

ECOLOGY

Misinformation tactics protect rare birds from problem predators

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Efficient decision-making integrates previous experience with new information. Tactical use of misinformation can alter choice in humans. Whether misinformation affects decision-making in other free-living species, including problem species, is unknown. Here, we show that sensory misinformation tactics can reduce the impacts of predators on vulnerable bird populations as effectively as lethal control. We repeatedly exposed invasive mammalian predators to unprofitable bird odors for 5 weeks before native shorebirds arrived for nesting and for 8 weeks thereafter. Chick production increased 1.7-fold at odor-treated sites over 25 to 35 days, with doubled or tripled odds of successful hatching, resulting in a 127% increase in modeled population size in 25 years. We demonstrate that decision-making processes that respond to changes in information reliability are vulnerable to tactical manipulation by misinformation. Altering perceptions of prey availability offers an innovative, nonlethal approach to managing problem predators and improving conservation outcomes for threatened species.

INTRODUCTION

Decision-making is vulnerable to misinformation because deciphering uncertain information is cognitively taxing (1, 2). Although heuristic approaches (or rules of thumb) can reduce cognitive costs (3), they can result in misguided and costly decisions. Instead, when negotiating information-rich environments, many decision makers are thought to become “Bayesian updaters” (4), using both previous experience and new information to guide optimal choices. Information that proves useful or reliable motivates positive future responses, while useless or unrewarding information is filtered into the perceptual background and ignored thereafter (1). Tactical misinformation, or “fake news,” can succeed if it diverts the selective attention of decision makers by changing the perceived value of information.

Experiments in highly simplified environments with both humans (5) and animals (6) show the ease with which different forms of misinformation can exploit selective attention processes to alter choice. However, whether such processes occur in real world, complex situations are less clear (7). Predators, for example, depend on reliable information because they face considerable cognitive challenges in finding food in information-rich environments where much information about potential prey is unrewarding. Foraging optimally requires constant updating of an animal’s information state, so that only information with high probability of reward should be pursued when searching for food is costly (8). Signal detection theory predicts that if particular information about prey becomes unreliable, predators should abandon it in their search for food (1).

Here, we test whether tactical use of sensory misinformation can be deployed to manipulate Bayesian updating strategies by animals and thereby reduce undesirable predator impacts on vulnerable prey. Predator management is a vexed problem globally because

many predators provide vital ecosystem services but can sometimes affect other vulnerable species, leading to their persecution (9). To prevent extinctions, reducing predation by both native and non-native predators is an urgent priority, but current methods can cause ecological harm when predators are removed (10), are often ineffective (11), and increasingly lack social license (12). New techniques to solve this dilemma are urgently needed.

Decision-making theory offers an innovative, nonlethal solution that draws on principles of information search, nonassociative learning (habituation), and camouflage (13–16). It underpins the decision-making behavior of predators, predicting that individuals will give up and move from areas that provide little or no reward (17) and will stop searching for prey that are too costly to find when other food is available (18). Sensory cues, such as odor, that reveal the identity and location of prey help predators make these foraging decisions (19, 20). Decoupling cues from rewards have been demonstrated on a small scale in wild rats searching for artificial nests baited with quail eggs (21), but it is unknown whether this relatively simple sensory manipulation can deceive multiple predator species in complex environments into ignoring available natural prey and deliver population-scale benefits over ecologically relevant spatial and temporal scales. Behavioral modeling and captive animal trials suggest that this is achievable (22, 23), but it has never been tested with vulnerable secondary prey species at a landscape scale.

Here, we report two results demonstrating the mechanism and outcome of using tactical misinformation to reduce predator impacts: (i) the response of invasive mammals (ferrets *Mustela putorius furo*, cats *Felis catus*, and European hedgehogs *Erinaceus europaeus occidentalis*) to repeated exposure to three unrewarded bird odors (chicken *Gallus gallus domesticus*, quail *Coturnix japonica*, and kelp gull *Larus dominicanus*) before the arrival and during nesting of native ground-nesting shorebirds (double-banded plover *Charadrius bicinctus*, wrybill *Anarhynchus frontalis*, and South Island pied oystercatcher *Haematopus finschi*) over two breeding seasons in natural braided river ecosystems in New Zealand; and (ii) the subsequent effects on shorebird hatching success (HS) and population projections (see Fig. 1 for general methodology). We focused on a suite of introduced mammalian predators because they are a major threat

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to shorebirds in New Zealand and globally (24, 25), are rapidly attracted to prey odor (26), show reduced foraging efficiency when prey odor is widespread and abundant (19, 27), and are sensitive to the foraging costs imposed by unrewarded odor cues of different prey species (23, 27). Mammalian predation is a major cause of shorebird population decline and extinction (28), with climate change predicted to exacerbate nest predation rates in higher latitudes (29).

