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Supplementary feeding can attract red squirrels (*Sciurus vulgaris*) to optimal environments

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Running head: Effects of supplementary feeding

ABSTRACT

A number of conservation approaches are used to manage threatened species. However, some of these approaches require intensive planning and can often be restricted by funding. Supplementary feeding is a non-invasive and cost-effective approach to manage vulnerable populations, but we lack data on its usefulness. Here we investigated the effects of supplementary feeding on a population of red squirrels (*Sciurus vulgaris*), a UK priority species which faces competition from the non-native grey squirrel (*Sciurus carolinensis*). The study took place October-December 2015, lasting 8 weeks. Twenty feeders were installed 1 week prior to the beginning of the study in a protected woodland free from grey squirrels, either containing food (full feeders) or no food (empty feeders), and squirrel abundance before and after feeding was recorded at each feeder (for a total of 27 feeding and recording events). Six times more squirrels were seen at full feeders, and numbers increased by 7 fold after feeding. We also observed that the activity of red squirrels in the vicinity of full feeders increased during the course of the study. Eighty-five hair samples were collected during the study, all of which were found at full feeders. Results demonstrate red squirrels can differentiate between full and empty feeders, suggesting their awareness increases when supplementary food is present. Increased abundance of squirrels at full feeders after feeding times not only implies that squirrels are attracted to and can benefit by supplementation, it also shows that food supplementation can be used to regulate the movement of individuals across habitats. Understanding how red squirrel populations are affected by supplementary feeding will contribute towards existing conservation efforts to improve this species future survival.

Keywords: Conservation; Feeders; Food supplementation; Invasive species; Squirrel abundance

INTRODUCTION

Many species across the world are threatened by anthropogenic factors, in particular human population growth, habitat conversion, agriculture, and the introduction of alien species (Wake and Vredenburg 2008). Small populations and species that are sensitive to environmental changes caused by human activity have a particularly high propensity to extinction (McKinney 1997). The management of wildlife can ensure the protection of animal populations (Blanco et al*.* 2011), normally by preventing damage to and restoring their habitats (Allan et al. 2013). Conservation is however costly and resources can be limited, therefore ecologists must be equipped with realistic approaches and strong theoretical bases for constituting conservation priorities when aiming to stabilise populations and restore habitats (Ceballos and Ehrlich 2002).

The introduction of alien species is a pervasive problem normally having detrimental ecological impacts on native species, through competition, habitat alteration and spread of disease (Manchester and Bullock 2000). Invasive species are a leading cause for the global decrease in biodiversity (Davis 2003; Clavero and García-Berthou 2005), although in some cases it is not clear whether invasive species are a direct cause of the extinction of native species, or whether they are taking advantage of ecological changes that are primarily responsible for such extinctions (Gurevitch and Padilla 2004; Di Febbraro et al. 2016). Eradication of well-established invasive species is costly and challenging, therefore controlling populations and restricting their habitat range may be preferable. Early recognition of invasiveness would prevent harm to biodiversity, however characterisation of an invasive species can be unclear (Williamson 1993), which has led to difficulties in predicting intensity of invasiveness.

Reintroduction of a native species is a common management strategy, used to supplement existing wild populations or to re-establish them in areas where they have disappeared (Wilson et al. 2014). Successful reintroductions are likely to occur when a large number of individuals are released and the main factor responsible for the population decline has been eradicated (Fischer and Lindenmayer 2000). However, there are some drawbacks associated to reintroductions: time taken to evaluate success may be long, funding is not always available over long periods, and intense monitoring after relocation may be required.

One species for which reintroductions can be beneficial is the red squirrel (*Sciurus vulgaris*), which has experienced significant population decline over the past 60 years, with UK distributions presently restricted to Scotland and parts of northern England, formerly upholding a widespread distribution (Bryce et al. 2005). The native red squirrel faces competition from the non-native grey squirrel (*Sciurus carolinensis*), after its introduction from North America (Gurnell and Pepper 1993). Interspecific competition occurs between the two species, as they share the same food resources and woodland habitats (Wauters and Gurnell 1999; Bryce 2000; Gurnell et al. 2004). Grey squirrels have approximately twice the body size of reds squirrels (Bryce et al. 2005), and therefore a higher food demand. In addition, they have a higher tolerance to phytotoxins in acorns, making them better competitors (Kenward and Holm 1993). Importantly, the grey squirrel is responsible for the transmission of squirrel poxvirus (SQPV), which leads to high levels of mortality amongst red squirrels but not among grey squirrels (Rushton et al. 2006; White et al. 2016). SQPV has a significant impact at the population level (Tomkins et al. 2003). Once populations of red squirrels are weakened, grey squirrels out-compete and colonise habitats quicker than red squirrels can re-colonise (Bryce et al. 2005).

