

Pulsed food resources, but not forest cover, determine lifetime reproductive success in a forest-dwelling rodent

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Abstract

1. The relative contributions of habitat and food availability on fitness may provide evidence for key habitat features needed to safeguard population persistence. However, defining habitat quality for a species can be a complex task, especially if knowledge on the relationship between individual performance and habitat quality is lacking.
2. Here, we determined the relative importance of the availability of suitable forest habitat, body mass and food from masting tree species on female lifetime reproductive success (LRS) of Siberian flying squirrels (*Pteromys volans*).
3. We calculated LRS of 500 female flying squirrels based on a 22-year-long longitudinal dataset of two populations from western Finland. We assessed with generalised additive models the potential effects of availability of suitable habitat and cumulative lifetime availability of food from masting tree species on female LRS, longevity and fecundity. On a reduced dataset, we evaluated the importance of female winter body mass and conducted a piecewise path analysis to determine how variables were connected.
4. According to generalised additive models female longevity, fecundity and LRS were mainly determined by variation in cumulative lifetime availability of food from masting alder and birch. Instead, habitat and body mass had a smaller role. The path analysis indicated that lifetime food availability had a direct effect on longevity and fecundity, and these had an equal effect on LRS at both study sites.
5. Our results on LRS show that the occurrence of tree masting events during a female flying squirrel's lifetime has a profoundly larger effect on LRS than the cover of suitable forest habitat. Furthermore, this study emphasises the importance of both fecundity and longevity, and the indirect effects of food availability via those components, as determinants of lifetime fitness in female flying squirrels.

KEYWORDS

arboreal mammal, fecundity, forest specialist, habitat availability, longevity, *Pteromys volans*, Siberian flying squirrel, tree mast

1 | INTRODUCTION

Defining habitat quality for a species can be a complex task (Gaillard et al., 2010), especially if no knowledge on the relationship between individual performance and habitat quality exists. Consequently,

interpretations of habitat quality are often based on simple proxies that may be misleading (Gaillard et al., 2010; Van Horne, 1983). For example, forest cover and area of old growth forests are often used as proxies of habitat quality for arboreal animals. However, efficient conservation efforts of vulnerable species require not only

knowledge on their habitat use and food requirements but also an understanding of how habitat availability and food availability interact to affect individual variation in fitness (Colwell et al., 2010). This is particularly important for species living in environments with pulsed resources, such as forests dominated by masting tree species. The relative contributions of habitat and food availability on fitness may provide evidence for key habitat features needed to safeguard population persistence (Delibes, Gaona, Ferreras, & Doak, 2001; Robertson & Hutto, 2006).

A reliable and common estimate of fitness is lifetime reproductive success (LRS) or lifetime breeding success (LBS) which can be estimated from longitudinal data (Brommer, Gustafsson, Pietiäinen, & Merilä, 2004; Clutton-Brock, 1988; Newton, 1989). From initiation of first breeding, LRS and LBS are mainly determined by reproductive longevity (number of breeding seasons) and fecundity (average production per breeding season), with contribution from juvenile survival (Clutton-Brock, 1988; Newton, 1989). Environmental factors, such as food and habitat quality, can affect LRS through fecundity and longevity in conjunction with individual traits. For example, availability of food resources affect LRS directly (e.g. Millon, Petty, & Lambin, 2010) but can also be mediated through longevity (Bérubé, Festa-Bianchet, & Jorgenson, 1999; Bieber & Ruf, 2009; Wauters, Suhonen, & Dhondt, 1995). Habitat quality or habitat use are often important determinants of LRS in both birds (Herman & Colwell, 2015) and mammals (Bieber & Ruf, 2009; McLoughlin, Boyce, Coulson, & Clutton-Brock, 2006; Regan, Pilkington, Pemberton, & Crawley, 2016). For example, female St. Kilda Soay sheep that had high cover of key grass habitat within their home ranges had higher LRS than females with low cover of grass habitat (Regan et al., 2016). Of individual traits, body mass is most commonly related with LRS, longevity or fecundity, and usually heavier females achieve higher fitness (e.g. Bérubé et al., 1999; Clutton-Brock, 1988; Newton, 1989; but see Gaillard, Festa-Bianchet, Delorme, & Jorgenson, 2000a).