RESULTS

There was strong evidence for habituation to unrewarded bird odor by cats and ferrets before and during nesting (Fig. 2, A and B). Interaction times with odor were initially high but declined after 12 to 18 days. By the time nesting started, interactions with odor were only 5 to 9% of their initial levels. Conversely, hedgehog interactions with odor rose steadily, peaking 18 days into the nesting season and declining thereafter (Fig. 2C). We first detected hedgehogs in camera traps 11 to 28 days after odor deployment began, suggesting that they were gradually emerging from hibernation during much of the increase phase in interactions.

Odor treatments resulted in a 1.7-fold (range: 1.1 to 2.7) increase in HS of plover/wrybill nests and more than doubled the odds of

successful hatching (mean odds ratio: 2.2; range: 1.2 to 3.6). Treatment effects persisted for 25 days (Fig. 3A). Variation in daily survival rates (DSRs) of plover/wrybill nests ($n = 398$) was best described by treatment (odor versus no odor), day of nesting season, and matched site pairs (table S1). DSRs were higher on sites with odor, but the magnitude of this difference varied between site pairs. For oystercatchers, odor treatments also resulted in a 1.7-fold (range: 1.6 to 1.7) increase in HS and almost tripled the odds of successful hatching (mean: 2.8; range: 2.4 to 3.1). Treatment effects in this case persisted for 35 days (Fig. 3B). The three top models best explained variation in DSR of oystercatcher nests ($n = 72$), so these were averaged (table S2). The averaged model included treatment and day of the nesting season as significant predictors of DSR; however, there was no evidence of differences between site pairs for this species. Average HS for plover/wrybill and oystercatchers during the effective treatment periods on each site is shown in Fig. 4.

Forecasted plover populations from a starting population of 1000 birds show an additional 743 individuals [606 to 881, minimum/maximum differences in confidence intervals] after 25 years of annual odor treatment, compared with population declines with no treatment (Fig. 5).

Ferrets were the main nest-raiding predator on the Cass/Macauley sites (62% of predations, 26% by hedgehogs, and 4% by cats), while

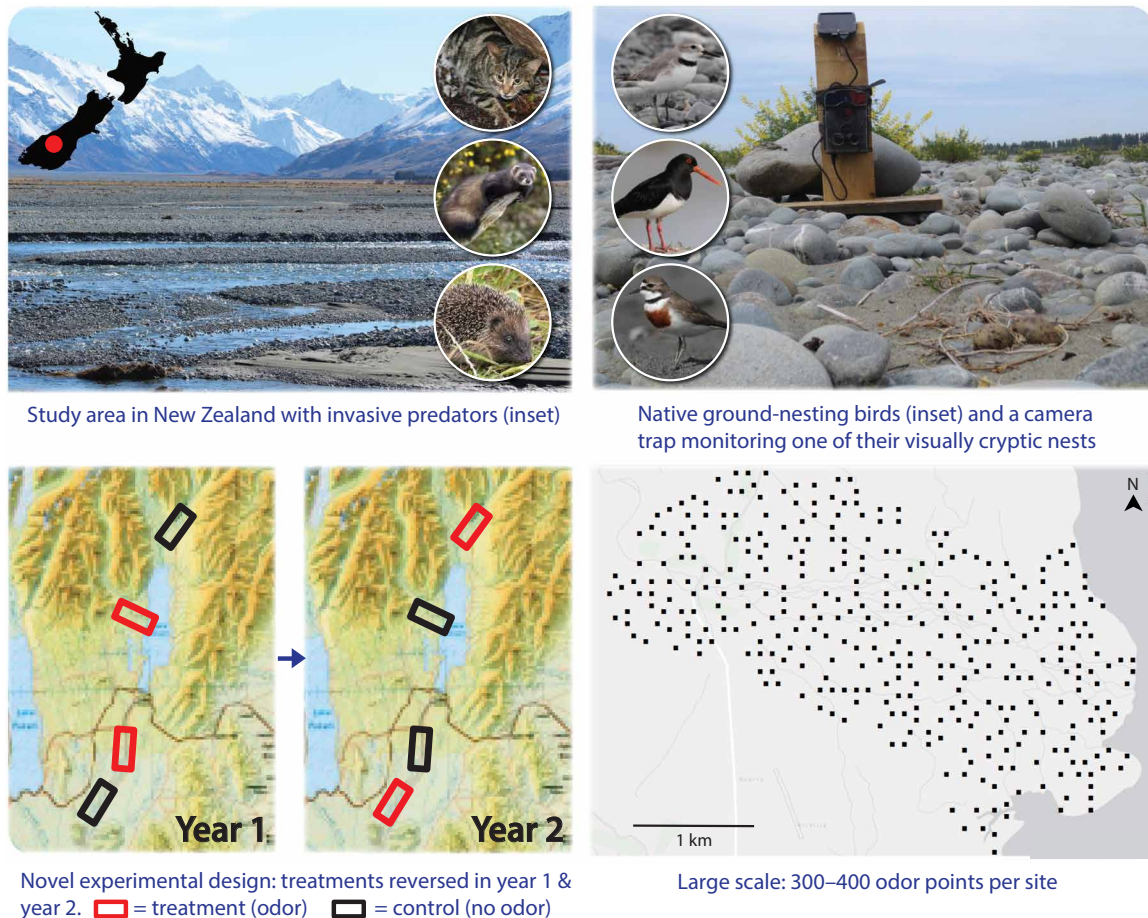


Fig. 1. The study area showing the study species (predators and native ground-nesting birds), the experimental design with treatments reversed at each of the four sites each year, and the scale of the deployment of the 300 to 400 odor points at each site. Photo credits (background images): Grant Norbury, Manaaki Whenua—Landcare Research.

