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Research Article

Mitigating the impact of forest management for conservation of an endangered forest mammal species: drey surveys and nest boxes for red squirrels (*Sciurus vulgaris*)

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Abstract

Timber harvesting practises can lead to loss of suitable nesting opportunities and thus have a negative impact on reproductive success and abundance of arboreal species. For many species, the impact of forest operations and the effectiveness of mitigation, such as pre-operational surveys, retention of trees with nests or the use of nest boxes, are unknown. This study aimed to assess the impact of forest operations and the utility of nest boxes as a conservation tool, using the Eurasian red squirrel (*Sciurus vulgaris*) as study species. We carried out the first quantitative assessment of drey survey effectiveness and tested the predictions that (1) red squirrel drey use increases post-thinning (2) nest box use increases post-thinning when their availability may be critical; (3) nest box use increases over time due to habitation and (4) nest box characteristics and placement affect nest box use. Our results show that thinning has led to squirrels changing their nesting behaviour with increased drey use post forest operations. We conclude that drey surveys are inefficient due the dynamic nature of drey use by red squirrels and that although foresters can detect a small proportion of active dreys, it is impossible to assess whether dreys are in use. Furthermore, nest box use increased after forest operations and nest boxes placed at a lower position in the tree were preferred. Our results suggested that red squirrels habituate to nest boxes over time as nest box use was higher during the second year after deployment. Overall, we propose that nest boxes can be a useful conservation tool to mitigate the impacts of forest operations and conclude that early deployment of nest boxes can contribute to red squirrel conservation by providing shelter for red squirrels after forest operations – and potentially for juveniles during natal dispersal.

Introduction

Foresters must often balance multiple, potentially competing objectives, for example when managing forests for timber production as well as for recreation and protected species conservation (e.g., Holbrook et al., 2018). For arboreal species, including small rodents and cavity-dependent birds, deforestation, and forest operations such as clear-felling or thinning can lead to a reduction of nesting opportunities and breeding sites, as well as potentially impact on breeding success, survival and forest carrying capacity and therefore species abundance (Lurz et al., 2003; Berthier et al., 2012; Michał amd Rafał, 2014; Sotola and Garneau, 2014). For some species, impact of forest management such as felling regimes are documented (e.g., Capercaillie *Tetrao urogallus*; Mikoláš et al., 2015), whereas for other species, including pine marten (*Martes martes*; O'Mahony et al., 2014) and the Eurasian red squirrel (*Sciurus vulgaris*), they are still completely unknown.

The Eurasian red squirrel (hereafter "red squirrel") is a small, diurnal tree squirrel that builds nests (dreys or dens) in trees. Red squirrels use dreys not only for breeding and raising young but also for resting during the day and for sleeping during the night (Edwards and Guynn, 1995; Wauters and Dhondt, 1990), as well as for shelter during bad weather (Pulliainen, 1973). Dreys contain an inner, soft core made with moss, leaves and grass (depending on availability), and an outer shell of twigs (Andrén and Delin, 1994; Linnell et al., 2018) and in coniferous forests are generally found in tree canopies often up in the crown next to the main trunk.

Due to disease-mediated competition from the introduced Eastern grey squirrel (*Sciurus carolinensis* G.), habitat loss and fragmentation, red squirrel populations have been in decline (Wauters et al., 1994a; Gurnell and Pepper, 1993; Bertolino and Genovesi, 2003) and are considered endangered in Great Britain. It is estimated that 75% of the remaining UK red squirrel population live in Scotland (Harris et al., 1995) and more recent estimates put this figure even higher at 80% (Mathews et al., 2018). Red squirrels and their dreys are protected under Schedules 5 and 6 of the Wildlife and Countryside Act 1981, the Nature Conservation (Scotland) Act 2004 and the WANE Act 2011. Consequently, red squirrel presence needs to be carefully considered in forest management plans and potential disturbance or damage to red squirrels or their dreys due to forest operational activity needs to be mitigated.

Current mitigation for the impact of forest operations on red squirrels include pre-operational visual surveys to locate and mark trees containing red squirrel dreys and to retain these drey trees, together with immediately adjacent trees, where practicable, during thinning operations. Red squirrel drey surveys are carried out up to 18 months before forest operations are due to take place, with a further pre-operational

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check within a maximum of three weeks of the start of operations. Depending on habitat, drey surveys are acknowledged to have a varying degree of success (e.g., in dense spruce it is very challenging to locate dreys), but drey survey effectiveness has never been quantified using empirical evidence.