Red squirrels are listed as a priority species in the UK Biodiversity Action Plan (UK Biodiversity Action Plan Steering Group 1995) and are under legal protection (Bryce et al. 2005). Conservation efforts are vast within the UK, with involvement from numerous organisations such as National Trusts, Wildlife Trusts, Natural England and Forestry Commissions, who utilise a diversity of strategies including habitat improvement, grey squirrel control and reintroduction programs (Pepper and Patterson 1998). Reintroduction has the potential to be a highly successful conservation tool for this species, however a number of parameters need to be met for it to be deemed practical, such as habitat suitability and availability of individuals to be released (Fornasari et al. 1997; Gurnell et al. 2009).

Food supplementation can be used to sustain reintroduced populations by improving nutritional condition and breeding success (Boonstra and Krebs 2006; Robb et al. 2008). Whilst many studies report significant outcomes, others have found no benefits or even detrimental effects associated with supplemental feeding (Hoodless et al. 1999; Newey et al. 2010). For example, food scarcity is a major limiting factor for bird populations and supplementation can increase over-winter survival and reproductive success (Newton 1998); however, birds tend to form larger aggregations around feeders, leading to spread of disease and increased predator attraction (Robb et al. 2008). Research into the importance of food supplementation for the conservation of red squirrels remains limited (López-Bao et al. 2008; Lioy et al. 2016).

The aim of this study was to investigate how supplementary food affects a wild population of red squirrels within a nature reserve where supplementation had not previously occurred and to discover if there are any benefits of introducing feeders in a new area. This was achieved by providing squirrels with food and recording the differences in squirrel abundance before and after feeding, and making comparisons with areas with no supplementation. It was predicted that by increasing food availability with supplementation, squirrel abundance would increase in the supplemented areas. If so, food supplementation could be used as a management tool to increase red squirrel abundance in protected areas that are deemed suitable for the reestablishment of healthy red squirrel populations.

MATERIAL AND METHODS

Study Site

Ainsdale National Nature Reserve (NNR) consists of frontal and fore-dunes, grassland, frontal pinewood, scrub and rear woodland (WS Atkins Consultants Limited 2004). The dunes are rich in biodiversity, with some representative species including the natterjack toad

(*Epidalea calamita*), the great crested newt (*Triturus cristatus*), and the sand lizard (*Lacerta agilis*). The woodlands are located centrally within the dunes, covering 21.43 ha and being comprised primarily of Corsican pine (*Pinus nigra*). Ground flora is absent or limited in most woodland areas (Clarke & Ayutthaya 2010). Grey squirrels were not present in the area at the time of study. Grey squirrels had been previously present but they were eradicated from the area. Since their removal, the area of study has been monitored regularly, ensuring that grey squirrels have not moved back into the area. Monitoring by the Wildlife Trust takes place across the red squirrel stronghold and buffer zone in spring and autumn, including the study woodland, and involves direct sightings, field signs and hair samples collected from hair tubes (Bertolino et al. 2009; Gurnell et al. 2011). To date the area of study is confirmed to be a grey-squirrel free area.

Feeders

Prior to data collection, we selected an area within the woodland that was deemed as preferred habitat for the red squirrel, based on feeding signs, tree species present, tree density, and distance from public footpaths. We selected and mapped 20 grid points within this area, with a distance of approximately 100 m between each grid point. We used these grid points to accurately position feeders in the woodland (Fig. 1). We installed one feeding box in each one of these grid points. Feeding boxes were positioned at head height and attached to a tree using cable ties (Fig. S1). We did not use red-only feeders, as grey squirrels were not present in the study area. Red-only feeders are more expensive but they are recommended in areas were grey squirrels can be present (Gurnell & Pepper 1993). Ten feeders contained no food (control) and 10 contained food (a mixture of peanuts and shelled sunflower seeds). Feeders containing food (full feeders) alternated in the woodland with those containing no food (empty feeders). Feeders were cleaned weekly with animal-safe disinfectant. Feeders were taken down once the study was concluded.

