Translocated native pine martens Martes martes alter short-term space use by invasive non-native grey squirrels Sciurus carolinensis

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RESEARCH ARTICLE

Translocated native pine martens *Martes martes* alter short-term space use by invasive non-native grey squirrels *Sciurus carolinensis*

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Abstract

1. Predators can shape the distributions and dynamics of their prey through direct and indirect mechanisms. Where prey animals are regarded as pests, the augmentation of predator populations might offer a potential tool in their management.

2. Declines in invasive non-native grey squirrel *Sciurus carolinensis* populations in Ireland and Scotland have been related to an increase in range and density of native pine marten *Martes martes* populations. These reductions in grey squirrel abundance have, in turn, been linked to recovery of native red squirrels *Sciurus vulgaris*.

3. Taking the opportunity presented by a conservation translocation of pine martens from Scotland to Wales, we investigated the short-term effects of exposure to translocated martens on the space use and survival of resident grey squirrels.

4. Grey squirrel range size and daily distance travelled increased significantly with increasing exposure to martens but we found no effect of marten exposure on the recapture probability (i.e. apparent survival) of the sampled squirrels within the study time frame. This is suggestive of contemporary, non-lethal effects changing the ranging or foraging regimes of squirrels, due either to predator avoidance and/ or earlier lethal effects associated with a reduction in intraspecific competition.

5. *Synthesis and applications.* Our evaluation mimics the conditions experienced by grey squirrels at the front edge of naturally recovering pine marten populations and presents direct evidence that pine marten translocations could play an influential role in the behaviour and dynamics of invasive non-native grey squirrel populations. Translocations of native predators, undertaken primarily for biodiversity conservation, could therefore find additional application in managing the ecological and economic impacts of invasive non-native prey.

KEYWORDS
biological control, grey squirrel, home range, invasive species, landscape of fear, pine marten, reintroduction, translocation

1 | INTRODUCTION

The direct effects of a predator on its prey are often obvious but indirect effects can play an equally influential role on prey demography and distribution (Brown, Laundre, & Gurung, 1999; Preisser, Orrock, & Schmitz, 2007). In a 'landscape of fear', cues to predator activity can elicit behavioural changes in prey species (Laundré, Hernández, & Altendorf, 2001; Suraci, Clinchy, Dill, Roberts, & Zanette, 2016) that manifest in anti-predatory behaviours, including modifications of space use, that often come at the expense of foraging and reproduction (Heithaus et al., 2007; Suraci et al., 2016). Regulation of prey populations, their behaviour and ecosystem impacts, can stem from fear-mediated responses (Jacob & Brown, 2000; Ripple & Beschta, 2004). Raccoons *Procyon lotor*, for example, exert impacts on potential prey animals by reducing the time they spend foraging (Suraci et al., 2016). Prey animal fitness can also be linked to anti-predatory responses; Green turtles *Chelonia myda*s generally avoided the areas of high tiger shark *Galeocerdo cuvier* predation risk, but turtles in poorer body condition took greater risks to exploit the areas of higher forage quality. These condition-dependent decisions affected not just turtle fitness but extended to alteration in seagrass community composition (Heithaus et al., 2007). Thus, fear of predators not only affects fitness of prey but can also result in trophic cascades with ecosystem effects.

Diversity in the responses of prey animals to their predators (Parsons et al., 2017) is related to the forms that cues to predation risk can take. These range from direct evidence of predator presence through sounds and scents (Apfelbach, Blanchard, Blanchard, Hayes, & McGregor, 2005; Suraci et al., 2016), to the association of risk with particular habitat types (Heithaus et al., 2007; Lima, Valone, & Caraco, 1985). The variability and complexity of non-lethal effects of predation and predator presence can therefore make the relatively simple concept of a landscape of fear difficult to demonstrate or quantify, particularly in a natural setting or when lethal and non-lethal effects co-occur (Polis, 1991).

The direct and indirect effects of predators upon their prey may result in comparable population effects, i.e. reduced abundance of prey animals, and so patterns observed at landscape scales might not reveal mechanistic drivers. By investigating the mechanisms underlying observed patterns relating the distributions and abundances of predators and their potential prey at finer temporal and spatial scales, we might predict and understand landscape-scale trends (Levin, 1992). This study therefore takes advantage of an opportune situation in which predator abundance, and hence the risk environment of prey animals, has been manipulated and monitored on a fine scale.

The manipulation of predator–prey relationships has long been used as a method of population control. In some circumstances, biological control agents provide a 'natural' method of managing problem species, reducing the need for ongoing human interventions (Atkins, Redpath, Little, & Amar, 2017; Wanger et al., 2010). However, the introduction of predators has often led to unexpected outcomes, many of which have been detrimental to non-target, native species (Doody et al., 2009; Parkes & Murphy, 2003; Simberloff & Stiling, 1996). Although the use or restoration of native predators to control non-native prey is relatively untested, it has potential in invasive species control. In North America the native blue crab *Callinectes sapidus* limited the abundance and range of the introduced European green crab *Carcinus maenas* through predation (DeRivera, Ruiz, Hines, & Jivoff, 2005). In Indonesia, the endemic Celebes toad *Ingerophrynus celebensis* negatively affected invasive ant *Anoplolepis gracilipes* populations through predation, thereby enhancing native ant abundance (Wanger et al., 2010). In these cases, the density of the native predator was an important factor in their impact on the invasive prey. More importantly, the differing evolutionary histories of native predator and invasive prey have resulted in a spectrum of ineffective anti-predatory responses by naïve prey, from failure to recognize predation risk to anti-predatory responses that do not enable predator evasion (Salo et al., 2007; Sih et al., 2010; Wanger et al., 2010).

