evaluation of a kairomone is needed to determine the direction in which a predator travelled, which can be assessed by variation in odor intensity along a scent trail. Informed prey are more difficult to capture and as stoats and hedgehogs are predominantly solitary foragers, these species should gain greater benefit from eavesdropping than gregarious species that can be warned by conspecifics (Ridley et al. 2014). However, inspection behavior is not without risk as the scent depositing predator may remain in the vicinity or an intended recipient (conspecifics) could be attracted to the odor. The persistence of eavesdropping behavior suggests that kairomone investigation provides fitness benefits to a species, despite the associated danger.

Close approach to the predator odor may be necessary to activate the appropriate olfactory receptors. The vomeronasal organ (VNO), which is a chemoreceptor, detects non-volatile compounds and requires direct physical contact with the source (Papes et al. 2010). Most mammals, including studied Mustelidae such as ferrets, possess a functioning vomeronasal organ (Estes 1972, Woodley et al. 2004). The purpose of the VNO was thought to primarily relate to the detection of chemical cues from conspecifics, but recent discoveries have demonstrated that, when the VNO is destroyed, it inhibits an animal's ability to perceive predator odor (Zhao and Liu 2015). Mesopredators may therefore approach the predator scent to assess non-volatile compounds encoded in the chemosignal. This need for direct contact suggests that predator odor could be an effective attractant, as it increases the likelihood of a target species interacting with a camera trap or control device.

The response of stoats to ferret odor differed from those of other mesopredators. This may be because stoats are primarily competitors of ferrets, whereas the other mesopredators are primarily prey. A kairomone may provide important additional information to a competitor, such as the foraging activity of a rival species (van

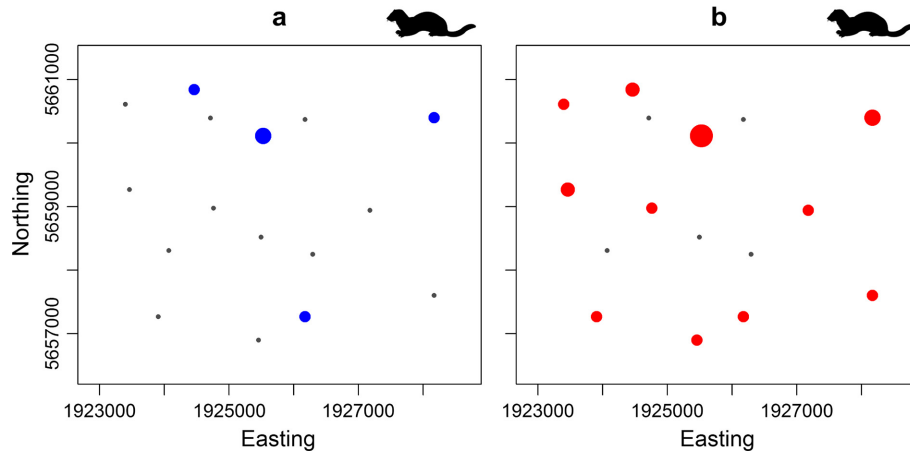


FIG. 4. Stoa site detections with (a) rabbit (blue points) or (b) ferret + rabbit (red points). The size of a point indicates the number of observations at a particular monitoring site. Monitoring sites that did not detect stoats are illustrated with black dots. Distance between consecutive ticks on the x and y axis are 1 km. [Color figure can be viewed at wileyonlinelibrary.com]

Dijk et al. 2008) or the location of common den sites (Dowding and Elliott 2003), whereas the freshness of the scent may be the most important characteristic for prey, facilitating risk assessment (Bytheway et al. 2013). Stoats, given their greater agility, would be at less risk of injury or death than the other mesopredators if a ferret was encountered in an open area. Mesopredator' responses may therefore be additionally influenced by the level of risk posed by the dominant predator.