Additional conservation measures to mitigate habitat loss and loss of nesting opportunities may include the implementation of artificial nest boxes as a tool to enhance availability of suitable nesting sites (Sotola and Garneau, 2014). This can be especially useful in the UK where forest stands often lack suitable, mature trees with natural cavities (e.g., for pine martens *Martes martes*; Croose et al.,, 2016). Nest boxes also play a key role in small mammal research and have been used in studies on forest fragmentation (e.g., dormice, *Muscardinus avellanarius*; Zapponi et al., 2013) and in relation to forest management practices (e.g., Siberian flying squirrel *Pteromys volans*; Santangeli et al., 2013). In red squirrels, nest boxes have been used to study litter size, litter sex ratio, mortality, as well as species presence and interactions with other species (Shuttleworth, 1999, 2001; Shuttleworth and Schuchert, 2014), however, many aspects remain unexplored (Shuttleworth and Schuchert, 2014) and no information is available on the effectiveness of nest boxes to mitigate for the impact of forest operations.

The aim of this study therefore was to investigate the impact of forest operations on red squirrels, to assess the effectiveness of current mitigation and to assess the utility of nest boxes as a conservation tool for red squirrels. We carried out the first quantitative assessment of drey survey effectiveness and in addition, we tested the predictions that (1) red squirrel drey use increases post-thinning (2) nest box use increases after forest operations when their availability may be critical due to habitat loss (and therewith potential drey locations), unintentional drey loss or disturbance; (3) nest box use increases over time (i.e. the year following initial deployment) due to habitation and (4) nest box placement and nest box characteristics (including local drey density, nest box height, nest box type, tree species in which the nest box is deployed) affect nest box use. We provide essential information for the potential deployment of nest boxes as a tool in forest management to balance the need for timber production with red squirrel conservation.

Materials and methods

Study area

Fieldwork was conducted in 28 ha of mixed-conifer forest near Ferness, in the Highlands of Scotland (57°29′29″ N, 3°43′47″ S) between February 2017 and May 2018. The forest is dominated by Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) with some small patches of Japanese larch (*Larix kaempferi*) and Sitka spruce (*Picea sitchensis*). Trees were planted in the early 1950's and thinning, mainly of the Norway spruce habitat, took place from 11/05/2017 – 31/05/2017. Approximately 10 000 m^3 was removed from the study area and the basal area of trees was reduced from 42 $m^2\,ha^{-1}$ to 32 $m^2\,ha^{-1}$, based on a thinning prescription that accorded with yield class models for silvicultural management of these tree species in this area (Matthews et al., 2016). Typical forest operations like these, represent a relatively sudden event by which red squirrel dreys may be removed or may become so exposed or unconnected due to removal of nearby trees as to render it no longer suitable to use.

Drey use

We captured red squirrels from 3/2/2017 to 13/2/2017, using 20 single-entry, modified, live-mink traps (dimensions 584×178×145 mm) (Bethel Rhodes & Sons Ltd, Keighley, UK). Traps were laid out with a 88 ± 22 m spacing and attached to trees at a height of approximately 1.5 m. Traps were baited with whole hazelnuts and a "squirrel whole nut mixture" (Ark Wildlife Ltd, Herts, UK) and were checked every three hours and closed to capture each night.

We fitted 22 red squirrels with tracking units (G10 UltraLITE GPS/VHF with 120 mA h, Advanced Telemetry Systems, Isanti, USA) weighing <5% of body mass and carried out daily radio-tracking of tagged squirrels from 15/02/2017 to 11/08/2017. Squirrels were located using a hand-held, three-element Yagi antenna and a TRX-1000 receiver (Wildlife Materials, USA). Each squirrel was radio-tracked until it was sighted or the tree in which it was located was identified. Their locations (waypoints) were recorded using a hand-held Garmin model GPSmap60 CSx (Garmin International, Olathe, KS) GPS receiver. For each waypoint we recorded whether the animal was active (squirrel seen), in a drey (drey observed) or unknown.

To investigate drey use and local drey density, only "drey waypoints" obtained during radio-tracking were analysed, and "active" or "unknown" waypoints were discarded. To test our first prediction, drey use of individual red squirrels was investigated in response to forest operations and data were analysed before (15/02/2017 – 10/05/2017), during (11/05/2017 – 31/05/2017) and after (01/06/2017 – 11/08/2017) forest operations. In addition, drey data for all animals were compiled and plotted per month to provide further insights of changes in drey use in response to forest operations. Local drey density, defined as the number of dreys within a 30 m radius of each nest box, was calculated in ArcMap™ 10.4 (ESRI, 2016) using drey locations identified throughout the study.

