Evaluating diversionary feeding as a method to resolve conservation conflicts in a recovering ecosystem.

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Abstract

1. The recovery of mammalian predators of conservation concern in Europe is a success story, but their impact on some prey species of conservation concern may cause conservation dilemmas. This calls for effective intervention strategies that mitigate predator impacts without compromising their recovery.
2. We evaluated diversionary feeding as a management intervention tool to reduce depredation on nests of rapidly declining Western capercaillies in Scotland. We studied the influence of diversionary feeding provision on the fates of artificial nests deployed using a replicated and representative randomised landscape-scale experiment. This comprised paired control (no diversionary feeding) and treatment (diversionary feeding applied) sites, each with six artificial nests distributed across 600 km^2. The experiment was conducted over two years, and in the second year, the control-treatment pairs were swapped.
3. Diversionary feeding substantially reduced depredation of artificial nests, translating into an 83% increase in predicted nest survival over 28 days of incubation. The increase in survival was mostly accounted for by a reduction in the probability that a pine marten, the main nest predator, consumed or cached eggs. Diversionary food also significantly reduced nest predation by badgers, although the magnitude of this effect varied by year.
4. Diversionary feeding is an easily employable method shown in this study to reduce predator impact (functional) without lethal (numerical) intervention. Managers should proceed with its application for conserving capercaillie in Scotland without delay.

Introduction

Many conservation interventions lack sufficient evidence of effectiveness before being implemented, despite multiple pressing issues requiring effective intervention owing to limited resources and vast demands. This often leads to inefficient and ineffective management that fails to achieve, or worse, are detrimental to, broader conservation goals. The result is often conflict among managers, stakeholders, scientists, and the public.

With legal protection and reduced lethal predator control, the recovery of many mammalian predators in Europe is a success story for conservation. However, many of these predators exploit a range of prey, some of which are also of conservation concern or financial interest, leading to conservation conflict (Redpath et al., 2013). Lethal control of generalist predators is widely used as a management intervention, aiming to maximise a harvestable surplus or to improve the conservation status of declining species (Gibson, 2006). Lethal control is widely accepted when it eradicates or controls some damaging non-native predators (Zavaleta et al., 2001). In contrast, lethal control of native predators to protect native species is ethically debatable and has often been shown to be ineffective, except at small spatial and short temporal scales.

Many generalist predators readily compensate for losses through increased immigration and reproduction, leading to only short-term reductions (months) in predator density unless control is applied continually, with culling foxes during breeding periods showing recovery by the following February (Lieury et al., 2015)). Accordingly, many programmes cannot achieve the standards required to have a substantial impact (Kämmerle and Storch, 2019). Additionally, protected predators cannot easily be lethally controlled, requiring relevant authorities to change conservation goals, policy, and licensing (Sainsbury et al., 2019). This means lethal control may only extend to a portion of the predator guild, and the most impactful species may not be influenced. Culling also disrupts the predator guild, with consequent changes in the behaviour and density of non-target species (Rees et al., 2023) while disrupting regulatory ecosystem services that some predators provide (Sheehy et al.,

2018; Williams et al., 2018). Moreover, even for species that are not presently protected, ethical and public perception issues are associated with the acceptability of lethal control of predators (Santiago-Ávila et al., 2018). Therefore, interventions to alter the impact of predation, as opposed to interventions that seek to reduce the abundance of predators, may be more effective for conservation.

The diet of mammalian generalist meso-predators is often dominated by the most abundant prey within the system, typically small mammals (e.g., voles), but in the face of episodic scarcity of (cyclic) primary prey species, prey switching results in increased predation on alternative preys, such as ground-nesting birds and their nests (Kjellander and Nordström, 2003). Increased nest loss to generalist predators has been implicated as contributing to the decline of multiple ground-nesting birds, including forest grouse and waders (Ewing et al., 2022; Ibáñez-álamo et al., 2015). Roos et al. (2018) systematic review found compelling evidence that ground-nesting seabirds, waders, and gamebird populations can be suppressed by predation. Specifically, populations of long-lived species with high adult survival and late onset of breeding are more likely to be impacted by predation.

Many ground-nesting birds have adaptations to reduce the impact of nest predation, such as laying large clutches and re-laying, which reduces variation in population growth rate (Lima, 2009, 1987). Via these adaptations, native predators and prey have historically coexisted. However, the level of nest loss a population can withstand depends on its demographic and ecological context (Banks, 1999). For example, if nest depredation rates are increased under human influence, whether owing to the elevated density of generalist predators (e.g. via food subsidy (Pringle et al., 2019) or lack of competitors (Petty et al., 2003)) or more vulnerable nests (e.g. a reduction in safe nesting habitat (Kaasiku et al., 2022)) and compounded by deleterious climate and habitat influences (Ibáñez-Álamo et al., 2015) losses may become additive. Therefore, there is a threshold below which decline will eventually lead to deterministic extinction and where management intervention may be warranted or, in some cases, is the only option.

One promising non-lethal management option is diversionary feeding: the deliberate provisioning of food to change the behaviour of target species and reduce unwanted behaviour (Kubasiewicz et al., 2016) by exploiting the propensity of foraging individuals to exploit the most easily accessed resources (Pyke, 1984). It has been used to reduce the predation impact of single predator species, such as red kites (*Milvus milvus*) preying on lapwings (*Vanellus vanellus)* (Mason et al., 2021) or kestrels (*Falco tinnunculus*) exploiting little terns (*Sternula albifrons*) (Smart and Amar, 2018).

A notable 22-year-long diversionary feeding management trial, supplemented with a short-term experiment, in a boreal forest landscape (Norway) resulted in increases in black grouse (*Tetrao tetrix)* and Western capercaillie (monitored via brood counts with pointer dogs), attributed to a reduction in fox predation (Finne et al., 2019). A similar experiment that provisioned foxes with dog food (Lindström et al., 1987) found decreases in nest predation during cyclical vole crashes. These studies are valuable starting points for understanding how diversionary feeding may influence nest predators specifically. However, as noted by Kubasiewicz et.al (2016), the success of diversionary feeding is often species and context-specific. Therefore, assessing species not evaluated in previous studies is crucial for understanding the effectiveness of diversionary feeding for multiple species. Landscape-scale experimental evidence is limited yet vital in establishing how diversionary feeding can function as a widely applied conservation intervention to alleviate nest predation pressure.

Forest grouse species' (Tetraonidae) are the focus of much interest from a game and conservation management perspective. Culling nest predators is often promoted as a key intervention for grouse population maintenance (Fletcher et al., 2010). One species with a significant conservation focus across Europe is the Western capercaillie *(Tetrao urogallus)*. In Scotland, several well-funded conservation initiatives have failed to durably halt the pronounced decline of capercaillie since the 1970s, with evidence of a further 50% reduction from 2016 to 2020 and extinction is predicted within the next 50 years (Baines and Aebischer, 2023). Climate change is the likely ultimate driver of decline through reduced food sources for chicks and hens (Wegge et al., 2022). However, multiple proximate

factors are also implicated in the decline (i.e. fence collisions (Baines and Summers, 1997)), including a significant impact of predation of nests and chicks (Summers et al., 2004).