Field Method

For each measurement, the observer was positioned 15 m from a feeder and carried out a 5-minute scan for red squirrel activity. This was recorded as the 'before feeding' measure (Fig. 2). The observer then proceeded towards the feeder, filled the box with food (or pretended to do so, as explained below), then took another position 15 m from the feeder and made an additional 5 min scan for red squirrel activity. This was recorded as the 'after feeding' measure (Fig. 2). If the feeder was a control (empty feeder), the action of filling the feeder with food was replicated, but no food was put in the feeder. The same procedure was repeated for all 20 feeders. This protocol was repeated on 27 different days over an 8-week period between October and December 2015.

Sticky tape was positioned under the lid of each feeder to catch hair from any animal using the feeder, an approach which was adapted from hair tube surveys (Finnegan et al. 2007). Hair was collected and analysed in the lab to identify whether it was from a red squirrel or another animal. To determine whether feeders were being used by multiple individuals, GoPro time-lapse cameras were installed on trees adjacent to two trees with full feeders that we knew were being used by squirrels. Photos taken with these cameras were examined to determine how many individuals were present at a feeder and to validate feeder usage by squirrels (Steen & Barmoen 2017). Data from these cameras were not statistically analysed. Photos from these cameras showed only red squirrels (range: 1-3 red squirrels).

Permission was obtained from the Ainsdale National Nature Reserve to install the feeders and conduct the project within the National Nature Reserve. However, given the observational nature of the experiment, the authorization of an animal care or ethics committee was not required.

Statistical Analysis

We conducted our statistical analyses using R, version 3.3.1 (R Core Team 2016). We set significance at $p < 0.05$. Unless otherwise noticed, we implemented generalized linear mixed models (GLMMs) using the *glmer* function (package lme4, version 1.1-12), with a Poisson distribution and log link. In one GLMM the number of squirrels observed in the vicinity of empty or full feeders was entered as the response variable in the model. The fixed effects in the full model were treatment (two levels: empty feeders and full feeders), observation time (two levels: observation before placing or pretending to place food in the feeder, depending on the treatment, and observation after placing or pretending to place food in the feeder), temperature, wind speed, and rain occurrence (binary variable). We included observation day (the day in which the first observation took place being day 1) as a random effect. In another GLMM we used the number of feeders in which we observed red squirrels in any particular day as the response variable. Following Crawley (2002), we included all probable terms in the full model and excluded non-significant terms sequentially until the model contained only statistically significant terms.

RESULTS

The number of squirrels observed around full feeders was significantly higher than around empty feeders (z value = 8.33, $p < 0.0001$; Fig. 3), and it was also higher during the second phase of observation (after placing food in a "full" feeder or pretending to place food in and "empty" feeder) than during the first phase of observation (z value = -8.41, $p < 0.0001$; Table 1). The maximum number of squirrels observed at empty feeders were 1 (first phase of observation) and 3 (second phase of observation), whereas at full feeders the maximum number of squirrels were 5 and 10 (first and second phase, respectively). Temperature, wind speed, and rain had no effect on the observed number of squirrels ($p > 0.05$).

The number of full feeders around which we observed squirrels was higher compared to empty feeders (z value = 6.74, $p < 0.0001$; Table 1). The number of feeders with squirrels in their vicinity was also higher during the second phase of observation than during the first phase of observation (z value = -6.85, $p < 0.0001$). Temperature, wind speed, and rain had no effect on the number of feeders visited by squirrels ($p > 0.05$).

The number of full feeders in which we observed red squirrels increased during the course of the study (Spearman's rank correlation: r = 0.53, p = 0.005; Fig. 4). As for empty feeders, there was not a significant correlation between the number of feeders with squirrels and observation day (r = 0.04, p = 0.84).