Drey survey

A pre-operational drey survey was carried out by an Environment Forester from Forestry and Land Scotland on 18/04/2017 and 19/04/2017 (three weeks before the start of forest operations at the study site) using grid-based sampling with a distance of 50m between transect lines. All observed dreys were located and marked and data on location, shape (sherical or platform) and condition (1–3; whereby 1 is best condition and 3 the worst condition) were recorded. Under condition category 1, a drey would be expected to be a fully, complete structure (no gaps) and have fresh (green) material added. Under category 3, dreys would have significant gaps in the structure, or even have partially collapsed and no fresh material would be present. Category 2 covers dreys that do not fall into categories 1 or 3 and would normally show a clear structure, but no signs of recent use such as fresh or green material. Where dreys in categories 1 and 2 are expected to be in use, category 3 dreys are expected to be abandoned.

Nest box use

Nest boxes were constructed (Ewan Buxton Joinery Ltd., Carrbridge, UK) with and without insulation, whereby internal dimensions of both nest box types measured the same at 32×35.5×55 cm (Shuttleworth, 1999; Sotola and Garneau, 2014), but insulated nest boxes had and additional intermediate layer of 10 mm foam board and were therefore larger in outside dimensions (Fig. 1 a-b). A 5 cm diameter entrance hole was cut in the top corner on one side of the box and positioned next to the tree trunk.

In total, 32 nest boxes (16 insulated and 16 non-insulated) were deployed across the study area with a nearest neighbour distance of 58 ± 16 m (Fig. 2). We placed the nest boxes at a low height (approximately 2.5 m) or at a high height in the tree canopy (approximately 6 m) in Norway spruce or Scots pine trees (Fig. 2) and filled them initially with a layer of hay to provide material within which red squirrels could potentially nest.

Entrances of nest boxes were monitored by trail cameras (Bushnell NatureView Camera model 119439) placed 1m away using a wooden

Figure 1 – Nest boxes used were a) non-insulated or b) insulated; whereby the inside dimensions were the same, and c) nest box entrances were monitored by trail camera.

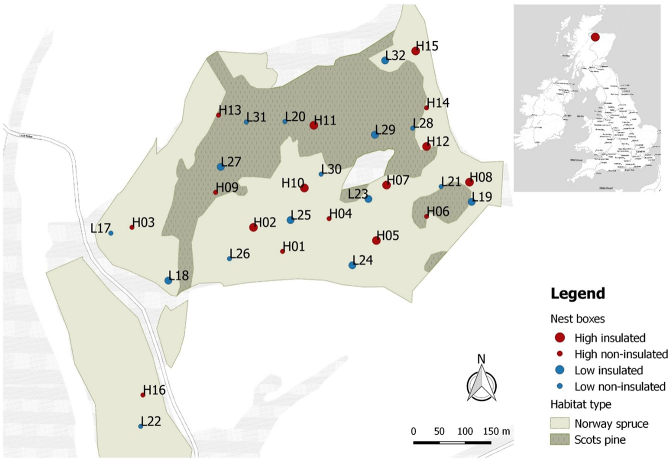

Figure 2 – Locations of insulated (large circles) and non-insulated (small circles) nest boxes placed in Norway spruce (light area) or Scots pine (dark area) at a low height (L – blue circles) or high height (H – red circles). Labels represent the nest box height followed by their ID number.

arm attached to the nest box to minimise the likelihood of photos being taken due to moving branches and other vegetation (Fig. 1c). Cameras were motion triggered 24 hrs/day with an interval of 1 second and set to take 3 consecutive photos (at 3.1 Mpx resolution) (per "burst") with a trigger speed of 0.7 second. The sensitivity of the cameras' passive infrared sensor was set to normal level and the intensity of the infrared flash was set to "low".

Camera data were obtained between 18/02/2017 and 31/05/2018 and categorized into period 1 from 18/02/2017 to 31/05/2017, period 2 from 01/06/2017 to 12/09/2017 and period 3 from 10/02/2018 to 31/05/2018, whereby period 1 represents the period before and during forest operations and coincides with spring breeding season, period 2 represents the period after forest operations and coincides with summer breeding season. Period 3 coincides with spring breeding season the year following forest operations and is comparable in duration as period 1 to allow assessment of nest box uptake over time (with habituation), without including a potential confounding effect of forest operations on nest box use. Cameras were removed between period 2 and period 3. Due to malfunctions (e.g., water ingress, chewed sensors or technical issues resulting in unusable time stamps) no data were available for nest box H03 (all periods), L20 (periods 2 and 3), H08, H13, H16, L22, L25, L26, L29, L31 and L32 (period 3) and 31, 30 and 21 functioning cameras remained for periods 1, 2 and 3 respectively.