Increased stoa detections across sites with the addition of the kairomone are more likely the result of multiple stoa detections, rather than increased activity by a few stoats. The average home range of a stoa (King and Powell 2007) equates to a diameter of 1.36 km (male) and 0.98 km (female), based on a circular home range. Using these estimates and stoa detections across sites, there was one pair of cameras that a female could travel between and three pairs that a male could travel between, at the maximum extent of an average home range. Home ranges of stoats overlap within and between the sexes in all seasons (King and Powell 2007). Breeding cycles would not influence stoa detections, but dispersing sub-adults could appear or reside in our study area. Given the topography of the study area, distances between cameras, and overlapping home ranges, it is more likely that we detected multiple stoats. Similarly, detections of other mesopredators are unlikely to be a function of movement given the distances between cameras and the circular diameter of home ranges: rat (male 0.22 km and female 0.11 km) and hedgehog (male 0.35 km and female 0.23 km).

Visits by mesopredators may have increased the olfactory information available at a monitoring site. Kairomones have been shown to influence the behavior of sympatric predators (Garvey et al. 2016) and the build-up of chemical information at a site may influence subsequent visitations. Odors deposited unintentionally, as an individual moves around in its environment, would attenuate quickly and their attractiveness would be superseded by

fresh odor deposits. However, odor signals (scat, urine, or body odor) that are deposited intentionally, may persist for longer in the environment and these signals may create a web of information among sympatric predators (Banks et al. 2016). Stoats were the only mesopredator recorded intentionally scent marking beside the ferret odor, both by body rubbing and defecating, which occurred during 21% of observations. This behavior is difficult to explain if the subordinate species wished to remain inconspicuous. Based on our information, scent marking did not increase the detection probability of conspecifics or sympatric mesopredators, as visitation rates were consistent before and after scent marking. However, there were only six documented instances of scent marking, which makes these results inconclusive.

Mesopredators may be attracted to dominant predator odor to locate prey, carrion, or den sites, as eavesdropping for resources occurs between species that occupy the same trophic levels (Peake 2005, van Dijk et al. 2008). Stoats do not make their own dens, but use those of other animals (King 2005) and may eavesdrop on ferret scent to help locate appropriate sites. In support of the idea that stoats investigated the odor to acquire resources, one study that radio-tracked mustelids recorded nine occasions where dens were shared sequentially by both ferrets and stoats (Dowding and Elliott 2003). Scavenging for food may also potentially explain attraction to kairomones, as stoats, hedgehogs and rats may associate aging ferret odor with the possibility of locating the partial remains of prey.

Our study fell within the breeding season of hedgehogs in New Zealand (King 2005) and the attraction displayed by hedgehogs, i.e., repeatedly circling the kairomone vial, is a behavior that appears very similar to the "cart-wheeling" performed by males during courtship (King 2005). Hedgehogs were also photographed self-anointing on more than 30 occasions: they are known to self-anoint with a range of novel, strong-smelling, or toxic substances.

The basis of this behavior is unknown; it may act as a deterrent to predators or alternatively self-anointing may play a role in mating behavior (Weldon 2004, King 2005).