Lethal control of foxes and crows is common practice across many shooting estates in Scotland; even with this intervention, capercaillies have disappeared from all but a few shooting estates, with the core remnant populations now found in regions where predator control is not carried out (Baines and Aebischer, 2023). In contrast, two other potential grouse predators, badger (*Meles meles)* and pine marten (*Martes martes,* marten hereafter), are UK-protected species and cannot be routinely controlled in the same manner (MacPherson and Wright, 2021). A correlative study in Scotland implicated martens in the decline of capercaillie (Baines et al., 2016). As a result, lethal control of martens has now been suggested as a possible capercaillie conservation option. However, tension exists because this would risk undoing conservation gains (marten recovery) whilst also requiring significant scale, effort, and cost to overcome compensation through immigration. Given these legislative restrictions, practical difficulties, a lack of scientific consensus on efficacy, and the intraguild complexities resulting from the disruption of predator communities, there is an urgent need for alternatives, such as diversionary feeding, to be evaluated. Particularly given its potential to influence the behaviour of multiple members of the predator guild simultaneously.

Considering that evidence on the effectiveness and practicalities of diversionary feeding has been mixed, we respond to a need to evaluate the extent to which diversionary feeding could decrease nest predation by a guild of predators and to assess the practicalities and feasibility of diversionary feeding as a management tool. We do this through large-scale, experimental deployment of diversionary feeding paired with control sites with no feeding. Specifically, we focused on the protected marten as an important nest predator and the critically endangered capercaillie. Our experiment compared artificial nest survival in a control and treatment design to evaluate how diversionary feeding influences the rate at which nests are depredated. We also aimed to establish how the distance of nests from feeding sites may influence the effectiveness of diversionary feeding. Our experimental

approach provides a robust, accurate, and comparable index of predation change, with nest failure purely being related to predation pressure and not alternative factors, such as nest abandonment due to adverse weather, as may be true with actual nests.

Materials and Methods

2.1 Study Area

This study was conducted in the Cairngorms Connect landscape (FLS, Wildland Ltd, RSPB, Naturescot), a 600km^2 ecological restoration project on the western side of the Cairngorms National Park, Scotland (57°09'47.5"N 3°42'47.0" W, Figure 1). The landscape consists of remnant Caledonian and plantation pine forests (mainly *Pinus sylvestris*), with a mixture of bogs, heaths, and some deciduous woodlands. Management includes intense culling of *Cervidae* (red and roe deer) to allow forest regeneration, and, unlike in more traditional neighbouring estates, there is no control of predators. The area encompasses the core of the remaining population of Scottish capercaillie (Baines and Aebischer, 2023). The predator community includes badger, fox, marten, carrion crow (*Corvus corone)*, common buzzard (*Buteo buteo)*, and ten scarcer raptor species.

2.2 Experimental Design

We performed a randomised landscape-scale experiment with paired control and treatment sites swapped between years. The sampling units were 60 paired, 1km^2 square grid cells restricted to forested areas (National Forest Index, min of 1.7 hectares of forest cover) and the size of the grids was chosen to encompass the typical daily home range of a marten (49 ha in females and 54 ha in males (Zalewski et al., 2004)). Diversionary feeding treatment was assigned to all but 8 cells randomly, and the paired control cell was selected to be approximately>1km^2 from its matching diversionary feeding cell to maximise treatment independence, using empty cells as spacing (Figure 1). The centre of treatment cells had a feeding station (see below), and each pair of treatment and control cells contained six artificial nests as response variable (see artificial nests below). Due to constraints

resulting from the convoluted shape of the study area, 8 cells with edges closer than 1 km were given the same treatment to maintain the independence of treatment. The response variable to treatment was the fate of six artificial nests. The experiment was conducted over nine weeks between 24th April and 1st July, coinciding with tetraonids' nesting, re-nesting, and early brooding periods (Summers et al., 2004) in 2021 and 2022. Diversionary feeding and control treatments were swapped within pairs between years.

2.3 Diversionary Feeding Stations

To maximise the applied relevance of the experiment, we provided supplementary by-products from ongoing deer culling. This is a resource known to be consumed by predators when left in situ as gralloch (organs left after culling) and carcasses, which was more cost-effective than provisioning other food sources. The nine-week timeframe selected for our feeding provisioning was deliberately short to avoid any numerical predator response, a potential risk with diversionary feeding (Kubasiewicz et al., 2016). The feeding period also coincides with the time of more abundant food (Spring), meaning that diversionary food is more likely to provide an alternative, not a supplement. By-products from deer culling presented in times of food scarcity (winter) are more likely to be supplements (Whitney et al., 2018)

Inception of diversionary feeding was timed close to egg laying to avoid any increase in predator abundance within the vicinity of feeding stations after territories and breeding decisions of predators were likely fixed. Feeding stations were deployed within ~100m of the centre point of grid cells and were replenished every two weeks with ~10kg of deer carrion (for 8 weeks), and the remaining food weights were recorded with a spring scale to monitor depletion. Replenishment ensured food was always available, even if predators were to have found decaying meat unappealing (Moleón and Sánchez-Zapata, 2021). When possible, food movement and the distance from central feeding stations were also recorded.

All feeding stations were monitored using remote camera traps (Browning Recon Force Advantage model: BTC-7A), set to record three-shot bursts with a five-second interval between captures to establish uptake of diversionary feeding treatment by target and non-target species. These settings were selected to allow detection of predators quickly moving through sites and removing food. We considered an independent detection as an image taken within >30 minutes of each other.

2.4 Artificial Nests

We used the fate of artificial nests rather than nests of wild capercaillie and black grouse as the response variable owing to the scarcity of these focal prey and to minimise disturbance. Approximately 7 days after establishing the feeding sites, we constructed 3 artificial nests, containing 7 eggs, in each control and treatment grid (N=180). The three nests were placed 100m, 300m and 500m from the centre of the cell. A second deployment of nests, mimicking re-laying, occurred at the predation date or hatch date of the first deployment at the same distance interval from the cell centre but 50-100m away from the previous nest to avoid predator bias. Secondary nests contained only 3 hen eggs plus one wax egg, mimicking the lower clutch size seen in relaying (Storaas et al., 2000) and were not replaced once depredated or if they survived 28 days. Meaning 360 nests were deployed each year. All nests were checked every 14 days, with two visits spanning the 28-day capercaillie incubation. Checks were conducted visually from 3-5 m away. The location of the artificial nests at each distance was determined using a randomly generated compass bearing from the centre of the grid at the specified distance.