We used "citizen science" and uploaded our photos onto Mammalweb (www.mammalweb.org) for the public to help identify which photos displayed red squirrels. Mammalweb creates "sequences" of photos that are taken <10 s apart and in total 28543 sequences were classified of which 2.02% (n=578) displayed red squirrels. For the purposes of data analyses nest boxes were considered "in use" when a red squirrel was identified on one (or more) of the photos in a sequence. When sequences within 3 minutes of each other both displayed a red squirrel (n=113), these were considered the same nest box visit, resulting in 452 independent nest box visits. Nest box use is defined as the number of independent nest box visits per nest box per period (mean 5.60 ± 6.28, n=82).

Data analyses

Our dependent variable nest box use are repeated measurements (for each nest box) and cannot be treated as multiple independent observations. To account for these circumstances, we modelled nest box use using a generalized linear mixed model (GLMM) with a Poisson distribution, using the function glmer in the add-on package `lme4` (Bates et al., 2015) in R 3.4.3 (R Core Team, 2016), with nest box ID as random effect factor. Fixed effect factors included local drey density (continuous), forest operations (categorical), nest box height (categorical), nest box type (categorical), tree species (categorical) and year (categorical) (Tab. 1).

As our aim was to specifically test the predictions that nest box use increased a) after forest operations and b) over time, we built two separate generalized linear mixed models. Model 1 was built to test for a potential increase of nest box use after forest operations and was therefore based on data collected in 2017 only, including fixed effect factor 'forest operations' (i.e., period 1 and period 2) (but not including factor "year", i.e., excluding data collected during period 3), in addition to the other factors in the model (Tab. 1). Model 2 was built to test for a potential increase of nest box use over time, and was based on spring data only, included fixed effect factor "year" (i.e., period 1 and period 3) (but not factor "forest operations", i.e., excluding data collected in period 2), in addition to the other factors in the model (Tab. 1). We excluded data from period 2 from the second model, because if we had included all periods and forest operations indeed increase nest box use, this would have confounded our results for uptake over time. The best fit models for all response variables were chosen based on the Akaike Information Criterion (AICc) (see Supplemental Information for model selection results). Next, we performed pairwise comparisons between and within groups with Tukey post-hoc tests on the best fit models (for Model 1 and Model 2), using `emmeans` R Package.

Results

Drey use

We recorded a total of 215 drey locations across the field site throughout the study period. Due to mortality or animals losing their collars, drey data were available for 16 individuals throughout the entire study period to assess drey use in response to forest operations. On average, red squirrels used 12.8 ± 6.2 different dreys (n=16) throughout the study period. Red squirrels used a significantly different number of dreys before, during and after forest operations (one-way ANOVA: $F_{(2,45)}$=10.5; p<0.001). Post-hoc comparisons using the Tukey HSD test indicated that the mean (± 1 SD) number of dreys used per squirrel

Table 1 – Random and fixed effect factors.

Independent variable	Description
Nest box use	number of independent visits to the same nest box per period model 1: mean 5.98 ± SD 7.00, n=61 model 2: mean 4.33 ± SD 3.89, n=52
Fixed effect factors	
Local drey density (continuous)	number of dreys in a 30 m buffer zone around each nest box model 1: mean 1.90 ± SD 1.86, n=61 model 2: mean 1.88 ± SD 1.83, n=52
Nest box height (categorical)	High (model 1: n=30, model 2: n=27) Low (model 1: n=31, model 2: n=25)
Nest box type (categorical)	Insulated (model 1: n=32, model 2: n=28) Non-insulated (model 1: n=29, model: 2 n=24)
Tree species (categorical)	Norway spruce (model 1: n=40, model 2: n=36) Scots pine (model 1: n=21, model 2: n=16)
Forest operations (categorical) (Model 1 only)	before operations (period 1: 18/02/2017 to 31/05/2017) (n=31) after operations (period 2: 01/06/2017 to 12/09/2017) (n=30)
Year (categorical) (Model 2 only)	2017 (period 1: 18/02/2017 to 31/05/2017) (n=31) 2018 (period 3: 10/02/2018 to 31/05/2018) (n=21)
Random effect factor	
Nest box ID	ID of the nest box (H01 to H17, excl. H03 and L18 to L32) (n=31)