The recovery of the native pine marten *Martes martes* in the United Kingdom and Ireland, after an extended period of decline and near-absence (Langley & Yalden, 1977; Sainsbury et al., 2019), has been hailed as an advance in controlling invasive non-native grey squirrel *Sciurus carolinensis* populations (Sheehy & Lawton, 2014; Sheehy, Sutherland, O'Reilly, & Lambin, 2018). Grey squirrels are classified as a pest in the United Kingdom due to the damage they cause to timber through bark stripping (Kenward & Parish, 1986), as well as competing with, and spreading infection to, native red squirrels *Sciurus vulgaris* (Rushton et al., 2006). In regions of Ireland (Sheehy & Lawton, 2014) and Scotland (Sheehy et al., 2018) where pine martens have been recovering for a substantial period and are living at high, medium and even low densities, grey squirrel populations have been negatively affected. The resulting lower densities of grey squirrels have in turn been associated with increases in red squirrel populations, thereby indirectly linking pine marten recovery to that of red squirrels. To date, the mechanistic basis of these observations remains unknown. Where they co-occur, grey squirrels, along with other native squirrel species, feature in the diets of both the American marten *Martes americana* and the ecologically and taxonomically similar fisher *Pekania pennanti* (Arthur et al., 1989; Hales, Belant, & Bird, 2008). However, range overlap between grey squirrels and these arboreal mustelid predators is somewhat limited and the grey squirrel thus largely evolved in an environment containing primarily terrestrial and aerial predators, and has been exposed to arboreal mustelids at only the limits of their native range. It might therefore be expected that grey squirrels are unlikely to demonstrate effective anti-predatory responses to arboreal mustelids. As a result, this prey species population is likely to suffer directly from the native predator's recovery. Understanding the grey squirrels' response to perturbations, such as introducing a novel predator, is therefore important in predicting the impact of increasing pine marten populations on the future status of grey squirrels in their non-native range.

The translocation of pine martens as part of a species conservation programme has created a unique opportunity to investigate the responses of resident, non-native grey squirrels to the arrival of native, but newly establishing, pine martens. By simultaneously tracking martens and squirrels we were able to record how the distribution of the martens influenced the spatial behaviour of the squirrels. We predicted that in areas experiencing higher pine marten activity, grey squirrels would: (a) occupy restricted home ranges, due to increased vigilance and reduced foraging or roaming behaviours which are associated with the presence of other predators (Lima et al., 1985); (b) show little shift in the location of their home range; and (c) move less per day in order to reduce their encounter rate with martens by restricting their ranges. We would also expect grey squirrels to (d) exhibit lower survival, when compared to squirrels in areas with lower pine marten density, as a result of direct predation.