The nests were made to resemble actual capercaillie nests: a shallow depression at the base of a tree filled with plant material, covered with dwarf bushes twigs to mimic the visual camouflage an incubating hen provides. We ensured that at least 1.5 eggs were visible to an observer standing 3-5 m away from the nest to allow for nest detection by a visual (avian) predator. Each artificial nest had six small domestic hen (*Gallus gallus domesticus)* eggs, resembling capercaillie eggs in size and colour (Mortola and Al Awam, 2010; Rosenberger et al., 2017). A 7th egg was drained and filled with “Parasoy”

soy wax blend to aid in identifying predators through tooth and bill marks. Wax eggs had a 50cm clear fishing line attached to a 3mm nail inside the egg, with the other end tethered to the ground with a 30cm tent peg. To reduce human scent that may affect discovery rates (Weldon, 2021), eggs were stored on pheasant feathers for seven days before deployment, rubber gloves were worn when handling eggs, and rubber boots and field clothes worn during deployment were stored outdoors.

If a nest site was disturbed or the 1.5 visible eggs could not be seen during nest checks, the nest was inspected in more detail. Depredation was deemed to have occurred if any hen egg was damaged or removed. Field signs, including marks on wax eggs and patterns of nest disturbance, were recorded to ascertain which predator was likely responsible (Summers et al., 2004). The assumed predator was assigned for each depredation event before checking camera trap data to allow unbiased validation.

In addition to the 14-day visual checks, camera traps were set up at one-third (60, per treatment, per year) of nests (Browning Recon Force Advantage model: BTC-7A or Browning Recon Force Elite Model: BTC-7E-HP4). This allowed the specific identification of nest predators and was used to validate field interpretation of wax egg markings and nest signs. Cameras trained on artificial nests were set to record 10-second-long videos and distributed equally, but randomly, between treatments and distances. Thus, 10 nests per distance from the cell centre had a camera for each treatment.

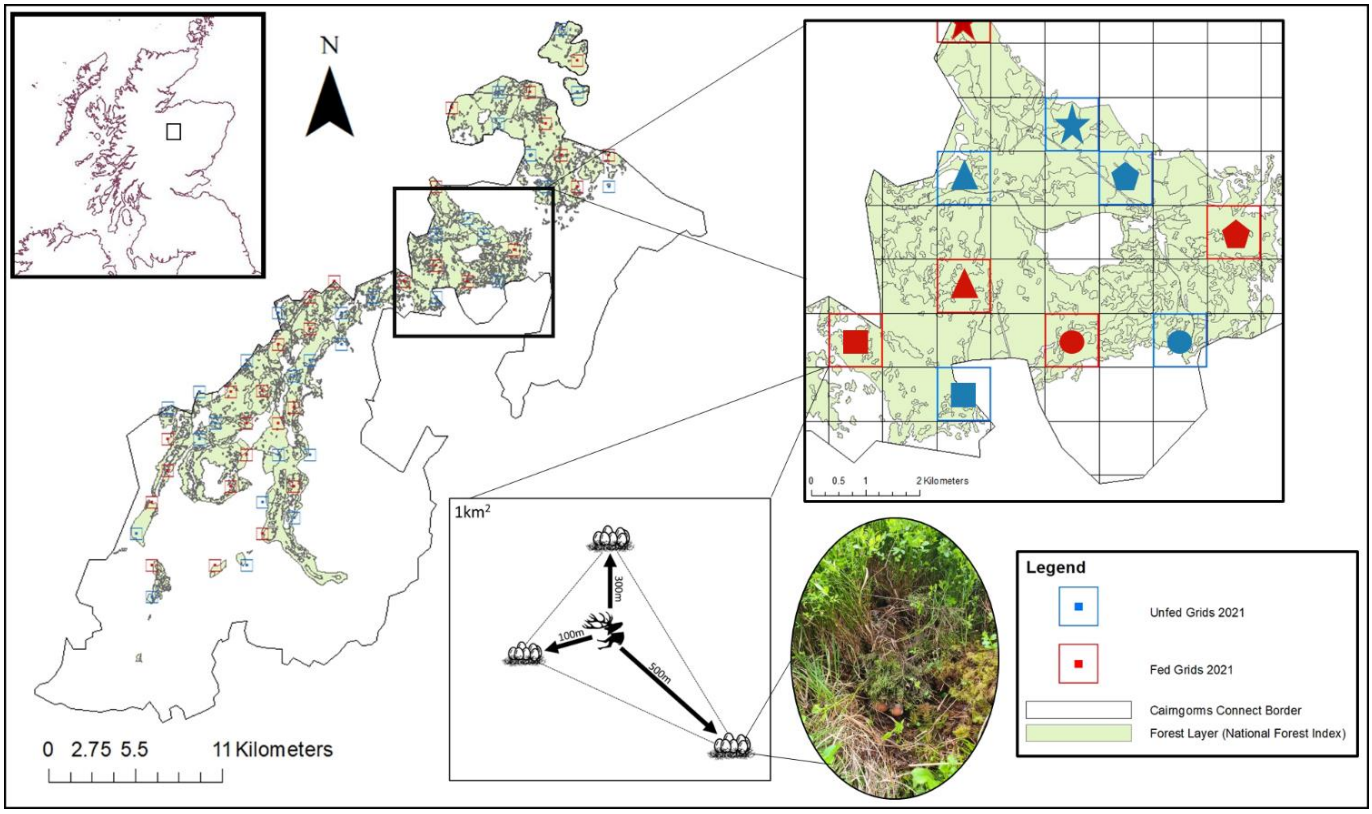

Figure 1. Illustration of the experimental design. The main map shows the forested areas of the Cairngorms connect landscapes, which was our scope of inference. The highlight region zooms into the sampling grid cell design (squares), showing the division of the sampling area into 1km^2 suitable sample grids (based on being within the CC area and containing the forest layer). The primary control and test deployments are colour coded, with feeding sites (2021) in red and control sites (2021) in blue. The bottom left 1km2 area shows an example of a sample grid showing the internal structure of a diversionary feeding site, including the general nest structure and a central feeding station. Control sites mimicked the structure without the feeding station. An exemplary artificial nest with heather cover is illustrated.

Data extraction

Camera trap photos taken at feeding stations were identified at the species level using the metadata tagging software DigiKam 7.3.0, following the 'camtrapR' workflow (Niedballa et al., 2016). Videos taken at artificial nests were viewed, and species-specific detection histories were generated manually by recording the time and date of a depredation event. The assumed responsible predator of

233 depredated nests for nests without cameras was inferred from field signs. Video footage from camera
234 traps allowed validation of assumed predators from signs with confirmed predators on camera traps,
235 showing a 99% (N= 109) success rate in correctly identifying nest predators when an assumed predator
236 was assigned (See Appendix 1). We excluded 15 nests, from further analysis, known to have been
237 depredated by a fox (n=2), corvids (n=7), or rodent (n=6) owing to low sample size and 28 nests
238 depredated by non-identified species as they likely formed a heterogeneous group (12 Test: 31
239 Control).