A total of 85 hair samples were collected from full feeders, whereas none was found on empty feeders. Of these 85 samples, 81 were assigned to red squirrels. The number of full feeders that were visited by red squirrels, based on the presence of their hair, was thus higher than that of empty feeders (Wilcoxon signed rank test: V = 0, $p < 0.0001$).

DISCUSSION

The main results of our study confirm our prediction that an increase in food availability by supplementation increases squirrel abundance, particularly after the event of replenishing a feeder. More squirrels were observed in areas with full feeders, indicating that red squirrels are able to distinguish between empty and full feeders. Further supporting the preference of red squirrels for full feeders, hair samples from red squirrels were obtained at full feeders but not at empty feeders. These findings seem to invalidate the suggestion that presence of a feeder (whether full or empty) influences an individual’s position within the woodland. Indeed, if squirrels associated any feeder with food, we would have expected to observe similar numbers of squirrels at each feeder.

In addition to the observed difference between empty and full feeders, squirrel abundance around full feeders increased by 7 fold immediately after replenishing the feeders with food. That is, squirrels favoured full feeders and became aware when feeders were replenished. It remains to be investigated whether squirrels use visual, auditory or olfactory cues, or a combination of these, to differentiate between empty and full feeders and to detect the replenishing events. Red squirrels are arboreal granivores (Molinari et al. 2006), and they rely on olfaction when using their memory to retrieve cached food (Vander Wall 1998), so a combination of visual and olfactory investigation may have been involved in their differential behaviour toward empty and full feeders and in their positive response to replenishment events.

If feeders were in close proximity to high amounts of natural food, the number of squirrels at these feeders might have been lower. Under these conditions, squirrels would be less inclined to use feeders, particularly as feeders may cause an increased predation risk through decreased ability to be vigilant (Jayne et al. 2015). Natural food abundance was not recorded during this study, and consequently patch quality and food distribution was unknown. However, our study was conducted between October and December, when natural food resources available to red squirrels are more predictable (Wauters et al. 2007), which suggests that squirrels may be attracted to supplementary food even when they also have access to natural food.

Squirrel abundance may have been affected by population spatial distribution, which is characteristically controlled by patch quality and natural food abundance; poor quality patches with fewer resources are expected to have less dense populations (Wauters et al. 2001). Additionally, optimal foraging theory suggests that energy is required to search for food, and that it is more efficient to reside in areas where food is abundant, which is also advantageous for caching behaviour (van der Merwe et al. 2014). Different studies on red squirrels indeed support the idea that squirrel density is positively associated with food availability (Kenward et al. 1998; Magris and Gurnell 2002; Wauters et al. 2008). Food supplementation can increase habitat patchiness and may lead to squirrels choosing to reside in areas with additional food resources, therefore supporting the idea that food supplementation can be used to manage populations. Our study further shows the potential practical use of supplementary feeding as a tool to control the movement of squirrels into optimal habitats chosen for their survival.

We found that squirrel abundance around full feeders significantly increased as the experiment progressed. This increased use of feeders is likely due to habituation to the feeder and learned reliance on an abundant and relatively predictable source of food. Squirrels may have spent gradually more time in the vicinity of a full feeder as the experiment progressed.

Such a behavioural response requires further investigation but has the potential to be used by managers to manipulate the movement of populations into areas that are considered better for the squirrels.

Food supplementation is widely used by wildlife managers, primarily due to its potential immediate benefits, and improvements are commonly observed (Blanco et al. 2011). It can, however, be wrongfully implemented, particularly when substantial evaluations have not been carried out, and it is unknown whether food is a limiting factor (Oro et al. 2008). Such misjudgements can lead to undesired counterproductive effects such as behavioural changes, disease, nutritional deficiency, poisoning and contamination (Blanco et al. 2011; Robb et al. 2008). Using food types that are naturally present can minimise nutritional deficiencies. A population can also become reliant on supplementation, which leads to a reduced ability to forage for natural food, something which is crucial for survival if supplementation is terminated (López-Bao et al. 2010). In addition, if predators learn that prey congregate around feeders, supplementation may lead to an increase in predation (however, see Karmacharya et al. 2013); stochastic filling of feeders could minimise this problem. In the case of red squirrels, careful implementation of supplementary feeding also needs to consider the competition with grey squirrels in areas in which the two species are present. Nevertheless, with a full comprehensive evaluation, continual maintenance and monitoring schemes, supplemental feeding has the potential to improve the conservation prospects of a population (Magris and Gurnell, 2002; López-Bao et al. 2008).