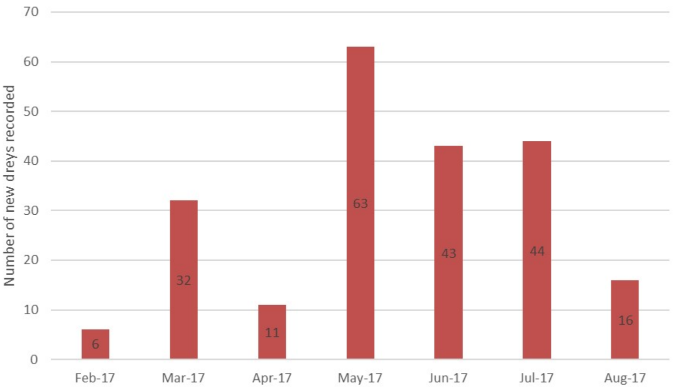

Figure 3 – Number of new dreys recorded for each month throughout the study period. Note that data was collected starting 15/02/2017 and ended on 11/08/2017 and Feb-17 and Aug-17 thus do not represent full months. Of the 63 new dreys identified in May-17, 6 were recorded before forest operations with the remaining 57 being recorded during forest operations took place (11/05/2017 – 31/05/2017).

after forest operations (7.50 ± 4.79) was significantly higher (p<0.01) than the mean (± 1 SD) number of dreys used per squirrel before (2.80 ± 1.43) or during (3.8 ± 1.9) forest operations (no significant difference in the number of dreys used before and during forest operations).

We pooled data for all individuals and investigated newly recorded dreys per month (Fig. 3), which showed a high number of new dreys being recorded during the months May-July. Of the 63 new dreys recorded in May, six were recorded before forest operations (01/05/2017 – 10/05/2017) and 57 during forest operations (11/05/2017 – 31/05/2017)

Drey survey

The drey survey identified 49 dreys (Fig. 4) of which we confirmed 47% (n=23) as being in use by the end of the study period (Tab. 2). It was expected that dreys categorised as having a spherical shape and scored to be in better condition would be more likely to be in use than platform dreys in worse condition. Although this assumption held true for spherical shaped dreys (percentage use S1>S2>S3), the opposite seemed to be the case for platform shaped dreys (percentage use P3>P2>P1) (Tab. 2).

Of the 215 drey locations we identified through radio-tracking, 193 (89.8%) fell within the area where forest operations took place (Fig. 4), and only 45 of these had been identified before the drey survey was carried out (< 18/04/2017). Seven of these 45 dreys had been identified during the drey survey, suggesting that at least 38 dreys (85.3%) had been missed during the survey. Finally, over the entire study period, a total of 171 dreys (88.6% of 193) were not identified during the drey survey, suggesting they were either missed or were newly build after the survey took place.

The results presented here are for the study area as whole, but we confirmed very similar results with high percentages of dreys missed during the survey or newly build after the survey for each of the dominant habitat types individually (Norway spruce: 87%, Scots pine: 71%, and Japanese larch: 83%).

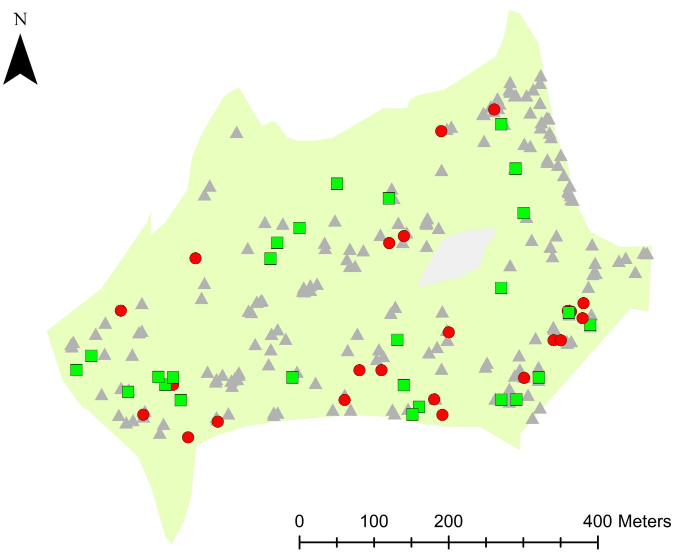

Figure 4 – Drey survey results with dreys being classed as either spherical-shaped (green squares) or platform-shaped (red circles). Drey locations identified throughout the study period through radio-tracking (193) are displayed as grey triangles.