240 Statistical analysis

241 We modelled the three fates of artificial nests using multinomial logistic regression: survived 28 days,
242 depredated by marten, and depredated by badger. We analysed the multinomial responses using
243 covariates that reflected the experimental design: diversionary feeding treatment to quantify the
244 effect of diversionary feeding, distance from the grid centre to quantify any spatial decay of the
245 feeding effect, and interaction between distance and treatment. We also included year as a fixed
246 effect to account for annual variation, e.g., in field vole prey abundance. We added grid cell identity
247 (n=60) as a random effect to account for any local influences on nest predation, such as local predator
248 abundance and habitat, across the two years of study.

249 Multinomial models were implemented using a generalised additive model (GAM) in package 'mgcv'
250 (Wood, 2017). We used the 'mn' response model as it allows the inclusion of random effects. We used
251 1000 simulations from the model using the function "Predict" to produce population-level (marginal)
252 estimated fate probabilities and confidence intervals. All statistical analysis was performed using R
253 (version 4.1.3).

254 **Results**

255 Uptake and usage of feeding stations

On average, 57.5kg (range: 38 - 81 kg) of deer meat was deployed per feeding station each year, with an average of 10.5kg (range: 6 - 14 kg) added every two weeks according to the weighed assessment of depletion at restocking visits.

Over 340,000 photographs were collected from the 60 feeding stations across 3,912 camera trap days. They include 142,179 images of potential egg predators recorded in 3,726 independent visits. Martens accounted for 13.0% of these visits (19374 images, 486 independent detections), badgers for 22.5% (54024, 839), and foxes for 10.3% (12946, 383). We also detected avian nest predators: 31837 (1306, 35.0% detections) of the visits were by raptor sp. (buzzard, golden eagle, red kite) and 20410 by corvids (639, jay, crow). Fifty-four out of 60 feeding stations were visited by predators (86.6% in 2021, 93.3% in 2022). Badgers, foxes, and buzzards visited similar proportions of feeding stations (58%, 57%, and 55%, respectively), followed by martens (43.33 %) (See Appendix 2). As predators had moved deer carrion away from the camera fields of view at 132 restocking visits (n= 240), it was not possible to estimate the amount of diversionary food consumed by each species.

Nest fate with diversionary feeding

Forty-nine percent of artificial nests (353/720) survived the full 28 days, meaning that 51% of nests experienced depredation. Recorded nest predators were martens (38%, 268), badgers (6.9%, 50), and other species (unknown, fox, corvid, and rodent (6.8%, 49)). However, fewer nests survived in control sites (128, 35.5%) than in diversionary feeding sites (228, 63.3%), reflecting fewer nests depredated by martens (Control: 170, Test: 98) and badgers (Control: 31, Test 19; (See Appendix 3).

Multinomial logistic regression revealed that nest fates were associated with the three experimental variables (treatment, distance, and year) but in different ways, see Table 1. The probability of marten depredation was substantially reduced when that nest was at a treatment site relative to a control site (-1.494, +/-0.309, p<0.00), and this did not vary between years (-0.007, +/-0.172, P= 0.969). There was an increase in the probability of depredation by marten with increasing distance between the nests and the feeding site. However, this effect was small and was only evident at the furthest distance

of 500m (0.698 +/-0.424, P= 0.099). The probability of badger depredation was also substantially and significantly reduced by diversionary feeding (-1.723 +/-0.622, p=0.006), with a significant additive influence of year reflecting higher badger depredation in 2022 (0.694 +/-0.325, P=0.033). Distance, with an interaction between treatments, did not show any significant effect. Predictions were based on the provision of diversionary food; we can see an increase in the mean predicted probability of nests surviving from 0.406 (CI 0.303- 0.523) up to 0.744 (CI 0.645- 0.828), an increase of 83%. This change occurs mainly due to the change in the predicted probability of marten depredation, reducing in value from 0.52 (CI 0.40 0.64) in control to 0.22 (Ci 0.151- 0.318) with diversionary food provision. There is also a change in predicted predation by badgers, with diversionary food treatment reducing predictions from 0.085 (CI 0.0187-0.227) control to 0.03 (0.005- 0.098) in 2021 and an increase in overall predicted badger predation in 2022 to 0.15 (CI 0.04-0.366) control and with 0.058 (CI 0.011-0.175) however, confidence intervals of badger overlap. See Figure 2.

When assessing the fate of all nests (N=720), including those not included in the multinomial model due to uncertain or sparsely represented fates, Kaplan-Meier analysis showed an increase in survival with treatment. Estimated 28 days survival of control nests was 0.345 (CI 0.281- 0.422), and that of nests in diversionary feeding treatment was 0.650 (CI 0.585-0.723), an 88% increase in line predictions from the multinomial model (See Appendix 4).

Table 1. Coefficients of multinomial logistic regression showing changes to log probability of fate of artificial nests. The reference fate for the model is that the nest survived for 28 days. Significant results are highlighted in bold.

	Dependant Variable (Fate)							
	Pine Marten (B)				Badger (C)			
Independent Variables	Coefficient	Std. Err.	z	P>|z|	Coefficient	Std. Err.	z	P>|z|
Intercept	0.278	0.235	1.184	0.237	**-1.794**	**0.409**	**-4.390**	**1.14e-05**
Treatment	**-1.494**	**0.309**	**-4.832**	**1.35E-06**	**-1.723**	**0.622**	**-2.771**	**0.006**
Distance 300m	0.005	0.285	0.019	0.984	-0.547	0.533	-1.027	0.304
Distance 500m	0.206	0.297	0.691	0.489	0.319	0.473	0.675	0.499
Year (2022)	-0.007	0.172	-0.038	0.969	**0.694**	**0.325**	**2.137**	**0.033**
Treatment*500m	0.155	0.425	0.366	0.715	1.170	0.839	1.394	0.163
Treatment*300m	0.698	0.424	1.647	0.099	0.736	0.795	0.926	0.355

Fate A (Survived) Calculated as Difference in
Interecept (100m, Control, 100*Control, 2021)
Significant Results in Bold