In conclusion, we showed that supplementary feeding increased local abundance of red squirrels around active feeders. Since this pattern might be partly due to small-scale woodland heterogeneity, further studies should undertake a comprehensive habitat survey prior to food supplementation to assess natural food abundance within different patches, in order to fully investigate feeder usage by red squirrels and how to maximise supplemental feeding depending on natural food abundance. Supplementary feeding is a non-invasive, easy to implement, and cost-effective conservation tool that can be used in addition with other management strategies to assist with the stabilisation or recovery of vulnerable populations.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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Table 1. Number of red squirrels and number of feeders with squirrels per observation day depending on observation phase (before and after "feeding") and type of feeder (empty and full).

	Empty feeders		Full feeders	
	Before	After	Before	After
Number of observed squirrels / day	0.22 ± 0.42	0.74 ± 0.86	0.7 ± 1.1	4.89 ± 2.53
Number of feeders with squirrels / day	0.22 ± 0.42	0.63 ± 0.69	0.59 ± 0.75	3.41 ± 1.31

Values represent the mean ± s.d

FIGURE LEGENDS

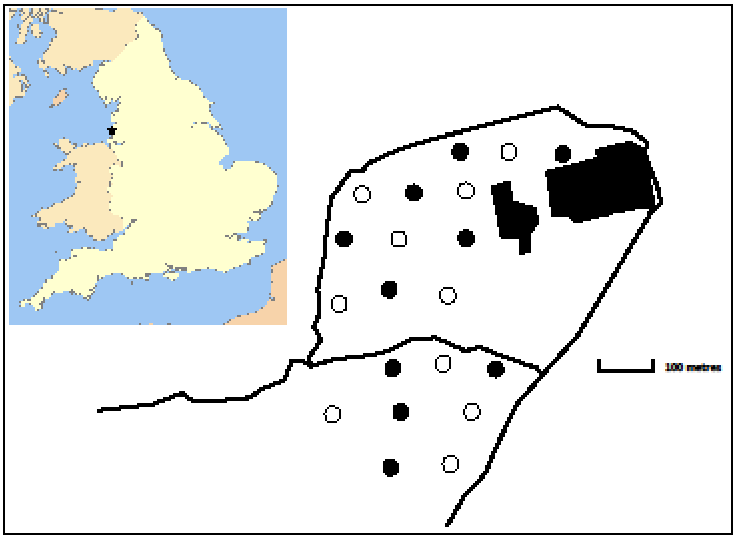

Fig. 1 Distribution of feeders within the woodland in the Ainsdale National Nature Reserve. Twenty feeders were randomly distributed, approximately 100 m apart. Full feeders are shown as filled circles and empty feeders as open circles. Lines indicate footpaths. Two small buildings located within the experimental area are also shown. The star symbol on the map shows the location of the study site.

Fig. 2 Observational procedure carried out at each feeder. (1) Observer position before "replenishment", (2) during the "replenishment" event (standing in front of the feeder), and (3) observer position after "replenishment".