2 | MATERIALS AND METHODS

The study was undertaken in mid-Wales at six locations comprised of mixed broadleaf and conifer woodland (Figure 1; Table 1). Squirrel trap lines were established in similar habitat at each site, i.e. in primarily broadleaf woodland compartments with relatively open understorey, which was a favourable habitat for grey squirrels. Tree species composition in the immediate vicinity of squirrel trapping locations typically comprised mature beech *Fagus sylvatica* and oak *Quercus* spp., interspersed with conifer trees, comprising Sitka spruce *Picea sitchensis*, Japanese larch *Larix kaempferi*, lodgepole pine *Pinus contorta* and Douglas fir *Pseudotsuga menziesii*. The wider sites over which squirrels ranged (Table 1) comprised multiple, diverse woodland compartments, which were in turn surrounded by large blocks of similar commercial conifer woodland (comprising >80% coniferous trees) and marginal upland farmland, largely comprising semi-improved and unimproved grasslands. In all woodland compartments there was minimal understorey and a closed canopy. The full methodology for determining habitat composition and a detailed account of woodland habitat at each site are provided in Supporting Information and Table S1. The six sites had a mean area of 56.8 ha (range 33.9–785.0 ha; Table 1) and were >3 km apart. Given the mean range size of grey squirrels in the United Kingdom is <5 ha (Gurnell, Wauters, Preatoni, & Tosi, 2001; Lawton & Rochford, 2007; Wauters, Gurnell, Martinoli, & Tosi, 2002), each site was assumed to host independent populations (Figure 1). Grey squirrels had been established in this area of mid-Wales for over
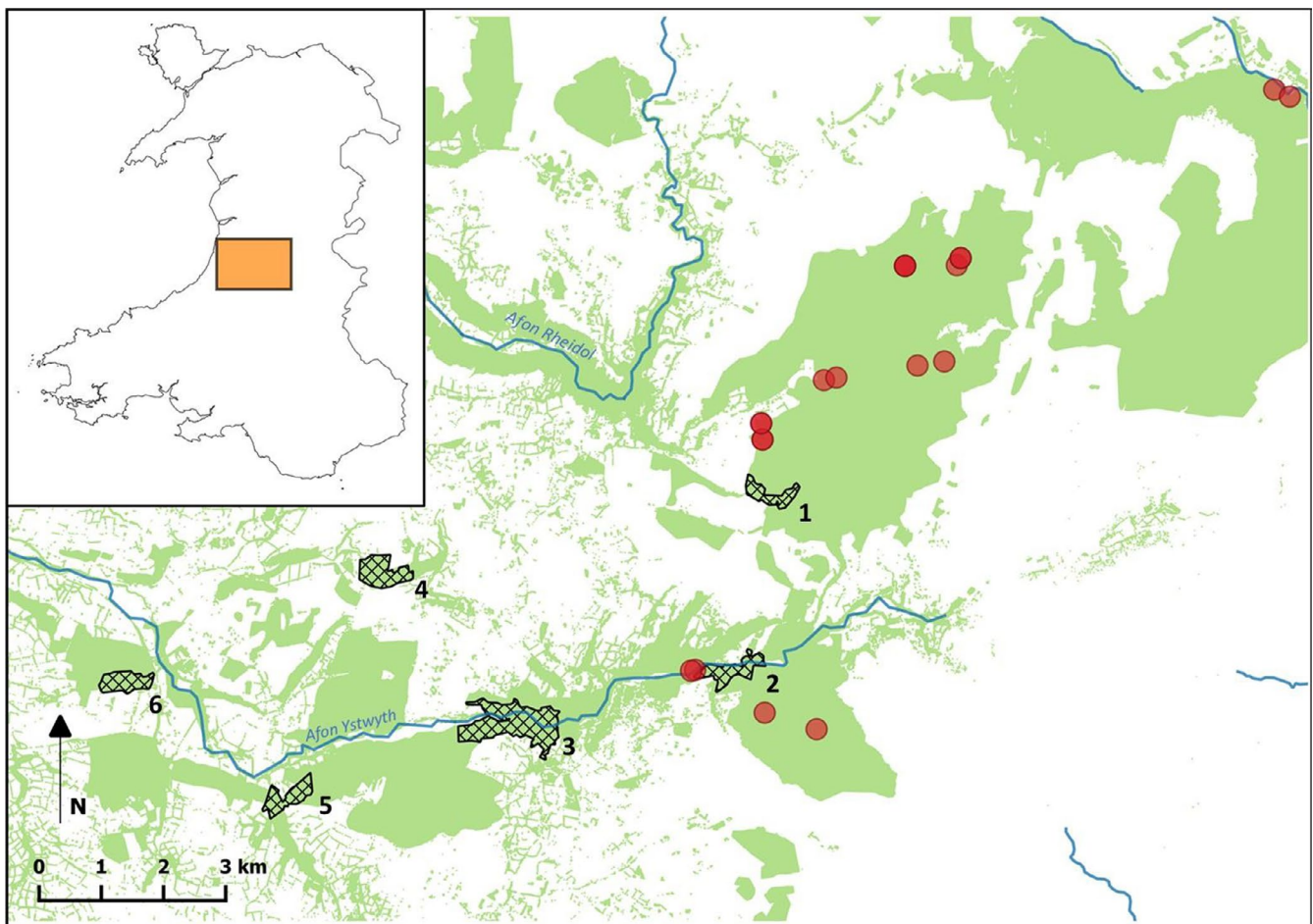

FIGURE 1 Locations of pine marten release sites and grey squirrel trapping sites in mid-Wales. Release sites are shown as red dots and grey squirrel trapping sites 1–6 as hatched areas. Insert shows location in Wales. Woodland is indicated in green

TABLE 1 Description of the six woodland sites used for grey squirrel trapping and the number of squirrels caught and used in analyses. Trapping area is defined as the squirrel trap line plus a buffer of radius 182 m (radius of mean squirrel home range in this study). Trapping of squirrels was undertaken to tag and collar squirrels rather than to estimate density. Dominant tree species comprise the three species with the highest % composition at each site. A detailed breakdown of habitat composition is provided in Supporting Information (Table S1)

Site	Trapping area (ha)	No. of traps	Trap density per ha	No. of individual squirrels trapped in first 7 days	Nearest marten release pen (km)	No. of squirrels in analysis (M:F)	Dominant tree species	Composition of site (%) Conifer	Broadleaf	Open
1	85.0	36	0.42	2	0.7	1:1	Sitka spruce (59.2%) Japanese larch (14.8%) Beech (3.2%)	74.9	6.5	18.5
2	70.3	22	0.31	13	0.4	0:8	Mixed broadleaf (13.1%) Noble fir (9.8%) Douglas fir (8.7%)	31.7	26.7	41.4
3	77.5	25	0.32	9	2.6	3:2	Japanese larch (22.8%) Beech (10%) Douglas fir (9.9%)	61.0	23.6	15.2
4	33.9	18	0.53	7	5.0	3:3	Japanese larch (45.9%) Sitka spruce (20.1%) Norway spruce (8.8%)	90.7	4.8	4.5
5	37.2	19	0.51	10	6.7	2:1	Douglas fir (42.5%) Mixed broadleaf (14.8%) Japanese larch (12.1%)	71.0	19.2	9.7
6	37.1	24	0.65	9	8.9	1:3	Norway spruce (30.2%) Douglas fir (14.9%) Beech (9.2%)	56.1	37.5	6.3

60 years (Lucas, 1997) and the sites had no record of grey squirrel culling, through trapping or poisoning, in the last 20 years. The nearest population of native red squirrels was 20 km to the south.