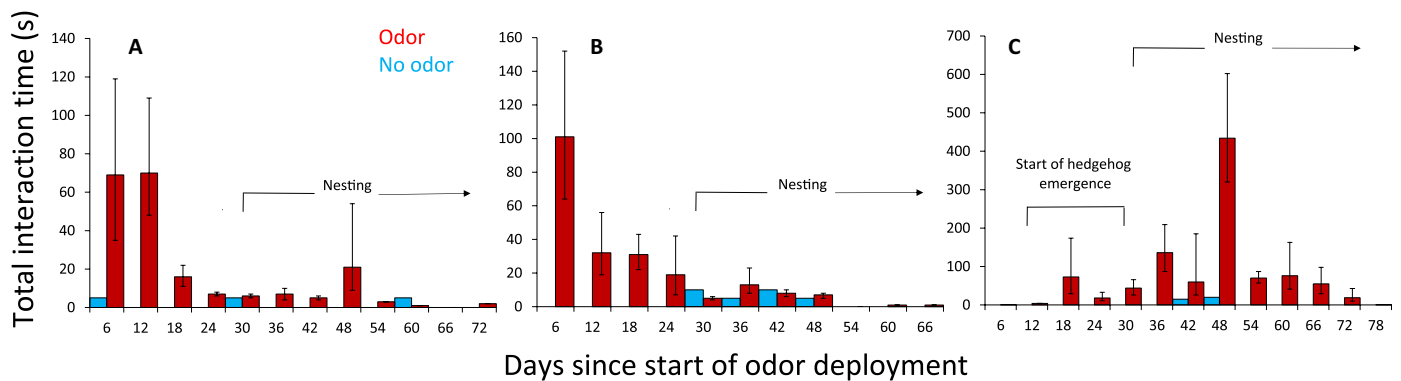


Fig. 2. Habituation of predators to unrewarded bird odor. Total interaction times (and 95% CIs) with bird odor for ferrets (A), cats (B), and hedgehogs (C). Background interaction rates with no odor are indicated by the blue bars (multiplied by 5 for visibility); 95% CIs not calculated for sparse data.

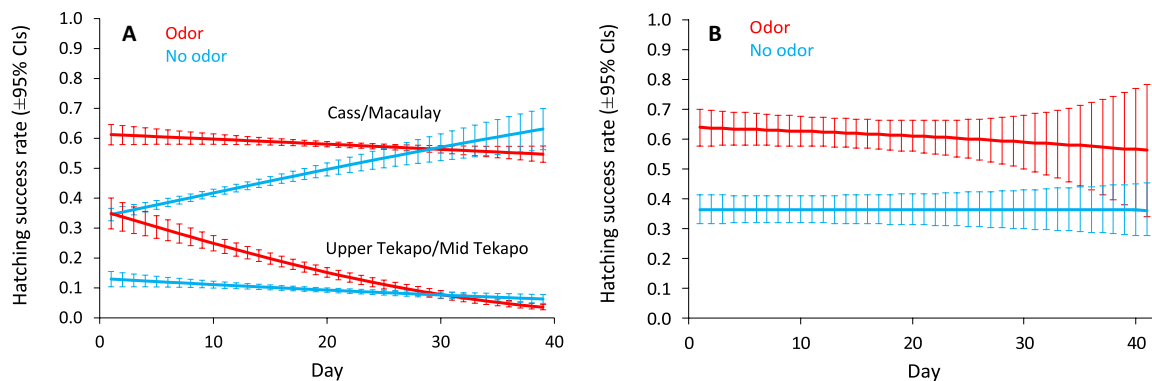


Fig. 3. Hatching success of birds with and without odor treatment. Predicted HS of plover/wrybill (A) and oystercatcher (B) nests during the first 40 days of the nesting season. 95% CIs for treatments and nontreatments overlapped from about day 25 onward for plover/wrybills and from about day 35 onward for oystercatchers. Sites were paired as Cass versus Macaulay and Upper Tekapo versus Mid Tekapo, according to similarities outlined in Materials and Methods. One site of each pair was treated with odor in year 1 of the study, and the other site was not treated. Treatments were reversed in year 2.

hedgehogs were the main nest raiders on the Tekapo sites (73% of predations, 18% by ferrets, and 6% by cats). Camera-derived indices of relative abundance of these main nest raiders showed differences between each treatment/nontreatment pair, but these remained when the treatments were reversed (fig. S1A). Tunnel-derived abundance indices (measured only in 2016) of hedgehogs were similar for the Tekapo pair, but ferret indices were higher on the treatment site of the Cass/Macaulay pair (fig. S1B), which would have tended to mask treatment effects.