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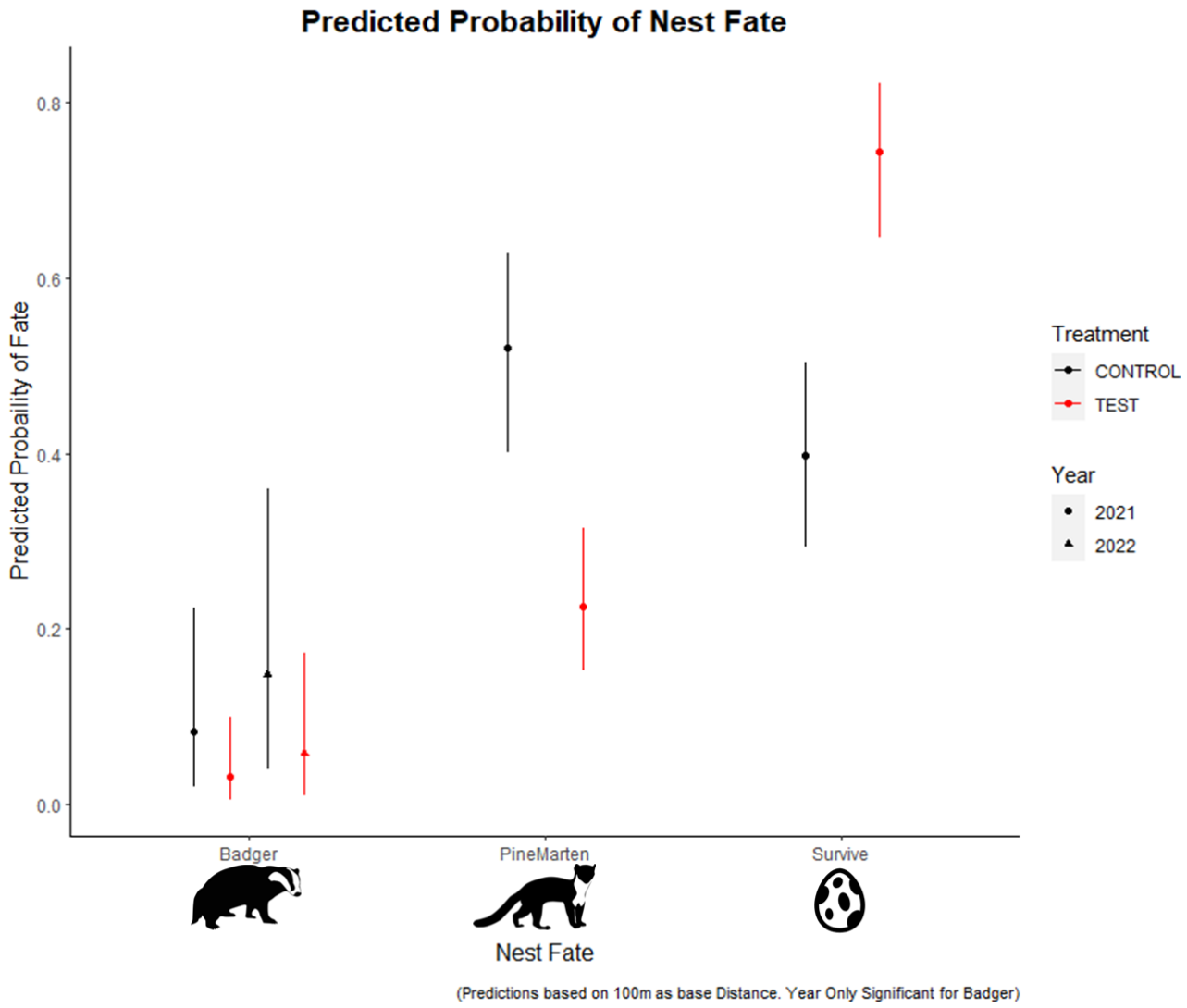

Figure 2. Multinomial logistic regression results show the predicted probability of nest fate: depredated by badger, depredated by marten, and survived. Predictions were created for nests at 100m from grid centres as the baseline for predictions. The year was not shown to influence the fates pine marten or survived with predictions based on 2021. We present predictions for Badger for both 2021 and 2022, as it was highlighted to have a significant difference within multinomial modelling (2021 circle, 2022 triangle). Treatment is shown with control in black and test in red 97.5% confidence intervals are shown via error bars.

Discussion

We evaluated how diversionary feeding alters the rates of nest depredation by meso-carnivores in a boreal forest landscape. We found that diversionary feeding almost halved depredation rates of pine

martens and badgers on artificial nests over the 28-day incubation period of tetraonid grouse. Predicted nest survival probability increased from 0.406 to 0.733 with the provision of diversionary feeding. Using a fully randomised, well-replicated, landscape-scale experiment allows us to infer causality between short-term provisioning of diversionary feeding and reduced depredation of artificial nest predation. Should they extrapolate to real capercaillie nests, our results present diversionary feeding as a viable non-lethal option for reducing nest predation on ground-nesting birds of conservation concern across the boreal zone, providing a form of control of the impact of predator presence without sacrificing ecosystem benefits, or garnering negative public interaction. The presence of a validated alternative to lethal intervention raises questions as to whether practitioners have the social licence to cull one protected species for the protection of another.

Intervention for Protected Predators

Diversionary feeding almost halved both marten and badger depredation rates but from different baselines. Because of these two species' reduction in nest depredation, artificial nest survival increased by 83% (Figure 2). The risk of depredation by marten was five times higher than badgers. Hence, the reduction of pine marten impact is proportionally greater for nest survival. This is despite martens having confirmed access at only 43% of feeding stations from cameras. This could be due to the localised redistribution of diversionary food into the area surrounding feeding stations by other predators, with large pieces of carrion found up to 50m away from feeding stations, causing imperfect detection. Similar food redistribution around carcasses by badgers and foxes has been seen at a maximum of 103m (Young et al., 2015).

Both badger and marten numbers have been suppressed historically due to persecution. Marten was driven to localised extinction but has recovered since the first re-sightings in the study area in 1994. It has been suggested that this recovery and the perceived high density of pine martens may be the reason for unsustainably high nest predation rates. Surveys in 2012 estimated 0.07 - 0.38 individuals per km^2 using spatially explicit capture-recapture of non-invasively collected hair in sites within our

research area (Kubasiewicz et al., 2017). A 2020 survey using similar field and analytical methods indicates no rise in density Hobson et al. (2023). These values are within density estimates for pine marten elsewhere, such as Bialoweiza Forest, ranging from 0.363-0.757 individuals per km^2 (Zalewski and Jedrzejewski, 2006). This indicates that modifying marten feeding behaviour through diversionary feeding is a realistic, sustainable, and evidence-based alternative to lethal control, especially if marten populations are not above normal densities.

Land manager perceptions (before this experiment) are that badger numbers have increased; while no formal estimates have been presented, we found that badgers were widely distributed, accessing 58% of feeding stations and depredating artificial nests in a pine forest, where historically, they were assumed mostly absent. This could reflect a recovery by badgers and another reinstated source of predation pressure that could also be halved by diversionary feeding.

Interpreting artificial nest data

There are known caveats to interpreting absolute predation rate on artificial nests and necessary conditions for interpreting differences in predation rate in an experimental context such as ours. To avoid overemphasising some predators' impact and underestimating others' impact, the predators responsible for actual nest predation must match those of actual nests (Pärt and Wretenberg, 2002). For marten, the main predator in this study, we can be confident that changes seen in nest predation may translate to actual nests, as they have been seen to predate actual nests at a similarly high rate in other studies. Summers et al. (2009) sampled actual capercaillie nests in the same region with camera traps (N=22); in this instance, all confirmed losses were due to marten predation.

Consideration of other studies on predation rates on the capercaillie nests reveals that the fate of artificial nests in this study aligns with what is seen elsewhere in their range. Predation rates of capercaillie nests in a stable population in southern Norway ranged from 48 to 90% according to the stage of the vole cycles (Wegge and Storaas, 1990). In Scotland, observed predation rates revealed by camera traps deployed on actual nests ranged between 42 and 68% (Summers et al., 2009). Our

353 estimates of 65% predation rates on our artificial nests in control sites are within these ranges, with
354 the observed 37% in the presence of diversionary feeding as low as the lowest value seen in Norway
355 in a peak vole year. Thus, present nest predation rates in Scotland are not abnormally high, especially
356 considering our study took place during low vole years when predation rates were expected to be at
357 the high end of observed rates.