Between September and December 2015, squirrel traps were positioned on the ground and pre-baited for 7 days before being set for 7–12 days and checked every morning and evening. Trap density was approximately 0.9 per hectare, with an average of 24 traps per woodland (Table 1). Adult squirrels were tagged with a subcutaneous passive integrated transponder (PIT: Avid Identification Systems Inc.) to enable identification upon recapture. Adult squirrels over 500 g were fitted with collars equipped with GPS loggers (modified i-GotU GT-120; Mobile Action Technology) configured to record locations at hourly intervals and VHF beacons (Biotrack) to enable confirmation of residency and recovery of the GPS unit by recapturing the squirrel after 3 weeks. GPS units successfully recorded between 5 and 24 days (SE 0.9 days) of movement data. A subsample (87%) of trapped individuals was collared, remaining individuals were only tagged. Juveniles, or individuals below 500 g, were excluded from all tagging or collaring. Locations taken within 1 hr of collar application (Delehanty & Boonstra, 2009) and 12 hr before collar removal were removed from the dataset. As a further part of data cleaning, individual points recorded further than 2 km from the edge of the trapping woodland block were considered spurious and were removed (n = 12 of 8,598 points). This conservatively allowed for movement outwith woodland patches, based on evidence that when woodland habitat is unavailable, or during dispersal, squirrels have been found to remaining within approximately 400 m of the nearest habitat patch (Stevenson et al., 2013).

Between September and November 2015, 20 pine martens were trapped in the Scottish Highlands, equipped with VHF radio collars (Biotrack) and transported to three release sites in Wales (Figure 1). They were held individually in soft release pens for up to 5 days, released, tracked and located 1–7 times per week for up to 10 months following release. Locations were triangulated from bearings using LOAS 4.0 (Ecological Software Solutions). Bearings that did not converge were excluded. Systematic scat surveys, undertaken as transects between 2011 and 2015, had found no evidence of pine martens in the region and the translocated martens were considered to be the only ones in the area (MacPherson et al., 2014).

2.1 | Squirrel ranging

We derived four measures of squirrel ranging; home range (90% kernel density estimate—KDE) and core range (50% KDE) sizes (ha), daily distance travelled (km) and home range centroid shift (m). Range sizes were calculated using the R package 'ADEHABITATHR' (Calenge, 2006) using reference smoothing parameter 'h-ref' (Borger et al., 2006; Laver & Kelly, 2008). We ensured there were sufficient data for all squirrels to have reached the asymptote of a home-range area curve before including them in analysis (Laver & Kelly, 2008) and one squirrel was consequently excluded (see Supporting Information). We checked for spatial autocorrelation by plotting the semi-variance of location positions against time

lag between each location using the R package 'CTMM' (Calabrese, Fleming, & Gurarie, 2016; Fleming et al., 2014). Variograms were visually inspected to ensure they reached an asymptote and there was no observable patterning. None displayed spatial autocorrelation and all were retained.

The mean daily distance (km) travelled was estimated using 'distm' in the R package 'GEOSPHERE' (Hijmans, Williams, & Vennes, 2017) by summing the straight line distances between consecutive locations across the whole of the squirrel's collaring period. Home range shift (Janmaat, Olupot, Chancellor, Arlet, & Waser, 2009) was the Euclidean distance (m) between the centroids of the home ranges in the first and last weeks of tracking using gCentroid (R package 'RGEOS'; Bivand, Rundel, Pebesma, Stuetz, & Hufthammer, 2017).

2.2 | Marten exposure

For each squirrel, we extracted locations of all pine martens during the same monitoring period, plus the week before to account for exposure before squirrels were collared. Marten locations were used to create a density surface (Sims, Witt, Richardson, Southall, & Metcalfe, 2006) using the package 'ADEHABITAT' (Calenge, 2006). The surface comprised grid cells (100 x 100 m) and the size and composition of the grid remained constant. The kernel density estimates of marten locations were then generated using increasing bandwidth resolutions (h) of 500, 1,000, 2,000 and 3,000 m which enable the effect of one point to extend through more adjacent cells, with increasing bandwidth size (see Supporting Information). The home range of each squirrel was then mapped onto its matched marten density surface. The underlying marten densities in each cell within this squirrel range were then extracted and summed to give the total 'marten exposure' (martens per km^2) for each squirrel. The number of individual martens present in the whole landscape, i.e. the number of animals that had been released by the start date of individual grey squirrel monitoring, was calculated to account for the increasing likelihood of a squirrel–marten encounter over time.

2.3 | Apparent survival

We estimated apparent survival for squirrels in relation to pine marten exposure at each woodland site, rather than at an individual squirrel level, as some PIT-tagged squirrels were not collared, preventing the calculation of marten exposure for these individuals across their home range. We used a measure of recapture probability as a proxy for squirrel survival, as the trapping was conducted primarily to tag and collar animals and protocols did not provide for direct calculation of density or survival. The encounter histories for all PIT-tagged squirrels were used and individual apparent survival was scored as 1 if an individual was caught in both the first and second trapping period, and 0 if it was only caught in the first. Trapping duration and interval between trapping periods

were unequal. To make sites comparable, we sampled, with replacement, 5 days on which trapping occurred. This was the lowest duration of trapping in one period at one site. We resampled 1,000 times and calculated the proportion of iterations that each individual had an apparent survival of 1. For every squirrel we had an indication of its likelihood of being recaptured in the second trapping period, if (a) it was captured in the first trapping period and (b) had that trapping period lasted 5 days. Marten exposure was estimated as above, but in this analysis we used the maximum grey squirrel home range size recorded over the entire study (25.5 ha), centred on the centroid of the squirrel trap line. This was taken as the most conservative characterization of marten exposure for each woodland site.