DISCUSSION

Our results demonstrate that predators rapidly learn to disregard unprofitable prey cues, providing a deceptively simple sensory technique that can significantly reduce predation rates and produce population-level benefits for vulnerable prey species. This approach offers new opportunities to mitigate the effects of mammalian predation on ecologically relevant scales by altering predators' perception of prey availability without any direct interference with animals. The method avoids problems associated with current lethal approaches (12) and safeguards native predators that affect threatened species. While the key sensory modality used for prey detection may differ between taxa, learning to ignore unrewarded cues encountered repeatedly is akin to habituation (13) and is therefore likely to be a

common behavior in optimal foraging species. The tactical use of misinformation to disrupt natural foraging behavior should therefore have broad application.

Ferrets and cats rapidly lost interest in the unrewarded bird odor, a predicted response for Bayesian updaters that prevents individuals wasting time or energy investigating irrelevant information (30). Our use of misinformation presumably created a perception of low probability of prey encounter associated with bird odors, creating an altered prior probability (as used in Bayes' theorem) of success when predators were deciding whether to pursue such odors to find nests in the future (4). The lack of reward associated with this misinformation also removed ambiguity about whether bird odors would be rewarding before the birds arrived, which can strengthen the decision-making response (8) and undermine prior learning (31). After this initial habituation to repeated deployment of unrewarded bird odors, most predators presumably lacked motivation to pursue the odor of real birds once they were available, at least during the effective treatment period. The temporary increase in hedgehog interactions with bird odor was probably a response to emergence from hibernation in a hungry state at the time birds were arriving to nest.

Our modeling predicted that the observed 1.7-fold increase in nest survival over the first 25 to 35 days of the nesting season will change the trajectory of bird populations that would otherwise be in decline. This effect size benchmarks well against the doubling of prey

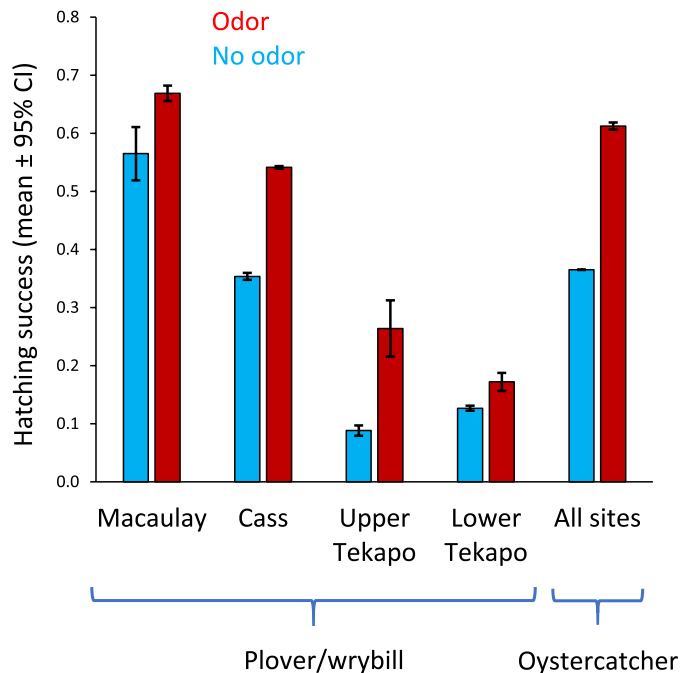


Fig. 4. Mean HS of plover/wrybill and oystercatcher nests during the 25- and 35-day effective treatment periods, respectively.

responses to the removal of invasive predators using traditional lethal techniques when they are effective (32). Protecting nests laid in the first third of the nesting season provides a disproportionately greater fitness value because their survival is naturally higher than for nests laid later (33–35).

We used three readily available bird odors, one, because we could not extract sufficient odor from local shorebirds, and two, because using more than one species increased the likelihood that predators would generalize between the prepared odor and the odor of real birds. Our results imply that, at least for ferrets and cats, individuals transferred their habituated response from these three bird odors to shorebird odor. Generalizing bird odors, rather than discriminating between species, is likely to enhance foraging efficiency and requires less cognitive effort when prey are similar, when similar hunting tactics are required, and when there are similar rewards (36). Our results show, counterintuitively, that the use of generalized prey recognition can be exploited to protect threatened prey species by creating virtual refuges from predation that result from a predator's altered perception of prey availability when searching. The likelihood of generalizing bird odors, however, appears to vary between predator taxa depending on their diet and life history. Hedgehogs, for example, eat mostly invertebrates. Eggs are relatively highly nutritious, so giving up on eggs incurs a greater cost compared with ferrets and cats who eat a high calorie diet of rabbit. Hedgehogs may therefore be more discerning between unrewarded and rewarded bird odors and therefore less likely to generalize (23).