The Siberian flying squirrel (*Pteromys volans* L., hereafter flying squirrel) is a nocturnal, arboreal forest species which has its westernmost distribution in Finland. Due to the long-lasting declining population trends across Finland (Hanski, 2006; Hokkanen, Törmälä, & Vuorinen, 1982; Selonen, Sulkava, Sulkava, & Korpimäki, 2010) and possible role as an umbrella species potentially indicating biodiversity values in old growth forests (Hurme, Mönkkönen, Sippola, Ylinen, & Pentinsaari, 2008), the species has a high conservation value and is strictly protected under European legislation (Habitats Directive 92/43/EEC). The population declines are probably linked with decreasing availability of suitable habitat due to current forestry management practises (Hanski, 2006; Santangeli, Wistbacka, Hanski, & Laaksonen, 2013b). Understanding how habitat characteristics and food availability contribute to the variation in LRS, life span and fecundity of flying squirrels may provide key evidence to the mechanisms involved in the population declines and clues to how conservation actions could be improved. Occurrence of flying squirrels is highly correlated with the presence and density of a suitable habitat, but species also seem to cope well with fragmentation (Santangeli, Hanski, & Mäkelä, 2013a; Selonen & Hanski, 2004).

In this paper, we take advantage of a 22-year-long longitudinal dataset on two populations of Siberian flying squirrels, combined with annual land cover data on habitat availability, to determine the relative importance of availability of food and suitable forest habitat on local and landscape scale on female LRS of this forest specialist. Furthermore, we evaluate the contribution of average annual reproductive success (fecundity) and breeding longevity on LRS, and which component is most influenced by habitat availability and/or food availability. Based on the known occupancy patterns and habitat preferences (Hurme et al., 2008; Santangeli et al., 2013a; Selonen, Hanski, & Stevens, 2001; Selonen & Wistbacka, 2016), we predict that LRS will be higher for females with large cover of suitable forest around their core territories and for females experiencing higher food abundance during their lifetime. Furthermore, we predict that females with higher body mass produce more offspring similar to findings in red squirrels (*Sciurus vulgaris*) (Wauters & Dhondt, 1995). Higher food availability and access to suitable habitat should lead to higher body mass and thus increased longevity or fecundity (Regan et al., 2016). High food availability also has a positive effect on annual reproduction in flying squirrels (Selonen & Wistbacka, 2016), and is therefore likely positively related with fecundity. However, as flying squirrels can live up to 7+ years, although most females are short-lived (<2 years, see Results), we expect that longevity is more important for LRS than fecundity, following, for example, Bérubé et al. (1999).

2 | MATERIALS AND METHODS

2.1 | Study species

Flying squirrels nests in tree cavities, nest boxes and dreys in spruce-dominated boreal forests. The mating season starts from mid-March. After the first litter born in April, the females can sometimes have a second litter born in June, especially when spring food availability is high (Selonen, Wistbacka, & Korpimäki, 2016). Litter size is 2.3–2.5 young for both first and second litters and about 15% of mothers produce summer litters (Selonen & Wistbacka, 2016). Weaning age for the species is at about 2 months, but exact estimates are lacking. Breeding dispersal is much shorter than natal dispersal, especially in females (average breeding movement distance: 72 ± 130 m, average natal dispersal distance: $1,830 \pm 1,390$ m, Selonen & Wistbacka, 2016). Females are territorial, living in non-overlapping home ranges (on average 7 ha) indicating that competition for nesting sites occur, while males live in overlapping home ranges (on average 60 ha) encompassing several males and females (Selonen, Painter, Rantala, & Hanski, 2013; Selonen et al., 2001). Annual local apparent survival in our populations is about 0.43–0.53 (Lampila, Wistbacka, Mäkelä, & Orell, 2009), and although most females disappear from the population after their first breeding season (probably from death, and not breeding dispersal, Brommer, Wistbacka, & Selonen, 2017; Selonen & Wistbacka, 2017) we have recorded individuals as old as 7+ years. Main predators of flying squirrels are larger owls, such as the Eurasian eagle owl (*Bubo bubo*), Ural owl (*Strix uralensis*), goshawk (*Accipiter gentilis*) and the European pine marten (*Martes martes*) (Selonen et al., 2010).