2.4 | Statistical analysis

To test the effect of marten exposure on grey squirrel ranging, we fitted a series of GLMs to the following three responses: home range (90% KDE) size (ha), core range (50% KDE) size (ha) and mean daily distance travelled (km). Response variables were log transformed to normalize their distribution and models used a Gaussian error structure. We included sex of the squirrel, marten exposure and number of martens as fixed effects and included the interaction between sex and marten exposure. We could not include site as a random effect due to uneven representation of the sexes among sites. All explanatory variables were standardized to have a mean of 0 and SD of 0.5 (for continuous variables). Sex was rescaled to have a lower value of −0.5 and upper value of 0.5 (Gelman, 2008). Each of these models was fitted four times using the estimates of marten exposure calculated at the four spatial bandwidths.

We evaluated the performance of models using Akaike's information criterion corrected for small sample size (AICc) and all models within ΔAICc ≤ 2 of the top model were included in the top model set (Burnham & Anderson, 2004). Model selection used the package 'MuMIn' (Barton, 2018). Full model averages were then used to identify main explanatory variables and generate effect sizes and 95% confidence intervals (Burnham & Anderson, 2004; Grueber, Nakagawa, Laws, & Jamieson, 2011). If 95% confidence intervals of variables did not overlap zero, variables were deemed significant. The relative importance (RI) of each variable within the top model set was also used. The explanatory power of full averaged models was then estimated using a likelihood-ratio based pseudo-R^2 where a value of 1 represents 100% of variance explained by the model.

One squirrel had exceptionally high levels of marten exposure and on close inspection of a Cook's distance plot, this individual had high leverage and was removed from analyses, but see Supporting Information for analyses including this outlier. To address the potential influence of habitat variation among sites on squirrel ranging and the potential indirect effect of links between habitat variation and marten exposure, we screened site-level habitat variables for

association with measures of both squirrel ranging and marten exposure, and refitted the above models of squirrel ranging to include any habitat variables that were significantly associated with squirrel ranging and marten exposure. Full details of this procedure are provided in Supporting Information.

2.5 | Survival analysis

A high number of squirrels were not recaptured in the second trapping period, resulting in zero-inflated indices of apparent survival. Therefore we used a zero-inflated beta-binomial Bayesian model to test the relationship between marten exposure and apparent survival. This approach simultaneously fits two processes to the data, one that models whether apparent survival is zero and another that models survival if greater than zero. Models were fitted in 'stan' (Carpenter et al., 2017) using the R package 'BRMS' (Burkner, 2015). Marten exposure was a fixed effect. Parameter values were estimated using Markov-chain Monte-Carlo (MCMC) methods, using 'brms' defaults for priors and initial values. Four chains were run for 2,000 iterations of which 1,000 were discarded as burn-in. MCMC chains for all parameters converged (R-hat < 1.01) and had an effective sample size greater than 2,000. From the remaining MCMC chains, we calculated the mean estimate and 95% credible intervals. The statistical significance of the effect of all model parameters was determined by the 95% credible interval not overlapping zero.

2.6 | Ethical statement

This study was approved by the University of Exeter Animal Welfare and Ethical Review Board and licensed by the Home Office, Scottish Natural Heritage and Natural Resources Wales.

3 | RESULTS

A total of 53 individual squirrels were collared over a 90-day period, 37 of which were recaptured and 16 collars were not recovered due to VHF antenna damage, animals dispersing, collars detaching in inaccessible dreys or mortality of animals in areas where they could not be relocated. Eight recovered collars could not be used due to GPS logger loss or failure. Ranging data from 29 squirrels (18 F and 11 M) were therefore suitable for analysis. These squirrels were tracked for a mean duration of 16 days (SE 0.9 days, range 5–23) and the mean number of locations per individual was 265 (SE 17, range 82–437). Mean home range (90% KDE) was 10.4 ha (SE 1.1 ha) and the mean core range (50% KDE) was 2.0 ha (SE 0.2 ha). Models of space use included 28 squirrels, after exclusion of an outlier with exceptional levels of exposure to martens, as detailed above. When marten exposure was considered at larger scales ($h \geq 2,000$ m) but not at a finer scale ($h \leq 1,000$ m), core and home ranges increased significantly

as marten exposure increased (Tables 2 and 3; Figure 2). The daily distance travelled was also significantly and positively related to marten exposure, and this effect was again detectable at larger spatial scales ($h \geq 1,000$ m) (Tables 2 and 3). There was a significant interaction between sex and daily distance travelled at $h = 1,000$ m. Males showed increased daily distance travelled with higher marten exposure, whereas females did not (Tables 2 and 3; Figure 3). There was no significant effect of marten exposure on shift in home range centroids (Table 3) at any spatial scale. Sex was retained in all top model sets as a main effect, though it did not appear to account for significant differences in range size or shifts. Site-level variation in the proportion of open ground habitats was correlated with squirrel home range (90% KDE) and with marten exposure ($h = 3,000$ m). No other habitats were correlated with squirrel ranging (Table S4). Inclusion of site-level variation in open ground habitats did not alter