We demonstrate that tactical use of misinformation can exploit vulnerabilities in natural decision-making processes. This result opens pathways for fundamentally new approaches to manage problem individuals and species using nonlethal approaches that address impacts rather than species. The Bayesian updating strategy used by predators when searching for prey, shaped by optimal foraging

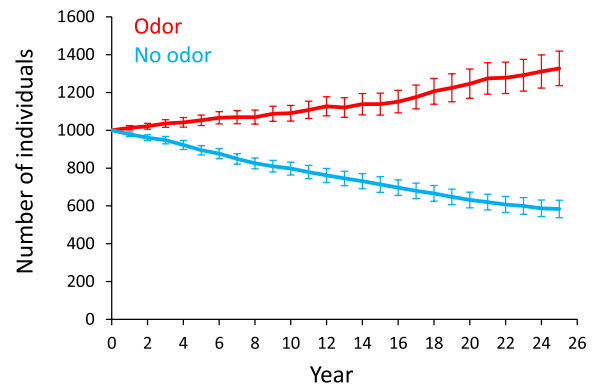


Fig. 5. Average VORTEX population projections (and 95% CIs) from a starting population of 1000 double-banded plovers over 25 years with and without odor treatment.

pressures and sensory learning behaviors, was unexpectedly easy to manipulate but had profound benefits for vulnerable prey. The cost of this method over the 66-day period from the start of odor deployment to the end of the effective treatment period (mean: 30 days) was about NZ \$33 per hectare (including odor extraction). Comparisons with conventional lethal methods, such as trapping and poisoning, are difficult because costs are highly variable and context specific. Some trapping operations, if conducted over the same 66-day period, cost about NZ \$35 per hectare (including purchase of traps) using live-capture leg-hold traps checked daily (the optimum trap type for cats) and lethal traps checked weekly. Trapping costs could be reduced considerably with less frequent checking, but additional costs would be incurred for leg-hold traps fitted with remote sensing equipment to indicate if an animal is captured and must be cleared. The cost of some aerial deployments of toxic baits is similar (NZ \$20 to \$40 per hectare), but licensing in New Zealand is currently restricted to rodents (which also kills stoats via secondary poisoning but not cats). Some ground-based poisoning operations of predators may be cheaper (c. NZ \$5 to \$15 per hectare), but licensing is currently restricted to stoats and cats and is in the early stages of development.

Altering perceived prey availability by applying bird odor before bird arrival deceived predators into ignoring an otherwise meaningful food cue, leading to reduced nest predation and improved conservation outcomes. Natural selection probably shaped evolution of economically rational decision-making tactics that are agile to changes in the value of information (4), especially in variable or novel environments, as faced by alien predators. A focus on the drivers and motivations of problem species will enable wildlife managers to manipulate them with counter tactics of deception and misinformation that are widespread in humans and primates (37) and that currently challenge human society (38, 39).

MATERIALS AND METHODS

The predator-prey system consists of indigenous avian prey species that are visually cryptic but highly vulnerable to a suite of introduced generalist mammalian predators (40). The predators primarily use olfaction to detect their prey and rely on other prey groups as their primary food resource. The study system comprised open, braided river ecosystems in the glacial outwash plains of the

Mackenzie basin in the South Canterbury region of New Zealand's South Island.

We measured nest survival of wild, native birds, mostly double-banded plovers (*C. bicinctus*, 81% of nests monitored), but also South Island pied oystercatchers (*H. finschi*, 15%) and wrybills (*A. frontalis*, 3%) at four study sites from August to November in 2016 and 2017. Study sites were 8 to 30 km from Lake Tekapo (44°00'26.47"S, 170°28'58.52"E). The birds nest on open, braided riverbeds and side terraces of rivers. Rivers consisted of dry boulders, gravels, sand, and silt dissected by numerous interconnected stream channels, and stable terraces on both sides. Water flows varied from 10 to at least 50 m³ s⁻¹, which predators can cross. Riverbed vegetation consisted of low herbaceous species (e.g., *Raoulia* spp.) interspersed with woody species (e.g., *Diiscaria toumatou*). Rivers were surrounded by extensive grasslands of uncultivated pasture species (e.g., *Festuca novaezealandiae* and *Poa cita*). Some riverbed margins supported introduced willow trees (*Salix fragilis*).

All terrestrial mammals present were introduced to New Zealand. The main nest predators were European hedgehogs (*E. europaeus occidentalis*, 56% of mammalian predations) and ferrets (*M. putorius furo*, 34%), but nests were also depredated by feral cats (*F. catus*, 6%), stoats (*M. erminea*, 3%), and rats (*Rattus* spp., 1%). Indigenous Australasian harriers (*Circus approximans*) destroyed 4% of monitored nests, and one nest was depredated by a South Island pied oystercatcher. Rabbits (and occasionally hares) are the primary prey species of ferrets, stoats, and cats in this area (41).