Nest box use

To aid visual identification of patterns in nest box visits in relation to forest operations, we first constructed a cluster heat map (Wilkinson and Friendly, 2009; Galili et al., 2018). This suggested that nest box use was higher in the period after forest operations than before forest operation, though this seemed mainly due to increased uptake in August 2017 (Fig. 5) and this trend did not seem to carry on into 2018. In addition, the heatmap suggests that low nest boxes were visited more frequently than high nest boxes (Fig. 5).

Results of our two final GLMM models are shown in Tab. 3. Best fit Model 1 showed that forest operations had a significant effect on nest box use (β=-0.92, SE=0.12, p<0.01) (Tab. 3). Tukey's post hoc test showed that nest box use was significantly higher after forest operations (mean ± SE: 1.904 ± 0.147) than before forest operations (mean ± SE: 0.983 ± 0.164). In addition, height at which nest boxes were deployed had a significant effect on nest box use (β=0.79, SE=0.28, p<0.05) (Tab. 3), with a significant preference for low nest boxes (mean ± SE: 1.840 ± 0.192) compared to high nest boxes (mean ± SE: 1.050 ± 0.211).

Best fit Model 2 also showed height being a significant effect on nest box use (β=0.88, SE=0.33, p<0.05) (Tab. 3), with a preference for low nest boxes (mean ± SE: 1.569 ± 0.223) compared to high nest boxes (mean ± SE:0.691 ± 0.251). Moreover, year had a significant effect on nest box use by red squirrels (β=0.34, SE=0.16, p<0.05) (Tab. 3), with higher nest box use in 2018 (mean ± SE: 1.299 ± 0.192) than in 2017 (mean ± SE: 0.961 ± 0.187).

Other nest box characteristics, including local drey density, nest box type and tree species in which the nest box is deployed, were not included in either of the final models and in the full models these main fixed effects were non-significant (all p>0.05) (see Supplemental Information).

Discussion

Despite thinning operations being routine in forest management, there is a critical knowledge gap when it comes to understanding the impact of forest operations on canopy-dwelling animals. We present data on the impacts of typical, standard thinning operations on red squirrels in a conifer forest in Scotland and assess possibly mitigation measures.

Table 2 – Drey survey results in comparison to dreys known to be used by red squirrels (through radio-tracking) by the time the drey survey was completed (⩽19/04/2017) and throughout the entire study period. Drey shape was recorded as spherical (S) or platform (P) and condition was estimated on a scale of 1–3 (best to worst condition) (see Methods for more details).

	Number of dreys (%)		
	Identified during drey survey	Confirmed as in use by the end of the drey survey	Confirmed as in use by the end of the study
S1	6	1 (17%)	4 (67%)
S2	19	4 (21%)	7 (37%)
S3	1	0 (0%)	0 (0%)
P1	3	0 (0%)	1 (33%)
P2	15	1 (7%)	7 (47%)
P3	5	1 (20%)	4 (80%)
Total	**49**	**7 (14%)**	**23 (47%)**

Table 3 – Results of the generalized linear mixed models for Model 1 (including forest operations: periods 1–2) and Model 2 (including year: periods 1 and 3). Boldface indicates significant predictors for nest box use.

Model 1				
Variables	**Estimate**	**Std. Error**	**z-value**	***p*-value**
(Intercept)	1.51	0.21	7.14	0.00
Nest box height	**0.79**	**0.28**	**2.80**	**0.01**
Forest operations	**-0.92**	**0.12**	**-7.74**	**<0.01**

Model 2				
Variables	**Estimate**	**Std. Error**	**z-value**	***p*-value**
(Intercept)	0.52	0.26	1.97	0.05
Nest box height	**0.88**	**0.33**	**2.69**	**0.01**
Year	**0.34**	**0.16**	**2.16**	**0.03**

Drey surveying is used by Forestry Land Scotland as part of their management and mitigation of over 400000 hectares of forest wherein the reconciliation of timber production and wildlife conservation is a key objective. Although it is acknowledged that drey surveys have a varying degree of success, drey survey effectiveness has not been quantified before. Our results showed that the standard drey survey missed 83.5% of the dreys that were known to be present (and in use) at the time of the survey, and that only 47% of dreys identified by the survey were confirmed to be in use by the end of the study (i.e., 53% of dreys identified during the drey survey were likely to be abandoned or no longer in use). This reflects both the difficulty in detecting squirrel dreys in dense conifer canopy, and the changeable nature of red squirrel nesting behaviour. Dreys can be built by squirrels over the course of a handful of days (Bosch and Lurz, 2013) and most squirrels adapt their drey use to changes in food availability in their local forest and a number of dreys are used at the same time (e.g., Lurz, 1995; Wauters and Dhondt, 1990). With the exception of breeding dreys, the use of dreys can therefore alternate over consecutive days and the use of up to 8 different dreys over a two-week period has been reported (Gurnell et al., 2008). Some of these dreys may be shared with other squirrels (both at different times and, occasionally, in cold winter nights, at the same time; Bosch and Lurz, 2012). This means that drey use across a forest is dynamic with drey switching, as well as old dreys being repaired or abandoned, and new dreys being built throughout the year. For example, Wauters and Dhondt (1990) showed that 35% of dreys were still in good condition one year after they had been first identified, but only 12% of dreys were in use for two years.