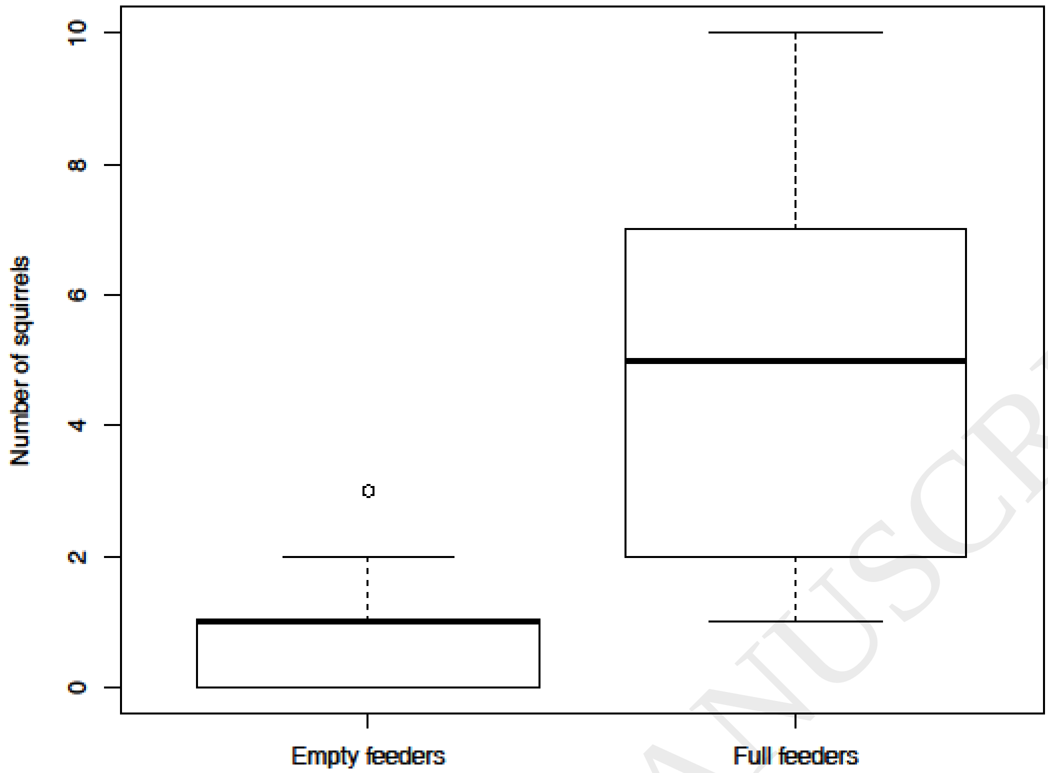

Fig. 3 Number of red squirrels found in the vicinity of empty and full feeders after the observer had pretended to place food or placed food in the feeder, respectively. For each boxplot, the bar within each box represents the sample median, each box represents 50% of the data around the median, and the two whiskers represent the 95% confidence interval.

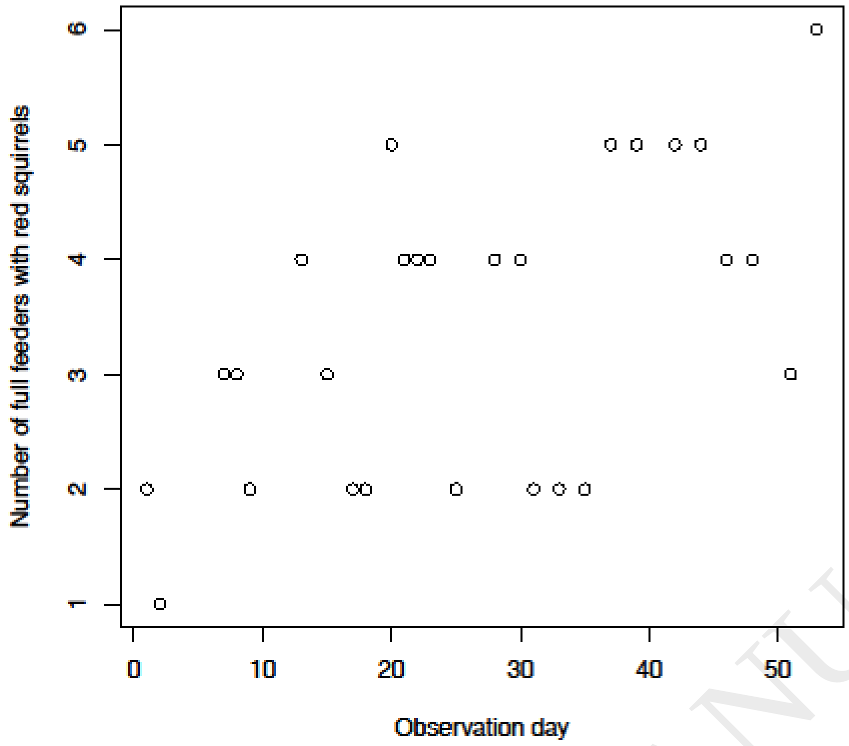

Fig. 4 Increase in the number of full feeders around which red squirrels were observed as the feeding regime progressed.