Management applications

A major challenge for controlling invasive species is monitoring populations at low densities. Responses to a dominant predator odor, such as increased attraction and engagement, can be exploited to improve conservation outcomes and the reliability of monitoring information. Exotic species that decline after intervention, or invade new ecosystems, are acutely aware of established competitors and conspecifics (Pyšek and Richardson 2010). New Zealand's pest-free islands are important refuges for native animals and a kairomone lure could be deployed for long term monitoring and interception. For example, a stoat that invaded Kapiti Island, 5 km off the coast of New Zealand, proved extremely difficult to locate and expensive to remove (Prada et al. 2014). Eventually, after an extensive operation, the stoat and its offspring were captured, with the sole male offspring entering a trap that was treated with the pheromones of a female stoat. Reduction in intra- and interspecific competition in managed ecosystems leads to greater resource availability and a non-food-based attractant would be advantageous in these situations (Glen et al. 2013). Stoats are extremely difficult to detect at low densities (Choquenot et al. 2001) and monitoring in this study using only a rabbit lure would have substantially underestimated their prevalence. When eradicating an invasive population, it is essential to put all animals at risk and variability in temperament between members of a population leads to inconsistent responses to chemical signals (Réale et al. 2007). Costs of eliminating the last few survivors may be disproportionately high (Nugent et al. 2007) so increasing the range of lures may improve capture rates, thereby ameliorating the costs of mop-up operations. In addition to the management of invasive species, animals are also live-trapped for translocation, to collect biological samples, and to fit monitoring devices. The scent of a dominant competitor may always be worth investigating, so a kairomone lure could function effectively in these situations.

Our findings could also have applications for invasive mustelid management outside of New Zealand. American mink (*Neovison vison*) are listed as one of 37 invasive alien species by the European Union and member states are required to take measures to ensure early detection and rapid eradication of listed species. Harrington et al. (2009) demonstrated that American mink are attracted to polecat odor. As ferrets are a sub-species of polecats, and considering the results from our study, ferret kairomone may be an effective management tool for mink.

Camera traps are being used increasingly in wildlife monitoring, and can operate for extensive periods (Meek et al. 2014). However, most scent lures do not remain attractive for comparable durations. This incongruence between camera capabilities and lure viability may lead to

inefficient monitoring devices or require labor-intensive refreshing of lures. Ferret pheromones have evolved to endure in the environment to maximize the probability of interception (Clapperton 1989), making pheromones an ideal natural long-life lure. Camera traps can also help assess wildlife populations by identifying naturally marked animals, a powerful nonintrusive technique requiring clear images to distinguish among individuals (Trolle and Kéry 2003). Increasing an animal's engagement at a monitoring site would help to reduce the number of unidentified individuals. Similarly, hair collected for DNA analysis requires the target species to interact with sampling devices. The significant increase in engagement observed by two mesopredators in our study suggests that dominant predator odor could be exploited in these situations.

Olfaction is the main sensory perception in many mustelids yet its potential role in wildlife management has not yet been fully realized. Monitoring with ferret kairomones changed our assessment of stoat abundance and distribution. Mustelidae are often considered rare, due to limited reliable records, making it difficult to accurately assess their distribution, abundances, and therefore their appropriate conservation status (Ramírez-Chaves et al. 2016). For example, accurate assessment of populations of cryptic mustelids, such as the marbled polecat (*Vormela peregusna*), Patagonian weasel (*Lyncodon patagonicus*), and Colombian weasel (*Mustela felipei*) are hampered by very low sighting rates and a scarcity of records (Ramírez-Chaves et al. 2016). The use of ferret kairomones to aid in the monitoring of these species may therefore generate more reliable population estimates. The technique of using dominant predator body odor could also potentially assist in reducing native mesopredator naivety to invasive predators or increasing the success of reintroduction programs for endangered native species. The critically endangered black footed ferret (*Mustela nigripes*) experiences 80% reintroduction mortality due to interference competition (Biggins et al. 2011). Ferret odor could potentially be deployed to encourage activity in particular areas of the habitat, to help with population monitoring, and dominant predator body odor could be used for pre-release behavior conditioning (Kleiman 1989, Biggins et al. 2011, Smith and Blumstein 2012).

Studying olfactory communication provides insights into predator ecology, but it is also of applied importance for population monitoring and invasive species management. Deploying dominant predator kairomones to monitor other predators may be a technique that is applicable worldwide. We hope our findings have practical applications for wildlife management and that future research continues to investigate the role of chemical communication among competing predators.

LITERATURE CITED

- Apfelbach, R., C. D. Blanchard, R. J. Blanchard, R. A. Hayes, and I. S. McGregor. 2005. The effects of predator odors in mammalian prey species: a review of field and laboratory studies. *Neuroscience and Biobehavioral Reviews* 29:1123–1144.