During drey surveys an attempt is made by foresters to estimate the likelihood of dreys being in use by assessing the shape and condition of dreys, whereby spherical shaped dreys in good condition are considered more likely to be in use than platform shaped dreys in bad condition. However, our findings showed that the opposite was true for platform shaped dreys and that those categorised as being in worse condition, were more likely to be in use than those categorised to be in better condition. Moreover, spherical shaped dreys were not necessarily more likely to be in use than platform shaped dreys. This indicated that although foresters can detect some dreys and drey like structures, it is nearly impossible to assess from these surveys whether dreys are in use. This is particularly important information, since these drey surveys may inform decisions about the possibility of felling in or outside the red squirrel breeding season.

Our first prediction was substantiated as we found that red squirrels used on average 12.8 ($\pm$ 6.2) dreys over the 6-month study period and more importantly, that the number of (new) dreys used per squirrel increased significantly after forest operations. Using different dreys can have a number of advantages or reasons; home range bequeathed to offspring with a shift in the adult range (Lurz et al., 1997), minimising parasite loads (Bosch and Lurz, 2012), or because of changes in food supply (Lurz et al., 2000). Dreys are also abandoned due to disturbance (Ognev, 1940) and the observed increase from a mean of 2.8 to 7.5 dreys used per squirrels suggests that the disturbance caused by thinning led to an adjustment of space (and thus drey use) by some squirrels.

An increase in the number of new dreys and therefore a need for new nesting locations should also result in an increased uptake of nest boxes. The second prediction we tested was whether nest box use increases after forest operations. Our model results indeed confirmed that nest box use by red squirrels increased after forest operations. This may be in response to habitat loss near existing dreys, the unintentional felling of