358 In this study, fox and corvid depredation of artificial nests was lower than on actual nests studied
359 by(Baines et al., 2004) in the same region. The presence of camera traps at some, but not all, false
360 nests may have deterred foxes, given the prevailing persecution (Zalewska et al., 2021). Conversely,
361 our efforts to reduce human activity at our artificial nests may have precluded the inflated corvid
362 predation that often occurs where humans interact with nests (such as trails and markers (Picozzi,
363 1975)). While some raptor species influence red grouse recruitment, the impact occurs through chicks,
364 not nest predation (Thirgood et al., 2000), so our results are not unexpected.

365 Consideration of risk factors:

366 The duration of our experiment, from late April to early July, was chosen to reduce the risk of a
367 numerical response through aggregation by predators potentially subsidised by deer carrion. Predator
368 territories and the number of embryos were long established before the deployment of diversionary
369 feeding. Thus, we infer diversionary feeding changed predator foraging (functional response), not
370 numbers (numerical response). However, deer culling activities mainly occur in winter in Scotland. It
371 is not unlikely that predators' numbers are elevated by the overwinter provision of gralloch (when it
372 is not removed) across the landscape and before our experiments. This is most likely in years of low
373 vole abundance, such as in 2021 and 2022. Anecdotally, case partners in Glenfeshie have been leaving
374 gralloch on the landscape across all seasons for over 10 years and have not seen any negative
375 influences of carrion.

376 Increased nest survival may not directly translate to more chicks reaching adulthood, hence
377 productivity (Saniga, 2002). If decreased nest predation and increased chicks make a breeding area

more attractive to predators aggregating in areas with diversionary feeding, this may elevate the predation rate (Pakanen et al., 2022). Capercaillie chick biomass is tiny relative to all other prey exploited by martens, badgers and other mesopredators. We view this as unlikely but worthy of further study.

Management Implications:

Using one fieldworker, this experiment covered most of Scotland's core residual range of capercaillie. Deployment of 30 feeding stations across five land ownership areas took five days. The focus on good experimental design for robust inference meant that deployment was labour-intensive; practical deployment would likely be easier, with no need for strict separation and designation of “control” and “test” sites. Using by-products from existing deer culling efforts means the cost of providing food was low and may even have reduced the disposal cost. Based on the total food deployed at each feeding station across our experiment, at maximum, a feeding station would require approximately 80kg of carrion, which is the equivalent of an adult male red deer (Reby and McComb, 2003). With large numbers of deer being culled, there is no limitation to the amount of deer viscera that could be made available by real-time supply or freezing byproducts during peak cull periods. Our design with nests at three distances from the food dump found no clear evidence that the depredation rate changed significantly with increasing distance from the feeding station up to 500m. A minimum effective density of one station per km^2 of suitable habitat was shown in this study. However, with no significant reduction in efficacy within that distance, the spacing could be more comprehensive for practical deployment. Logically, the influence of feeding on nest predation rate must reduce eventually, as seen with the 1.5 km^2 separation of feeding stations to control site nests. Thus, there is little doubt that diversionary feeding could be rolled out across the remaining range at little cost with potentially substantial benefits to a ground-nesting species in decline. To establish if a reduction in nest predation alone can lead to capercaillie recovery in the face of climate change, monitoring the influence of diversionary feeding should be performed, emphasising evaluating the full impact on productivity.

Another research priority is establishing if and when supplementary and diversionary food might inflate mesopredator abundance.

The observed substantial reduction in artificial nest depredation demonstrates the potential of diversionary feeding as an effective non-lethal intervention for conserving ground-nesting birds. It can be used with protected and recovering predators of conservation concern, hence alleviating conservation conflicts. Particularly, given pine marten recolonisation following legal protection, implementing non-lethal management action that mitigates the impact of predation is feasible and supported by the evidence presented here. No major obstacles should exist to implementing diversionary feeding whilst further monitoring impacts throughout the historical range of capercaillie now shared with the native pine marten.

Author contribution:

Conceptualisation: JB, CS, XL, KK, APP; **Fieldwork**: JB; **Statistical analyses,** JB, CS; **Data curation:** JB; **Writing—original draft preparation:** JB; **Writing—review and editing:** JB, CS, KK, XL, APP; **Funding acquisition:** XL, CS, KK. All authors have read and agreed to the published version of the manuscript.

Conflict of Interest:

None.

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Appendix Document:

Appendix 1: Nest Camera Trapping Assumed and Confirmed:

Comparison of assumed predators from signs with confirmed predators on camera traps showed a high success rate in correctly identifying nest predators when an assumption was made. In many cases where an observer was incorrect in assigning an assumed predator (pine marten only), the pine marten was the primary nest predator. Still, the nest site was visited afterwards by a secondary predator. When assigning an unknown mammal, in some instances, it was due to multiple predators interacting with the nest site before the observer could look at the predation signs, changing the indications, or, in the case of the fox, having so few instances of occurrence, signs were not clear. Out of 115 nest sites predated by predators with a camera trap deployed on them, 106 were able to detect the true nest predator successfully, and six failed to detect any interaction with the nest due to camera trap failure. Overall, observers were correct over 99% of the time when assigning an assumed predator. This gave us confidence to use assumed and confirmed predators in further fate analysis.

Table 1 Fates of nests of camera-trapped sites, with confirmed predation. The total number of assumed assignments is compared with the number of confirmed predators and if the assignment was correct. In the cases of incorrect assignment, the true predator was highlighted in “Incorrect

classification". In the case of unknown mammals, the incorrect classification highlights who the truly responsible predator was

Comparison of Assumed Accuracy (Nests with Camera Traps)					
Predator	Assumed Assignments (Total)	Number Confirmed	Correct Assignments	Accuracy (%)	Incorrect Classification
Pine Marten	72	72	70	97.2	1 Marten & Fox, 1 Marten & Badger
Badger	18	18	18	100	NA
Fox	0	2	0	NA	NA
Rodent	4	4	4	100	NA
Avian	0	0		NA	NA
Unknown_Mammal	13	NA	NA	NA	1 Badger, 8 Pine Marten, 2 Fox, 1 Dog & Pine Marten, 1 Badger & Pine Marten.
					N=109 (6 Camera traps failed to detect a predator)

Appendix 2: Feeding Station Access:

Feeding stations were monitored via camera traps across the entire sampling regime; camera images were tagged using the methodology described in the main text across the 9 weeks of camera trap monitoring of diversionary feeding. We highlight below the minimum number of feeding sites with at least 1 detection of a feeding predator. The minimum is due to a large amount of food dispersal from the central monitored point preventing perfect detection. Raptor species were grouped into one category to include rare detections, such as White-tailed eagles, but mostly were detections of buzzards. Domestic dogs were accidentally detected at 25% of feeding sites, with them not being kept on leads as is advised during the breeding season. Further breakdown of key predators can be found in the main text.