- Banks, P. B. 1998. Responses of Australian bush rats, *Rattus fuscipes*, to the odor of introduced *Vulpes vulpes*. *Journal of Mammalogy* 79:1260–1264.
- Banks, P. B., A. Daly, and J. P. Bytheway. 2016. Predator odours attract other predators, creating an olfactory web of information. *Biology Letters* 12:361–363.
- Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B (Methodological)* 57:289–300.
- Biggins, D. E., B. J. Miller, L. R. Hanebury, and R. A. Powell. 2011. Mortality of Siberian polecats and black-footed ferrets released onto prairie dog colonies. *Journal of Mammalogy* 92:721–731.
- Bramley, G. N., and J. R. Waas. 2001. Laboratory and field evaluation of predator odors as repellents for kiore (*Rattus exulans*) and ship rats (*R. rattus*). *Journal of Chemical Ecology* 27:1029–1047.
- Brinck, C., S. Erlinge, and M. Sandell. 1983. Anal sac secretion in mustelids: a comparison. *Journal of Chemical Ecology* 9:727–745.
- Brook, L. A., C. N. Johnson, and E. G. Ritchie. 2012. Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. *Journal of Applied Ecology* 49:1278–1286.
- Burwash, M. D., M. E. Tobin, A. D. Woolhouse, and T. P. Sullivan. 1998. Laboratory evaluation of predator odors for eliciting an avoidance response in roof rats (*Rattus rattus*). *Journal of Chemical Ecology* 24:49–66.
- Bytheway, J. P., A. J. R. Carthey, and P. B. Banks. 2013. Risk vs. reward: How predators and prey respond to aging olfactory cues. *Behavioral Ecology and Sociobiology* 67: 715–725.
- Campbell-Palmer, R., and F. Rosell. 2011. The importance of chemical communication studies to mammalian conservation biology: a review. *Biological Conservation* 144:1919–1930.
- Choquenot, D., W. A. Ruscoe, and E. Murphy. 2001. Colonisation of new areas by stoats: time to establishment and requirements for detection. *New Zealand Journal of Ecology* 25:83–88.
- Clapperton, B. K. 1989. Scent-marking behaviour of the ferret, *Mustela furo*. *Animal Behaviour* 38:436–446.
- Clapperton, B., and A. Byrom. 2005. Feral ferret. Pages 294–307 in C. M. King, editor. *The handbook of New Zealand mammals*. Oxford University Press, Melbourne, Australia.
- Clapperton, B. K., E. O. Minot, and D. R. Crump. 1988. An olfactory recognition system in the ferret *Mustela furo* L. (Carnivora: Mustelidae). *Animal Behaviour* 36:541–553.
- Clout, M. 2001. Where protection is not enough: active conservation in New Zealand. *Trends in Ecology and Evolution* 16:415–416.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* 122:661–696.
- Dickman, C., and C. Doncaster. 1984. Responses of small mammals to red fox (*Vulpes vulpes*) odour. *Journal of Zoology* 204:521–531.
- Dowding, J., and M. Elliott. 2003. Ecology of stoats in a South island braided river valley. Department of Conservation, Wellington, New Zealand.
- Erlinge, S., and M. Sandell. 1988. Coexistence of stoat, *Mustela erminea*, and weasel, *M. nivalis*: social dominance, scent communication, and reciprocal distribution. *Oikos* 53:242–246.
- Estes, R. D. 1972. The role of the vomeronasal organ in mammalian reproduction. *Mammalia* 36:315–341.
- Ferrari, M. C. O., and D. P. Chivers. 2009. The ghost of predation future: threat-sensitive and temporal assessment of risk by embryonic woodfrogs. *Behavioral Ecology and Sociobiology* 64:549–555.