Experimental design

Sites were independent of each other (between 5 and 23 km apart) and chosen because of their uninterrupted breeding habitat for birds, historically high numbers of breeding pairs, and ease of access. The sites were 1.7 km wide, on average, and were all around 1000 ha in area (lower Macaulay River: 1026 ha, 6.7 km long; Cass River delta: 780 ha, 4.1 km long; upper Tekapo River: 1010 ha, 6.7 km long; and mid Tekapo River: 1030 ha, 6.6 km long). The Macaulay and Cass sites were paired as both had unregulated water regimes, occurred at relatively high altitude [700 to 800 m above sea level (a.s.l.)], and had similar predator communities and greater bird productivity (42). The Tekapo sites were paired as they were part of the same regulated river system, occurred at lower altitude (500 to 600 m a.s.l.), and had similar predator communities and lower bird productivity. Before birds began nesting in early to mid-September, we exposed predators to odor extracted from readily obtainable bird species at one of each pair of sites. During nesting (September–November), we continued the odor treatment. In 2016, odor was applied to Cass cf. Macaulay untreated and upper Tekapo treated cf. mid Tekapo untreated. The treatments were reversed in 2017.

Odor preparation

Odor was extracted from three bird species. We used more than one species to increase the likelihood that predators would generalize between the prepared odor and the odor of real birds. Odor was extracted from thawed carcasses (freshly killed then immediately frozen) of wild kelp gulls (*L. dominicanus*), fresh carcasses of commercially available Japanese quail (*C. japonica*), and feathers extracted from commercially available freshly killed domestic chickens (*G. gallus domesticus*).

Bird odors were collected using a simple solvent extraction method. Typically, up to 12 individual quails, four gulls, or a 5-liter volume equivalent of chicken feathers were placed in a 20-liter

solvent-proof extraction vessel. Odor was extracted with approximately 4 liters of 1:1 dichloromethane:acetone (or enough to cover the bird carcasses) for approximately 12 hours.

The solvent was removed by rotary evaporation at mild vacuum in a 40°C water bath. Dried fatty triglyceride material was decanted while still warm and in a liquid state. Each extraction produced approximately 15 g of brownish quail material, 7 to 10 g of grayish gull, and 30 g of deep orange chicken material. Samples were reconstituted in Vaseline petroleum jelly to increase the persistence of the odor. We used a hot plate (approximately 50°C) to heat the Vaseline until it was liquid enough to allow mixing with the odor extract. Extract was added to achieve the desired concentration; for example, for 10% (w/w), we added 10 g of extract to 90 g of Vaseline to achieve a concentration that was just perceptible to human noses. The material was mixed thoroughly, transferred to plastic syringes, and stored at -20°C until required.

Odor deployment

We began deploying odor on the 2nd or 15th of August 2016 (to coincide with nesting commencing on each site) and continued for 95 and 82 days, respectively. The concentration of deployed odor was usually 10% (w/w) but increased toward the end of the trial in case 10% was ineffective [30% (w/w) of quail during the last 44 days of deployment and 20% (w/w) of chicken for an 11-day period, before increasing to 40% (w/w) during the last 62 days of deployment]. In 2017, odor deployment began on the 4th or 14th of August and continued for 93 and 84 days, respectively. Again, odor concentration was usually 10% (w/w), apart from 40% (w/w) of chicken on half of the chicken odor points (randomly selected) during the last 61 days of deployment.

Simulation modeling predicted that a single hedgehog would encounter 10 to 17 odor points, a cat 28 to 66 points, and a ferret 46 to 77 points over a 27-day period if odor was deployed on 40% of randomly selected points on a 100-m grid, with application rerandomized every 3 days (22). We deployed fresh odor every 3 days. To ensure that the odor was spread evenly across each site, we used a 50-m grid, and points receiving odor were no less than 100 m apart during each deployment session. The number of random odor points deployed during each deployment session ranged from 312 to 402 (mean: 379), depending on the size of the treatment area. This equated to about one odor point per 2.5 ha.

At every point, approximately 0.1 to 0.2 ml of the Vaseline matrix was smeared onto a small rock with latex gloves. On average, chicken odor was deployed at six consecutive points, quail odor at the next three points, and gull odor at the next single point, and then repeated. These ratios reflected the availability of the different odor types. It took three people about 7 hours to deploy odor at a single site. Walking routes between points were at the discretion of each person to complete deployments in the shortest possible time. Odor was applied for 26 to 40 days (average: 36 days) before egg laying began and continued for 45 to 56 days (average: 52 days) during nesting.

Predator habituation to odor

In 2016, we tested whether predators were habituating to the unrewarded bird odor by measuring the total time predators spent interacting with the odor on the treatment sites. Every 3 days, we randomly selected 80 of the above odor points on each treatment site and deployed motion-triggered cameras to record predator

interactions with odor over 5760 camera nights (figs. S2 to S4). A camera was mounted on a wooden stand 30 cm above the ground and placed 2 m from the odor, facing away from the sun. We used Bushnell Trophy Cam HD Aggressor No-Glow cameras, Reconyx PC900 Hyperfire professional infrared cameras, and Ltl Acorn Ltl-5210 infrared hunting trail cameras. Cameras were set to 24-hour mode, high sensitivity, and three photo bursts per trigger, with a 1-s interval between triggers. An interaction was defined as a predator sniffing the odor or within one body length of it. We summed the time that animals interacted with the odor during consecutive 6-day intervals (data from 3-day intervals were too sparse). Ninety-five percent CIs were bootstrapped by resampling (with replacement) interaction events 1,000,000 times.