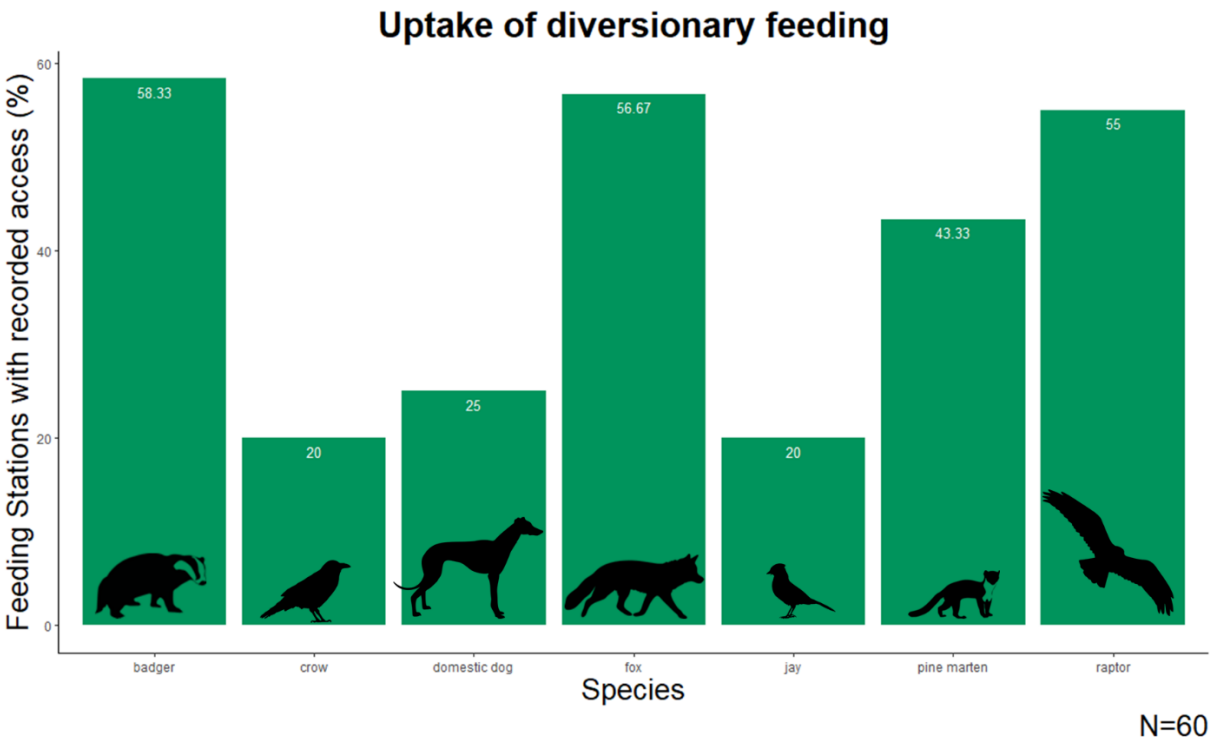
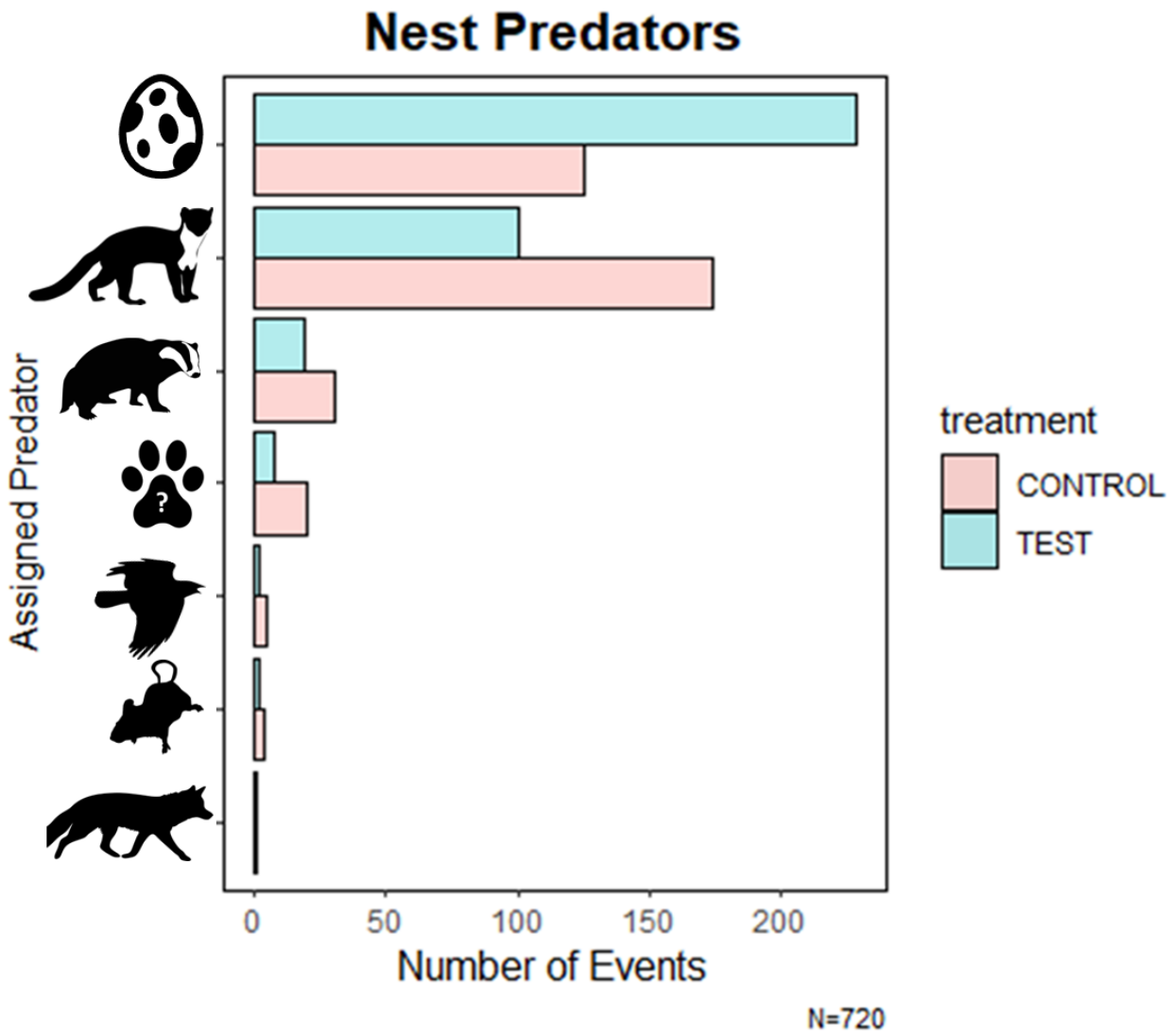


Figure 2. Shows the proportion of feeding stations with confirmed feeding by predatory species via camera trapping. The y-axis shows the percentage of all 60 sites that had a detection of each of the species listed on the X-axis.