- Garvey, P. M., A. S. Glen, and R. P. Pech. 2015. Foraging Ermine Avoid Risk: behavioural responses of a mesopredator to its interspecific competitors in a mammalian guild. *Biological Invasions* 17:1771–1783.
- Garvey, P. M., A. S. Glen, and R. P. Pech. 2016. Dominant predator odour triggers caution and eavesdropping behaviour in a mammalian mesopredator. *Behavioral Ecology and Sociobiology* 70:481–492.
- Glen, A. S., S. Cockburn, M. Nichols, J. Ekanayake, and B. Warburton. 2013. Optimising camera traps for monitoring small mammals. *PLoS ONE* 8:16–24.
- Glen, A., B. Warburton, J. Cruz, and M. Coleman. 2014. Comparison of camera traps and kill traps for detecting mammalian predators: a field trial. *New Zealand Journal of Zoology* 41:155–160.
- Harrington, L. A., A. L. Harrington, and D. W. Macdonald. 2009. The smell of new competitors: the response of American mink, *Mustela vison*, to the odours of otter, *Lutra lutra* and polecat, *M. putorius*. *Ethology* 115:421–428.
- Hemmi, J. M., and A. Pfeil. 2010. A multi-stage anti-predator response increases information on predation risk. *Journal of Experimental Biology* 213:1484–1489.
- Hines, J. E. 2006. Program PRESENCE. See <https://www.mbr-pwrc.usgs.gov/software/presence.html>
- Hughes, N. K., E. Korpimäki, and P. B. Banks. 2010. The predation risks of interspecific eavesdropping: weasel-vole interactions. *Oikos* 119:1210–1216.
- Hutchings, M. R., and P. C. L. White. 2000. Mustelid scent-marking in managed ecosystems: implications for population management. *Mammal Review* 30:157–169.
- Innes, J., D. Kelly, J. M. Overton, and C. Gillies. 2010. Predation and other factors currently limiting New Zealand forest birds. *New Zealand Journal of Ecology* 34:86–114.
- Jackson, D., and R. Green. 2000. The importance of the introduced hedgehog (*Erinaceus europaeus*) as a predator of the eggs of waders (*Charadrii*) on Machair in South Uist, Scotland. *Biological Conservation* 93:333–348.
- Jędrzejewski, W., L. Rychlik, and B. Jędrzejewska. 1993. Responses of bank voles to odours of seven species of predators: experimental data and their relevance to natural predator-vole relationships. *Oikos* 68:251–257.
- Jones, C., K. Moss, and M. Sanders. 2005. Diet of hedgehogs (*Erinaceus europaeus*) in the upper Waitaki Basin, New Zealand: implications for conservation. *New Zealand Journal of Ecology* 29:29–35.
- Kats, L. B., and L. M. Dill. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience* 5:361–394.
- King, C. M. 2005. *The handbook of New Zealand mammals*. Oxford University Press, Auckland, New Zealand.
- King, C. M., and R. A. Powell. 2007. *The natural history of weasels and stoats: ecology, behaviour and management*. Second edition. Oxford University Press, New York, New York, USA.
- Kleiman, D. G. 1989. Reintroduction of captive mammals for conservation. *BioScience* 39:152–161.
- Long, R. A., P. MacKay, J. Ray, and W. Zielinski. 2012. *Noninvasive survey methods for carnivores*. Island Press, Washington, D.C., USA.
- Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2000. 100 of the world's worst invasive alien species: a selection from the global invasive species database. Invasive Species Specialist Group, Auckland, New Zealand.
- Macdonald, D. W. 1985. The carnivores: order Carnivora. Pages 619–722 in R. E. Brown and D. W. Macdonald,