TABLE 2 Summary of models of variation in space use of invasive non-native grey squirrels in relation to exposure to introduced native pine martens. Full averaged models include terms from models in the top model set, where ΔAICc ≤ 2. Terms in the averaged models included the effect of variation in local density of translocated pine martens within the squirrel home range (*exposure*), the number of martens that had been released into the landscape (*martens*), squirrel *sex* and an interaction *exposure × sex*. For each squirrel behaviour variable, four models were run; one for each pine marten kernel bandwidth used to estimate marten density (500, 1,000, 2,000 and 3,000 m). Significant effects are where 95% confidence intervals do not cross zero (see Table 3) and are shown in bold. R^2 represents the likelihood-ratio based pseudo-R^2 value for the model

Response	Marten bandwidth (m)	Full averaged model	R^2
Core range (50% KDE)	500	Sex + martens + exposure	0.147
	1,000	Sex + martens + exposure	0.207
	2,000	Sex + martens + **exposure**	0.402
	3,000	Sex + martens + **exposure**	0.626
Home range (90% KDE)	500	Sex + martens + exposure	0.100
	1,000	Sex + martens + exposure	0.148
	2,000	Sex + **exposure**	0.327
	3,000	Sex + **exposure** + exposure × sex	0.636
Daily distance travelled (km)	500	Sex + exposure + exposure × sex	0.213
	1,000	Sex + **exposure** + **exposure × sex**	0.385
	2,000	Sex + **exposure** + exposure × sex	0.308
	3,000	Sex + **exposure** + exposure × sex	0.314
Centroid shift	500	Sex	0.058
	1,000	Sex + exposure	0.073
	2,000	Sex + exposure	0.132
	3,000	Sex + exposure	0.153

TABLE 3 Effects of variation in exposure to introduced native pine martens upon the space use of invasive non-native grey squirrels. For each behavioural variable, four models were run; one for marten exposure (martens/km²) calculated at each pine marten kernel bandwidth (500, 1,000, 2,000 and 3,000 m). Estimates of effect sizes are from GLMs (Table 2). For each squirrel space use metric the averaged standardized effect size across the top model set, lower and upper 95% confidence limits and relative importance (RI) of marten exposure is shown at each kernel bandwidth size. Significant effects are where 95% confidence intervals do not cross zero (see Table 2) and are shown in bold. NR indicates that pine marten exposure was not retained in the top model set. In one instance (daily distance, bandwidth 1,000 m), results are given for males and females separately because the effect of variation in marten exposure significantly interacted with the effect of squirrel sex (Figure 3)

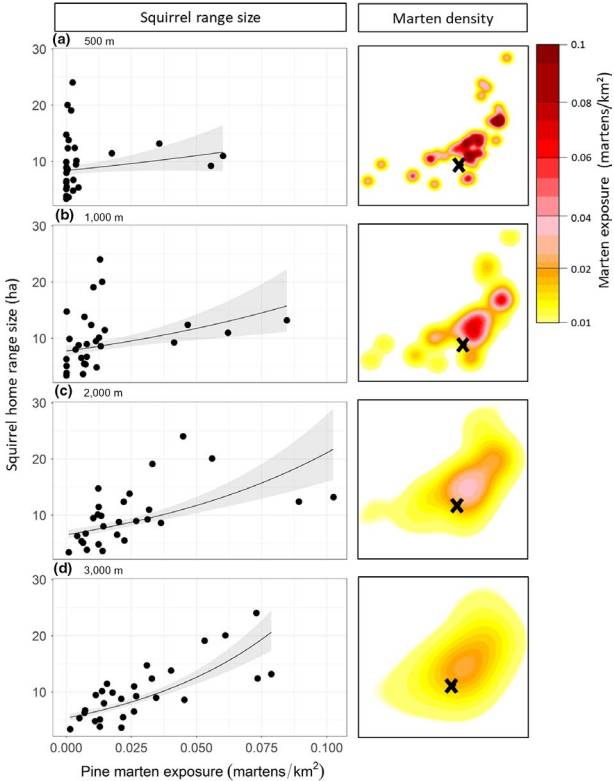| Kernel bandwidth (m)	Mean marten exposure (martens/km²)	Core (50%) range			Home (90%) range			Daily distance travelled (km)			Centroid shift (m)		
		Estimate	Confidence limits	RI	Estimate	Confidence limits	RI	Estimate	Confidence limits	RI	Estimate	Confidence limits	RI
500	0.007 ± 0.003	0.03	−0.20, 0.26	0.45	0.03	−0.18, 0.24	0.2	0.10	−0.13, 0.32	0.6	NR	—	—
1,000	0.014 ± 0.004	0.29	−0.25, 0.83	0.66	0.18	−0.25, 0.62	0.6	(M) 1.03	**0.41, 1.66**	1	0.05	−0.32, 0.42	0.18
								(F) 0.28	**0.09, 0.47**	1			
2,000	0.025 ± 0.005	**0.66**	**0.27, 1.05**	1	**0.56**	**0.21, 0.90**	1	**0.25**	**0.01, 0.42**	1	0.24	−0.46, 0.94	0.46
3,000	0.028 ± 0.004	**0.83**	**0.51, 1.14**	1	**0.76**	**0.48, 1.03**	1	**0.25**	**0.05, 0.45**	1	0.29	−0.46, 1.04	0.52