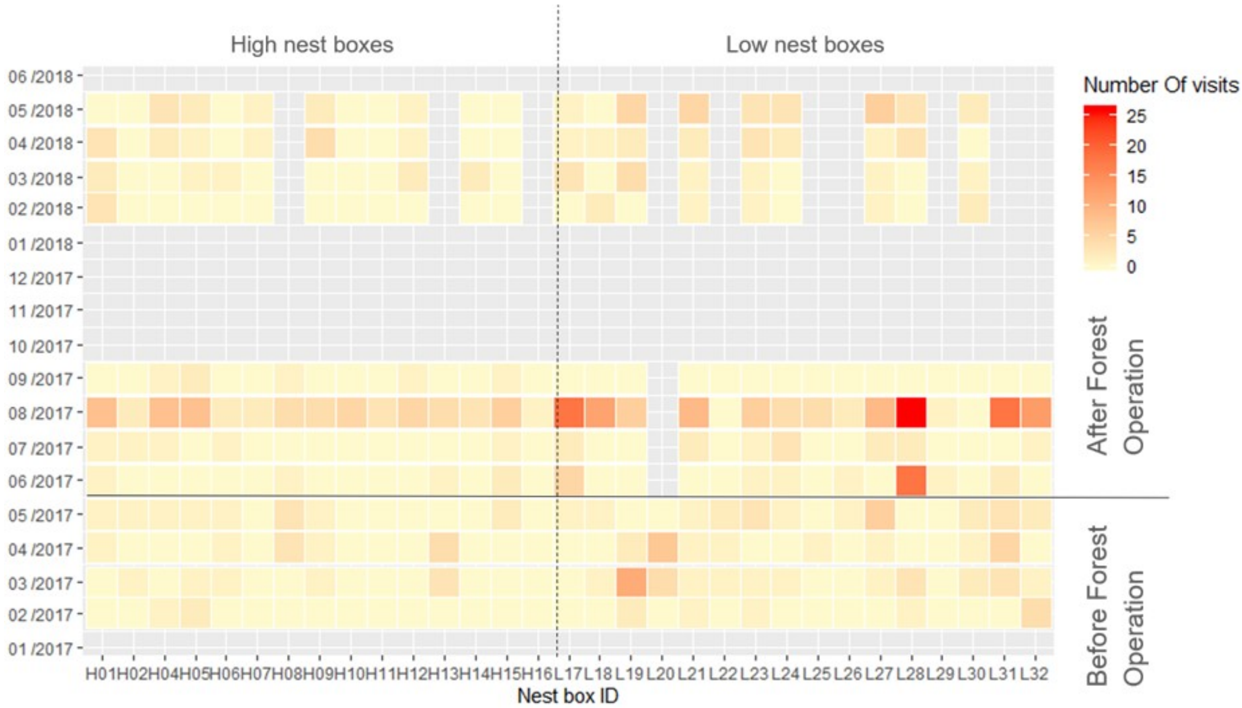

Figure 5 – Heatmap showing nest box use by red squirrels. High nest boxes are shown to the left of the dotted vertical line and low nest boxes to the right (nest box ID on x-axis). The period before the forest operations falls below the solid horizontal line and the period after forest operations above it. A colour scale from light to dark indicates the number of visits per nest box.

unidentified dreys, or due to the operations making existing drey locations risky (e.g., reduced canopy cover increasing the risk of predation) or unsuitable for continued use. As a general policy, trees with known dreys are left un-felled during thinning operations. Our findings on the effectiveness of the pre-operational drey survey, however, suggest there is a high risk of accidental removal of unidentified drey trees. In addition, disturbance caused by harvesting operations in the direct vicinity of dreys may also lead to a temporary abandonment of drey sites, increasing the need to find alternative shelter in the short term.

Whilst our data show a significant uptake of nest boxes following the thinning operations, a closer visual inspection of the data suggests that the increase in nest box use, reached its peak during the month of August, several weeks after the forest operations were completed. The dispersal of juvenile red squirrels from the natal nest after the first spring litter may therefore have contributed to nest box uptake and this highlights the changing and increased need for nesting sites at that time (Tittensor, 1970; Wauters et al., 1994b; Linnell et al., 2018).

Our third prediction was that nest box use would increase over time as animals discover and become familiar with them. This was substantiated as we found that nest box use increased during the second year of deployment. This finding provides an important management consideration, as it suggests that if nest boxes were to be used as mitigation tool, they could ideally be deployed the year before forest operations take place. Generally, red squirrel surveys are carried out 12 months before forest operations are due to take place (with a further pre-operational check four weeks in advance). Such surveys could provide a relative estimate of squirrel presence and population density and the results could therefore be used to decide whether or not to deploy nest boxes in the (surrounding) area.

Finally, we set out to test that nest box placement and nest box characteristics (including local drey density, nest box height, nest box type, tree species in which the nest box is deployed) affect nest box use. Our results showed an effect of height on nest box use, whereby red squirrels used nest boxes placed at lower heights (at approximately 2 m) more, but no other factors affected nest box use. This finding contradicts previous studies that showed a higher occupancy of nest boxes placed at heights greater than 2.5 m (Risch and Brady, 1996; Sotola and Garneau, 2014). Nest boxes at lower heights can be more easily and safely deployed and our findings clearly indicate that they are visited by red squirrels.

Conservation implications

Overall, our study suggests that thinning has led to squirrels changing their nesting behaviour with significantly more dreys being in use following forest operations. This apparent need for new nesting sites is also reflected in an uptake of nest boxes which reached its peak several weeks after the thinning.

We propose that nest boxes can be a useful conservation tool to mitigate the impacts of forest operations and conclude that early deployment of nest boxes in site specific sub-optimal habitats, in areas of low food availability or in areas with low population, can contribute to red squirrel conservation by providing shelter for red squirrels after forest operations — and potentially for juveniles during natal dispersal. We also found increased use of nest boxes placed at lower heights (approximately 2 m) compared to next boxes placed higher up in the canopy. In case of nest box deployment this would simplify the logistics and be highly advantageous from a health and safety point of view. Future research with a camera placed inside nest boxes would be useful to determine the length of nest box use by red squirrels to further our understanding in how far nest box use is temporary or permanent.

Finally, our study suggests that drey surveys are of limited use beyond establishing presence of red squirrels, and that they are less useful to confirm red squirrel absence. Our study highlighted the difficulty in detecting squirrel dreys and that dreys perceived to be in a bad condition, can be repaired and should not be assumed abandoned or unused. Felling during the breeding season should be avoided where possible, as breeding dreys are likely to be missed by surveying and although nest boxes can be a useful conservation tool to mitigate some of the impacts of forest operations, we found no evidence of breeding in the nest boxes.

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Statistics for full model 1.
Table S2 Statistics for full model 2.
Table S3 Model selection process for model 1.
Table S4 Model selection process for model 2.