- editors. Social odours in mammals. Clarendon Press, Oxford, UK.
- MacKenzie, D. I. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, Sydney, Australia.
- McKinney, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics* 28:495–516.
- McMurtrie, P., K. Edge, D. Crouchley, D. Gleeson, M. Willans, and A. Veale. 2011. Eradication of stoats (*Mustela erminea*) from Secretary Island, New Zealand. Pages 455–460 in C. Veitch, M. N. Clout, and D. R. Towns, editors. Island invasives: eradication and management. IUCN, Gland, Switzerland.
- Meek, P. D., et al. 2014. Recommended guiding principles for reporting on camera trapping research. *Biodiversity and Conservation* 23:2321–2343.
- Monclús, R., H. G. Rödel, D. Von Holst, and J. De Miguel. 2005. Behavioural and physiological responses of naive European rabbits to predator odour. *Animal Behaviour* 70: 753–761.
- Morris, D. W., and D. L. Davidson. 2000. Optimally foraging mice match patch use with habitat differences in fitness. *Ecology* 81:2061–2066.
- Murphy, E. C., and J. E. Dowding. 1994. Range and diet of stoats (*Mustela erminea*) in a New Zealand beech forest. *New Zealand Journal of Ecology* 18:11–18.
- Nugent, G., D. R. Morgan, P. Sweetapple, and B. Warburton. 2007. Developing strategy and tools for the local elimination of multiple pest species. Pages 410–417 in *Managing Vertebrate Invasive Species Conference*. National Wildlife Research Centre, Fort Collins, Colorado, USA.
- Papes, F., D. W. Logan, and L. Stowers. 2010. The vomeronasal organ mediates interspecies defensive behaviors through detection of protein pheromone homologs. *Cell* 141:692–703.
- Peake, T. M. 2005. Eavesdropping in communication networks. Pages 13–37 in P. K. McGregor, editor. *Animal communication networks*. Cambridge University Press, Cambridge, UK.
- Pierce, R. J., N. Miller, E. Neill, C. Gardiner, and M. Kimberley. 2007. Field trials of fresh and long-life stoat baits in Northland, New Zealand. Department of Conservation, Science and Technical Publication, Wellington, New Zealand.
- Prada, D., A. Veale, J. Duckworth, E. Murphy, S. Treadgold, R. Howitt, S. Hunter, and D. Gleeson. 2014. Unwelcome visitors: employing forensic methodologies to inform the stoat (*Mustela erminea*) incursion response plan on Kapiti Island. *New Zealand Journal of Zoology* 41:1–9.
- Pyšek, P., and D. M. Richardson. 2010. Invasive species, environmental change and management, and health. *Annual Review of Environment and Resources* 35:25–55.
- R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org>
- Ramírez-Chaves, H. E., J. F. González-Maya, and J. Schipper. 2016. Small Carnivore Conservation and its contribution to the knowledge of rare small carnivores. *Small Carnivore Conservation* 54:1–3.
- Réale, D., S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemans. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews* 82:291–318.
- Ridley, A. R., E. M. Wiley, and A. M. Thompson. 2014. The ecological benefits of interceptive eavesdropping. *Functional Ecology* 28:197–205.
- Ritchie, E. G., and C. N. Johnson. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* 12:982–998.
- Roberts, S. C., and L. M. Gosling. 2001. Economic consequences of advertising scent mark location on territories. Pages 11–17 in A. Marchlewska-Koj, J. J. Lepri, and D. Müller-Schwarze, editors. *Chemical signals in vertebrates*. Springer, New York, New York, USA.
- Rovero, F., and A. R. Marshall. 2009. Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology* 46:1011–1017.
- Roy, S. S., I. Macleod, and N. P. Moore. 2006. The use of scent glands to improve the efficiency of mink (*Mustela vison*) captures in the Outer Hebrides. *New Zealand Journal of Zoology* 33:267–271.