FIGURE 2 Relationships between grey squirrel home range sizes and increasing pine marten exposure (martens/km²). Home ranges are 90% kernel density estimates. (a)–(d) represent the different bandwidths used (500, 1,000, 2,000 and 3,000 m) in calculation of marten exposure. Panels on the right show example maps of the pine marten density surface at each bandwidth for an individual squirrel with its 90% home range represented by a black cross. Dark colours represent higher marten density and thus higher levels of exposure experienced by an individual squirrel in that location
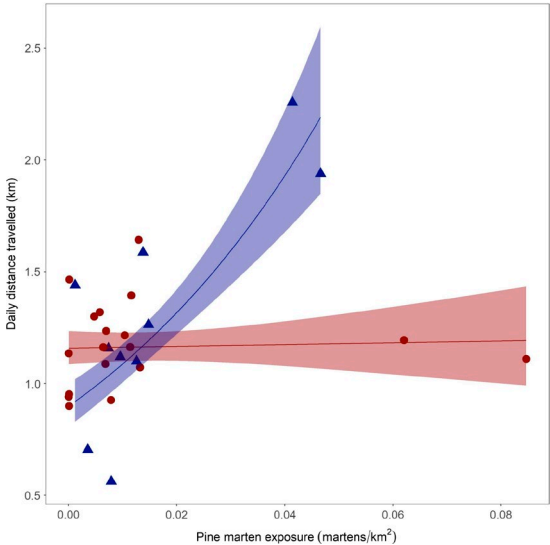

FIGURE 3 Effect of variation in exposure to translocated pine martens on daily distance travelled by grey squirrels. Sexes respond differently to pine marten exposure, male squirrels are shown as blue triangles and females as red circles. Pine marten exposure (martens/km²) is calculated using a bandwidth of 1,000 m

the effects of marten exposure on squirrel home range (Supporting Information, Table S5) and no interactions between habitat and marten exposure featured in the top model set.

Survival analysis included 61 PIT-tagged squirrels that were captured four times on average (*SD* 2.7, range = 1–11); 16 squirrels were captured only once. The number of consecutive trap days at sites ranged from 5 to 17 and the mean interval between the first and second trapping period was 37 days. There was no significant relationship between apparent squirrel survival and their exposure to martens for either the zero-inflated (estimate = 0.19, 95% credibility interval = −0.19–0.66) or beta-binomial (estimate = −0.05, 95% credibility interval = −0.15–0.08) parts of the model and the 95% credible intervals overlapped zero for both estimates.

4 | DISCUSSION

Using the opportunity presented by a conservation translocation of pine martens, our study sheds light on some of the processes potentially underlying the landscape-scale responses of non-native prey, grey squirrels, to the return of a native predator, the pine marten (Sheehy & Lawton, 2014; Sheehy et al., 2018). We found that, in contrast to our predictions of diminished ranging, squirrel range size and daily distance travelled increased with increasing exposure to the restored predator. This finding was not affected by among-site variation in habitat. We found that male and female grey squirrels increased the daily distances they travelled to different extents in response to marten exposure, likely reflecting the typical wider ranging behaviour of males (Gurnell et al., 2001). An increase in ranging behaviour may be a strategy utilized by squirrels to enable them to tolerate and respond to marten exposure without shifting their home range location. These differences in space use were observed over even brief time periods, during which new martens were still being released into the area, suggesting that the impact of pine martens in a landscape may be manifest almost immediately after their reintroduction to, or dispersal into, the area occupied by squirrels. Our results complement the observations of landscape-scale negative correlations between grey squirrel abundance and pine marten presence (Sheehy & Lawton, 2014; Sheehy et al., 2018). In contrast to expectations, particularly in view of the observed behavioural changes, we saw no relationship between squirrel survival and marten exposure. This is perhaps unsurprising given the relatively short time frame and small sample size, resulting in a low likelihood of detecting differences in mortality rates.

These findings might be interpreted in a number of ways. First, we could infer that pine marten presence does not directly affect the behaviour of surviving grey squirrels but that the observed changes are driven by changes in intraspecific competition. This may be a result of pine marten predation of grey squirrels in surrounding areas, prior to the study, or of un-monitored individuals, which in turn has changed the territorial and social environment

for surviving individuals. Alternatively, there may be an immediate, fear-mediated response, in contrast to predictions arising from Sheehy et al.'s (2018) models, and studies of squirrel responses to marten scent (D. Tosh, unpubl. data, cited in MacPherson, Denman, Tosh, McNicol, & Halliwell, 2016), which suggested grey squirrels were naïve to the presence of pine martens. In this scenario, we propose that grey squirrels are able to detect and identify the martens as a threat and consequently change their behaviour. This change could be permanent or plastic, resulting in either long-term population level changes or merely temporary behavioural changes which, after an initial period of disruption, return to 'normal'. The presence of such a landscape of fear would suggest that the prey species exposed to this novel threat then used the landscape differently to individuals not facing the new threat, or changed their behaviour in areas of high-perceived predation risk (Apfelbach et al., 2005; Jacob & Brown, 2000; Rosell, 2001). Due to the timing of this study, we were only able to compare grey squirrel behaviour across a spectrum of exposure to newly introduced martens, as opposed to a clear before-after-control-impact design. While the distribution and movement of prey can be dramatically altered by the presence of a predator (Heithaus & Dill, 2006), the temporal and spatial scales at which these changes occur depend upon the system being studied. Valeix et al. (2009) found that African herbivores displayed varying spatial and temporal habitat shifts in response to lion *Panthera leo* predation risk; grazers had limited habitat providing their required resources and did not alter their distribution while browsers altered their distribution to encompass the available alternative feeding habitats. In the face of high predation risk, a trade-off is made between resource acquisition and safety from predation (Lima et al., 1985) and these trade-offs may occur on a small scale, through behavioural changes while feeding (Laundré et al., 2001; Suraci et al., 2016), and on a large scale, through spatial expansions and shifts to alternative feeding areas (Heithaus & Dill, 2006; Maillard & Fournier, 1995; Valeix et al., 2009). The findings of our study are consistent with the latter of these responses, suggesting squirrels are extending, rather than shifting, their ranges in response to predation risk. The duration of such behavioural responses is therefore also important to consider. Behavioural plasticity may allow for a temporary change in squirrel space use during a time of novel perturbations, but a return to 'normal' ranging behaviour once this novel predator becomes 'familiar' (Bateman & Fleming, 2014). Such plastic or habituation responses in squirrels have been demonstrated by fox squirrels *Sciurus niger* across urban and rural gradients (Mccleery, 2009). One explanation for differences in space use by squirrels is a change in range utilization and foraging regime. Behaviour may be altered for the avoidance of predation in time (Griffin, Griffin, Waroquiers, & Mills, 2005), space (van Beest, Vander Wal, Stronen, Paquet, & Brook, 2013) or both. Some species under elevated risk of predation display higher vigilance and reduced time spent foraging at a particular location (Heithaus & Dill, 2006; Laundré et al., 2001; Maillard & Fournier, 1995; Valeix et al., 2009). Here, with increasing predation risk and reduced foraging returns, the trade-off