In 2017, we compared interaction rates between plain Vaseline (no odor) and no Vaseline using cameras deployed for indexing predator abundance on each site (details below) to ensure that predators were habituating to the bird odor and not the Vaseline. Cameras were equally apportioned to riverbed and terrace habitats, but we used data only from the terraces where predators were more abundant. Plain Vaseline was applied to a rock in front of a random selection of two or three of the five terrace cameras on each site, and the other two or three cameras had only a rock with no Vaseline applied (total of 630 camera nights). Vaseline was reapplied every 6 days and rerandomized between cameras. We fitted a linear mixed-effects model to the number of interactions, with Vaseline treatment as a fixed effect and site as a random effect [using the function `lmer` from the `lme4` package in program R (43)]. Apart from hedgehogs on the Cass site, predators did not appear to be attracted to plain Vaseline without odor (treatment coefficient = -0.005 , 95% CI: -0.030 to 0.019 , predator species pooled), suggesting that habituation was to the bird odor, not the Vaseline.

Nest monitoring

Experienced ornithologists repeatedly searched each site for occupied nests from 4 September to 9 November 2016 and from 11 September to 5 November 2017. Nests were located by systematically traversing areas of unvegetated gravels, locating birds as they flushed from their nests, and then watching as birds returned to their nests. Nest locations were Global Positioning System tagged. Motion-activated digital trail cameras were deployed on 94% of nests. Cameras were supported by small rocks and placed 2 m from the nest. Cameras were set to record either 10 s of video footage or a burst of three photographs whenever triggered by movement at the nest, with a minimum of 1-min stand-down interval between motion-triggered events. Nests were revisited every 2 to 4 days to check their status, service the camera, and download video footage. Deploying cameras at nests was considered necessary to accurately determine nest fates and the identity of predators, and any effect of the cameras or observers at nests on the fate of nests was assumed to be constant across sites and years (33, 44). Nest fates were determined either by direct observation of the hatch/failure event from the cameras (for the majority of nests) (see movie S1), by observing newly hatched chicks in the nest (for a minority of successful nests), or by eliminating the possibility of a hatch event by counting forward from known laying dates (for a minority of failed nests). We also noted whether nests were on islands in the river channel (defined as any area of gravel completely isolated from both banks of the river by one or more channels of open, flowing water) given that some predators have reduced access to islands (45), which could

result in higher nest survival (42, 46). No effect of nest location was found (tables S1 and S2).

We carried out a simulation-based power analysis to assess the ability of different nest sampling designs to detect a change in double-banded plover nest survival resulting from the odor treatment. We assessed the effect of two controlled factors on statistical power: number of nests monitored per site (20 to 60) and number of pairs of sites monitored (2 to 4). We also accounted for two uncontrolled factors: mean nest survival at nontreatment sites and natural variability in survival between nontreatment sites. We used nest survival data from a previous study (47) to conduct simulations using the minimum (0.239) and maximum (0.435) annual nest survival recorded, as well as two levels of variability around these values ($SD = 0.1$ and $SD = 0.2$). We then tested the power of each simulated design to detect increases of 0.2 and 0.3 (i.e., the effect size) in nest survival. Each simulation involved (i) drawing a mean nest survival value from a beta distribution (with parameters as defined above) for each of the nontreatment sites; (ii) adding the effect size to those values to obtain the mean survival for the paired treatment sites; (iii) drawing the fate of nests from a binomial distribution with means from (i) and (ii) for nontreatment and treatment sites, respectively; and (iv) fitting a binomial mixed-effect model to the simulated nest fate data. We simulated each combination of parameters 1000 times. Statistical power was determined as the proportion of simulations where a significant difference in nest survival between nontreatment and treatment sites was detected. The analysis showed that at least 50 nests were required per site, with two pairs of sites, to detect a minimum increase in survival of 30%, with 80% power. In the field experiment, we monitored 51 to 64 (average = 59) nests per site per season with known outcomes, or 470 nests in total, over two seasons.

Nest survival analysis

The incubation period for double-banded plovers is 25 to 28 days, wrybills 30 to 36 days, and South Island pied oystercatchers 24 to 28 days. Only 3% of the monitored nests were wrybill nests, and they occurred only on the Cass and Macaulay river sites. We pooled the wrybill and plover data and assumed the same incubation period to simplify the analysis. The incubation periods for plover/wrybill and oystercatchers were set to an average of 28 and 26 days, respectively. The date first nests were found varied among sites by about 10 days.

Because nests were often found partway through incubation, there was potential to positively bias nest survival estimates because unsuccessful nests were less likely to be found than successful nests. This was overcome by calculating DSRs for the period that nests were monitored. We calculated DSR using the nest survival model in MARK (48) and analyzed the data using the RMark package (49) in program R. Nest survival rates were essentially an inverse measure of predation rates, given that 89% of the nest failures observed in this study were due to predation.