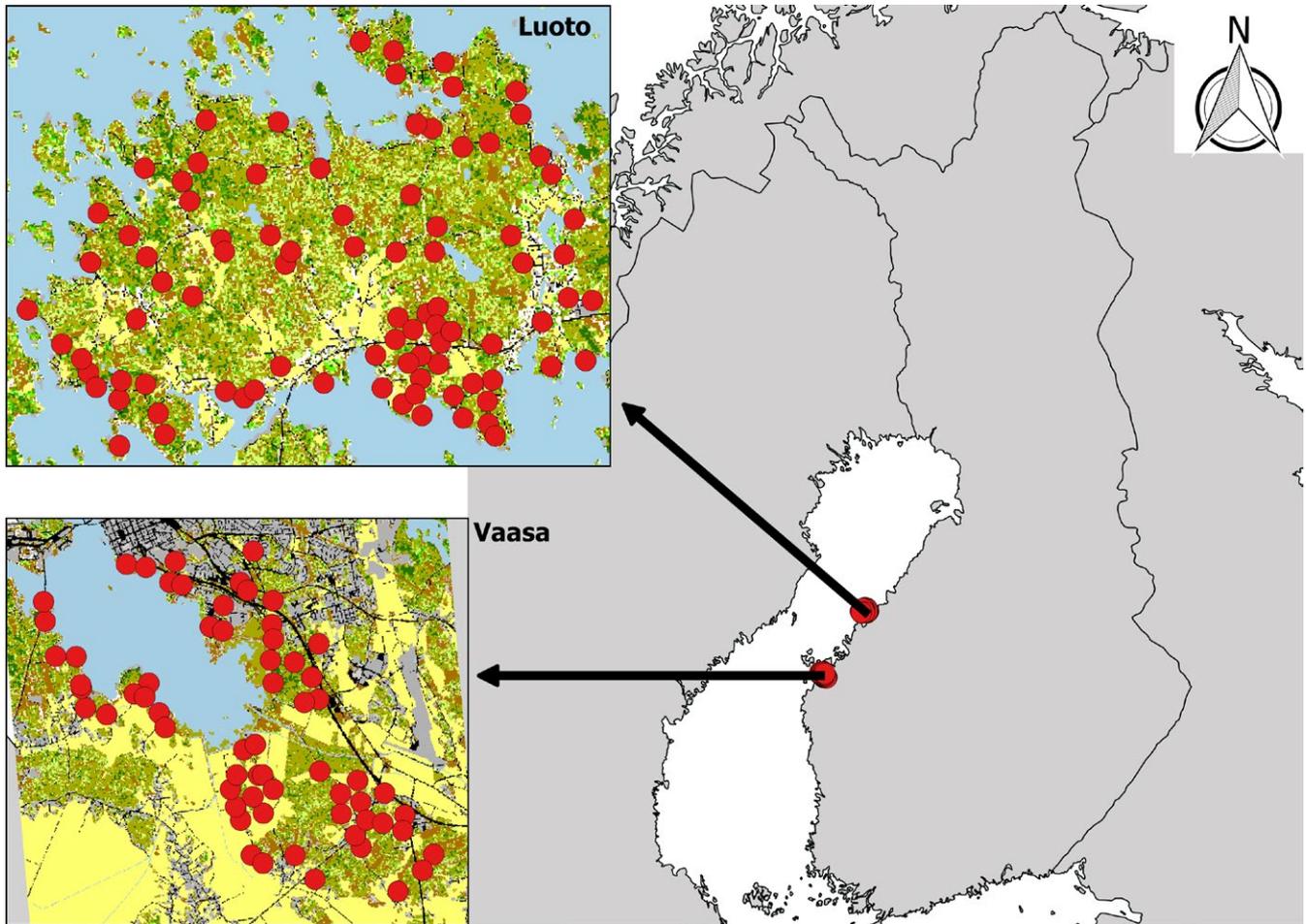


FIGURE 1 The map shows the location of the two study sites within Finland. Colours in the site-specific maps indicate the distribution and availability of different land cover types (light colour = agricultural land, dark mosaics = forests) where points indicate the approximate spread and location of nest boxes available for flying squirrels during the study period [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]

2.2 | Study sites and capture–mark–recapture data

The study was conducted at two study sites along the coast of West Finland from 1992/1993 to 2014 (Figure 1). One site is located in and around Vaasa city (hereafter: Vaasa region, 63°3'N, 21°41'E). The marking of flying squirrels started in 1992 in Vaasa within an area of 400 ha, after 2,000 the area was 25 km². Vaasa is covered by spruce forest patches, shoreline forests, clear-cuts and agricultural fields (for more information see Lampila et al., 2009; Selonen, Hanski, & Wistbacka, 2014). The other site is located about 90 km north-east at Luoto (63°49'N, 22°49'E; Figure 1) and covers an area of 44 km². The main forest types in Luoto are shoreline spruce-dominated mixed forests, clear-cuts and cultivated Scots pine forests. Capture–mark–recapture data have been collected since 1993 from this area.

At both sites, nest boxes for flying squirrels were placed in forest patches of various sizes in sets of two to four nest boxes per site, with an average of two nest boxes per mature spruce forest hectare. Box occupancy percentage by the flying squirrel was low (c. 25%), that is, in most cases a nest box was empty when checked. Flying squirrels (adults and juveniles) were captured by hand in nest boxes, sexed, weighed and marked with ear-tags (Hauptner 73850, Hauptner,

Germany). Natural cavities were rare in our study areas (on average 0.1 cavities/ha based on 742 spruce forest hectares surveyed within our study areas); we are thus confident that a large majority of breeding events occurred in monitored nest boxes. The nest boxes were checked during one to two sessions in June and August, depending on the presence of breeding females not only in June but also infrequently throughout the year.