between safety and resource acquisition becomes biased towards safety (Laundré et al., 2001; van Beest et al., 2013; van der Merwe & Brown, 2008). Consequently, increased vigilance and movement would likely reduce time foraging at single patches and increase the number of patches exploited, elevating the daily distance travelled between patches and range sizes.

Squirrel range size is a function of season, habitat quality and density of conspecifics (Lawton & Rochford, 2007; Wauters et al., 2002) and the link between marten density and quality of grey squirrel habitat may warrant further attention. Grey squirrels show preference for mixed broadleaf forests (Gurnell et al., 2001; Kenward & Tonkin, 1986) and our trapping locations were selected on this basis. Among-site variation in habitat contributed little to between-squirrel variation in spatial behaviour and the single habitat correlate of squirrel ranging (proportion of open ground) did not significantly detract from the effect of pine marten exposure. It is conceivable that within (as opposed to among) the study sites, habitat variation may have been a driver of between-individual variation in squirrel ranges and movement distances. In such a scenario of fine-scale selection, habitat that was unfavourable for grey squirrels but favourable for pine martens might mean that squirrels living where martens spent more time would require larger home ranges to acquire sufficient resources. However, marten habitat selection, and our measures of marten exposure, operate at a scale that is an order of magnitude, or more, greater than that for squirrels (Balharry, 1993; Caryl, 2008; Caryl, Quine, & Park, 2012; Pereboom et al., 2008). Seasonal variation and the associated reproductive and dispersal behaviours of squirrels may play a role in variation in space use, as squirrels might display different ranging behaviours in the latter months of the year, towards the end of the period of this study. In relation to dispersal, the tracked animals were resident during the observation period, and we have shown that they did not shift their range centroids. Our analyses suggest that the effects of marten exposure were independent of any main effects of sex, except in one model of daily distances, where there was a significant interaction between sex and marten exposure. Thus, squirrel reproductive and dispersal behaviours, although influential main effects upon ranging (Dubock, 1979), are unlikely to have introduced a systematic bias with respect to variation in marten exposure.

The impact of marten exposure on grey squirrel space use was calculated over a range of different spatial scales, by using different bandwidths for marten ranges (Figure 2) to capture the high mobility of this predator (Caryl, 2008; Zalewski, Jedrzejewski, & Jedrzejewska, 1995) and effectively 'allow' the effect of pine martens to be felt over a wider area. Pine marten ranges are highly variable, depending on habitat quality and conspecific density (Powell, 1979) and are likely larger for translocated animals that are exploring new landscapes. As models incorporated the greater potential extent of pine marten influence (through increasing bandwidths), we identified a more consistent effect on squirrel behaviours.

This study presents an initial insight into the fine-scale, short-term effects that a recovering native predator can have on its invasive, non-native prey. Our results suggest that even shortly after translocation and while living at low densities, pine martens affect grey squirrel behaviour. However, the exact timing of onset, duration and persistence of such changes remain unknown. We utilized a conservation translocation to simulate the natural range expansion of recovering marten populations and their use as a native agent of biological control. Our main methodological approach was not that of a capture–mark–recapture study, therefore the trapping periods were not consistent across sites, and so larger studies of grey squirrel density and survival across habitat types may provide an insight into direct, lethal effects of marten presence.

The re-establishment of martens may alter the abundance, behaviour and/or distribution of grey squirrel populations, not only in initial stages, as shown here, but over longer time periods, as shown in Ireland and Scotland. There is now a need to understand the wider implications of such behavioural changes for grey squirrel populations over longer time periods and whether this might help explain the downstream consequences for red squirrel populations described in Ireland and Scotland (Sheehy & Lawton, 2014; Sheehy et al., 2018) and for forestry economics.

AUTHORS' CONTRIBUTIONS

C.M.M., R.A.M., J.M., R.G. and S.B. conceived the ideas and designed the methodology; C.M.M., D.B. and M.F. collected the data; C.M.M. led analysis with input from C.E.D.G. and M.J.S.; C.M.M. led manuscript writing. All the authors contributed critically to drafts and gave approval for publication.

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SUPPORTING INFORMATION