Competing generalized linear models of DSRs were fitted using maximum likelihood, and their relative support was evaluated using the Akaike information criterion (AIC). Before evaluating the underlying drivers of survival rates, we examined general temporal trends in DSR by constructing a null model (time-invariant), a linear time-trend model, a quadratic time-trend model, and a model in which DSR was estimated separately for each year of the study. The null model (where all daily survival estimates are assumed to be equal to the mean value) was included as a baseline to evaluate the

importance of alternative models including covariates. Next, we developed models to explain variation in DSR with treatment, site, and paired sites (Cass/Macauley and Upper Tekapo/Mid Tekapo), and whether a nest was located on a river island. For the main effects of treatment and paired sites, we also included interaction effects with time to capture potential differences in temporal trends in DSR between treatment and nontreatment sites. In total, we fitted 10 models to the plover/wrybill data and six models to the oystercatcher data (more parameterized models could not be fitted because of the smaller sample size). Support for models for each species was evaluated with ΔAICc : Models with $\Delta\text{AICc} > 4$ (50) with respect to the model with lowest AICc were considered to have no support and were discarded. For those models with $\Delta\text{AICc} < 4$, we used model averaging to estimate model coefficients.

For both groups of species, we found most support for models predicting variation in DSR as a function of day of the nesting season (tables S1 and S2). Accordingly, we estimated HS as the product of 28 (plover/wrybill) or 26 (oystercatcher) consecutive DSRs, i.e., the lengths of the incubating periods. To illustrate temporal trends, we computed all possible estimates of HS during the study (i.e., $n = 39$ or 41 ; the maximum number of 28- or 26-day intervals in our 67-day nesting season). We computed the variances of the estimated HSs using the delta method (51).

To construct Fig. 3 for plover/wrybills, we derived an average treatment versus nontreatment effect for each individual site from a Site*Year*Time model (table S1), which gave DSRs for each day of the nesting season for each site and for each treatment or nontreatment year. These were converted to HS (see above) and averaged over the first 25 days of the nesting season (i.e., the “effective treatment period” where 95% CIs are nonoverlapping between treatment and nontreatment). For oystercatchers, we derived an average treatment versus nontreatment effect from the averaged model, which included a time \times treatment interaction but no differences between sites. DSRs from this model were averaged over the first 35 days of the nesting season (i.e., the effective treatment period).

The magnitude of the treatment effect was expressed in two ways: (i) the “relative risk” of hatching successfully during the effective treatment period, calculated as $p(T)/p(NT)$, where $p(T)$ = probability of hatching on a given day with odor treatment and $p(NT)$ = probability of hatching on a given day with no odor treatment; and (ii) the “odds ratio” for hatching successfully during the effective treatment period, calculated as $(p(T)/(1 - p(T)))/(p(NT)/(1 - p(NT)))$.

Bird population projections

We assessed the effect of the odor treatment on population growth rates of double-banded plovers because demographic parameters are best known for this species. We used VORTEX 10 (52) to simulate population projections using nest-HS for the treatment and nontreatment sites. Because we measured treatment effects on nest survival only, we used estimates of clutch size and chick and juvenile survival from (53). We simulated the observed waning of the treatment effect over 25 days by applying different values of nest-HS for successive renesting attempts: For first and second renesting attempts, we set HS as the mean of the first 25 days from the Cass/Macauley sites (0.592), and for third renesting attempts, we set HS as the mean from all days (0.580). We used values recorded from the Cass/Macauley sites because they were more typical for double-banded plovers (HS on the Tekapo sites was low) (42, 54). We set the starting population size to 1000 and the carrying capacity to five times

the starting population. We report the mean population size (and CIs) from 250 iterations run over 25 years with odor treatment applied annually.

Predator abundance indices

We measured relative abundance of predators in both years using motion-triggered cameras (18) and ink footprint tracking tunnels (55). Ten cameras were deployed for 60 to 93 days at permanent locations at 1-km intervals along each site (five cameras either side of the river, equally apportioned to side terraces and riverbed habitat). Animals detected in any part of an image and recorded more than 5 min apart were scored as a different individual. The data are expressed as the number of individuals detected per 100 camera nights (56), based on 5920 nights. The 5-min cutoff was derived by plotting histograms of time elapsed between consecutive images of the same species. This showed a prominent peak of elapsed times within 0 to 1 min, which dropped markedly for 3 to 5 min and declined further for 5-min intervals thereafter. In 2016, relative abundance was also measured using 24 footprint tunnels deployed for 60 to 70 days at 1-km intervals along each site equally apportioned to side terraces and riverbed habitat. Every 6 days, footprint cards were replaced with fresh ink, and tunnels were rebaited with a small amount of fresh rabbit meat. Footprints were identified as cat, hedgehog, or mustelid, and the data were expressed as the number of interceptions with tunnels per 100 tunnel nights, based on 6240 nights. Ninety-five percent CIs were bootstrapped by resampling (with replacement) camera and tunnel interaction events 100,000 times.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/7/11/eabe4164/DC1>

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Misinformation tactics protect rare birds from problem predators

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