- Russell, J., and M. Clout. 2005. Rodent incursions on New Zealand islands. Pages 324–330 in J. Parkes, M. Statham, and G. Edwards, editors. *Proceedings of the 13th Australasian Vertebrate Pest Conference*. Landcare Research, Lincoln, New Zealand.
- Schoepfner, N. M., and R. A. Relyea. 2009. Interpreting the smells of predation: How alarm cues and kairomones induce different prey defences. *Functional Ecology* 23:1114–1121.
- Smith, B. R., and D. T. Blumstein. 2012. Structural consistency of behavioural syndromes: Does predator training lead to multi-contextual behavioural change? *Behaviour* 149: 187–213.
- Smith, J. K., and G. Coulson. 2012. A comparison of vertical and horizontal camera trap orientations for detection of potoroos and bandicoots. *Australian Mammalogy* 34: 196–200.
- Smith, G., J. Ragg, H. Moller, and K. Waldrup. 1995. Diet of feral ferrets (*Mustela furo*) from pastoral habitats in Otago and Southland, New Zealand. *New Zealand Journal of Zoology* 22:363–369.
- Smith, D. H., R. Clayton, D. Anderson, and B. Warburton. 2015. Using home-range data to optimise the control of invasive animals. *New Zealand Journal of Zoology* 39:286–290.
- Taylor, B. D., R. L. Goldingay, and J. M. Lindsay. 2014. Horizontal or vertical? Camera trap orientations and recording modes for detecting potoroos, bandicoots and pademelons. *Australian Mammalogy* 36:60.
- Terborgh, J. 1974. Preservation of natural diversity: the problem of extinction prone species. *BioScience* 24:715–722.
- Towns, D. R., I. A. Atkinson, and C. H. Daugherty. 2006. Have the harmful effects of introduced rats on islands been exaggerated? *Biological Invasions* 8:863–891.
- Trolle, M., and M. Kéry. 2003. Estimation of ocelot density in the Pantanal using capture-recapture analysis of camera-trapping data. *Journal of Mammalogy* 84:607–614.
- van Dijk, J., T. Andersen, R. May, R. Andersen, R. Andersen, and A. Landa. 2008. Foraging strategies of Wolverines within a predator guild. *Canadian Journal of Zoology* 86:966–975.
- Venables, W. N., and B. D. Ripley. 2002. *Modern applied statistics with S*. Springer, New York, New York, USA.
- Verhoeven, K. J., K. L. Simonsen, and L. M. McIntyre. 2005. Implementing false discovery rate control: increasing your power. *Oikos* 108:643–647.
- Waite, T. A., and L. G. Campbell. 2006. Controlling the false discovery rate and increasing statistical power in ecological studies. *Ecoscience* 13:439–442.
- Wallach, A. D., W. J. Ripple, and S. P. Carroll. 2015. Novel trophic cascades: apex predators enable coexistence. *Trends in Ecology and Evolution* 30:146–153.
- Weldon, P. J. 2004. Defensive anointing: extended chemical phenotype and unorthodox ecology. *Chemoecology* 14: 1–4.
- Wiley, R. H. 1983. The evolution of communication: information and manipulation. *Animal Behaviour* 2:156–189.
- Wodzicki, K. A. 1950. *Introduced mammals of New Zealand. An ecological and economic survey*. Department of Science and Industry, Wellington, New Zealand.

- Woodley, S., A. Cloe, P. Waters, and M. J. Baum. 2004. Effects of vomeronasal organ removal on olfactory sex discrimination and odor preferences of female ferrets. *Chemical Senses* 29:659–669.
- Wyatt, T. D. 2010. Pheromones and signature mixtures: defining species-wide signals and variable cues for identity in both invertebrates and vertebrates. *Journal of Comparative Physiology* 196:685–700.
- Zhao, X., and D. Liu. 2015. Removal of the vomeronasal organ impairs predator odor detection in female golden hamsters. *Animal Biology* 65:1–12.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/eap.1483/full>

DATA AVAILABILITY

Data associated with this paper have been deposited in Datastore repository <http://doi.org/10.7931/J2PC308G>