Appendix 3; Nest Fates:

Raw nest data was explored to evaluate the primary visual effect of treatment on nest fate. Before robust monitoring, simply from base values alone, there is a noticeable difference between the number of nest predation events alongside the treatment variable. Overall, regardless of treatment, the two fates with the highest occurrences survived and were depredated by pine marten. Forty-nine per cent of artificial nests (353/720) survived the full 28 days, meaning that 51% of nests experienced depredation. Recorded nest predators were martens (38%, 268), badgers (6.9%, 50), and other species (unknown, fox, corvid, and rodent (6.8%, 49)). However, fewer nests survived in control sites (128, 35.5%) than in diversionary feeding sites (228, 63.3%), reflecting fewer nests depredated by martens (Control: 170, Test: 98) and badgers (Control: 31, Test 19).



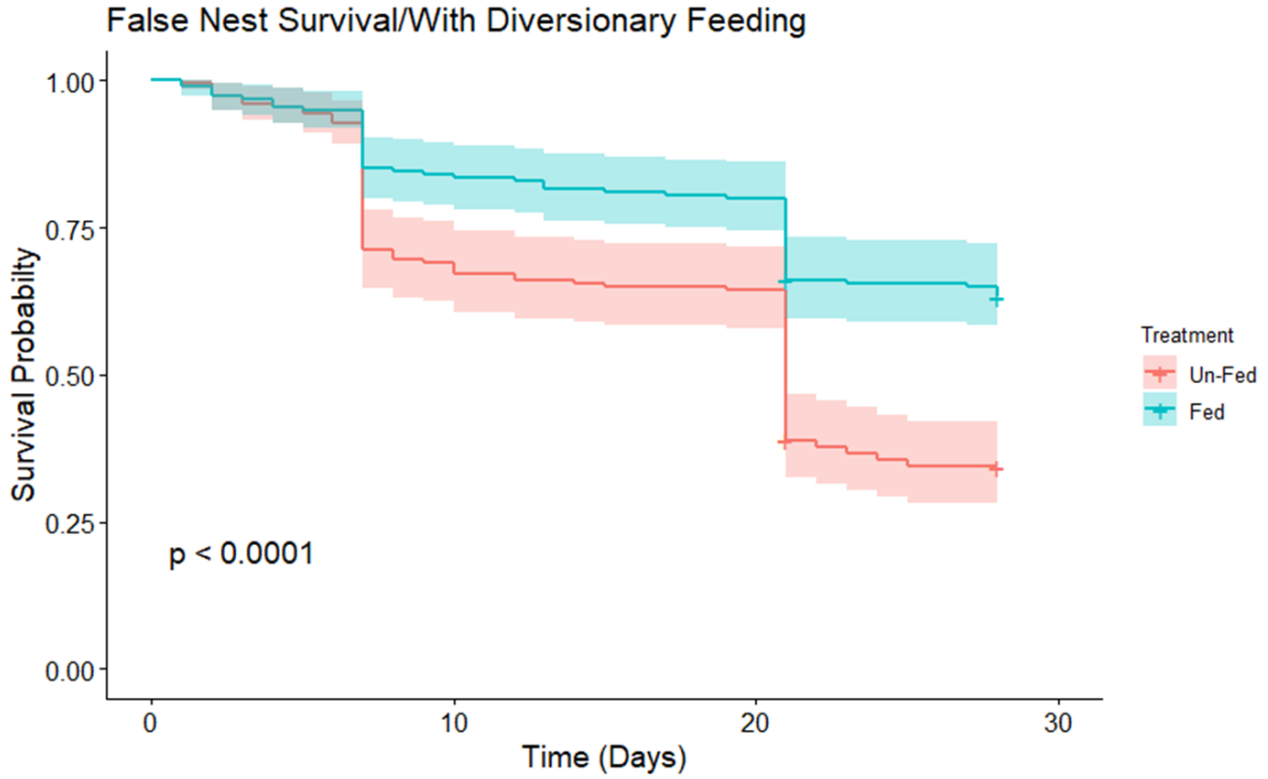
621

622 Figure 2. Proportional nest loss by all nests (confirmed and assumed combined), by treatment and
623 species. The figure is split by treatment type, with control (un-fed) and test sites (feeding). Sites are
624 ordered in order of overall prevalence from bottom to top.

625 Appendix 4; Survival without Fate Kaplan Meir:

626 The daily status of each artificial nest over 28 days was coded as a string of 1 (intact) and 0
627 (depredated) using the known predation date for nests with cameras and the mid-point between
628 visual checks for depredated nests without cameras. We estimated the influence of treatment by
629 fitting the Kaplan-Meier survival probability curve using the 'survival' package (Therneau *et al.,* 2023).
630 This allowed us to assess baseline fate (survived or predated) for all 720 nests over the 28-day
631 sampling period. Large numbers of deaths occur on day 7 and day 21 due to the assumption of a
632 central death date of nests between 14 and 28-day nest checks. These large dips indicate the trapping
633 regime, not actual deaths. Links with broader multinomial analysis are made in the main text.

634



635

636 Figure 3. Kaplan Meir survival curve visualising artificial nest survival over 28 days for control and
637 diversionary feeding (legend) diversionary feeding (N=720). Survival across our research period is
638 visualised using Kaplan Meier across 28 days of life for each nest; check days at 14 and 28 days are
639 shown with central death dates at days 7 and 21.

640

Table 1. The coefficient table of multinomial logistic regression shows the changes to the log probability of the fate of an artificial nest. The base reference fate for model (A) is that a nest survived for 28 days. Significant factors are highlighted in bold.

	Dependant Variable (Fate)							
	Pine Marten (B)				Badger (C)			
Independent Variables	Coefficient	Std. Err.	z	P>|z|	Coefficient	Std. Err.	z	P>|z|
Intercept	0.278	0.235	1.184	0.237	**-1.794**	**0.409**	**-4.390**	**1.14e-05**
Treatment	**-1.494**	**0.309**	**-4.832**	**1.35E-06**	**-1.723**	**0.622**	**-2.771**	**0.006**
Distance 300m	0.005	0.285	0.019	0.984	-0.547	0.533	-1.027	0.304
Distance 500m	0.206	0.297	0.691	0.489	0.319	0.473	0.675	0.499
Year (2022)	-0.007	0.172	-0.038	0.969	**0.694**	**0.325**	**2.137**	**0.033**
Treatment*500m	0.155	0.425	0.366	0.715	1.170	0.839	1.394	0.163
Treatment*300m	0.698	0.424	1.647	0.099	0.736	0.795	0.926	0.355

Fate A (Survived) Calculated as Difference in
Interecept (100m, Control, 100*Control, 2021)
Significant Results in Bold

641