In this study, we used only data on adult breeding females with their assumed full reproductive activity within the study period. Females were defined as dead or emigrated from the population when they had not been seen for three consecutive breeding seasons and thus analyses were based on females born before 2012 to avoid under-estimating LRS due to truncated longevity. Based on earlier analysis (Lampila et al., 2009) recapture probability of females was high in our study areas (around 0.9). Only a few females skipped breeding seasons, 15 females (3% of all females in the dataset) skipped one breeding season, one female skipped two seasons and 17 individuals (3.6%) were not observed breeding until second year after birth. Many of these females were likely not breeding as radiotracking data from the study area indicate that non-breeding females use dreys more than nest boxes during summer and are therefore less likely trapped (R. Wistbacka & P. Reunanen,

unpublished data). Most females were observed only once per breeding season, and we could not separate potential first and second litters in all cases as we observed juveniles close to weaning age. The fate of juveniles after leaving the nest and their mother (i.e. recruitment to the population) was not known for most individuals. Therefore, we defined LRS as the total number of offspring produced per female during the whole lifetime. Longevity is defined as the number of breeding seasons a female was observed in the study site, and fecundity is the average production of young per year (i.e. total number of offspring divided by the number of breeding seasons; annual variation in litter size is analysed in Selonen & Wistbacka, 2016; Selonen et al., 2016).

2.3 | Food availability data

The flying squirrel feeds on deciduous trees that occur within or at the edge of spruce (*Picea*) forests, and in our study sites birch (*Betula* spp.), alder (*Alnus* spp.) and aspen (*Populus tremula*) are the main forage items (Mäkelä, 1996; Selonen et al., 2016). These common species occur in all parts of the study area. During winter and early spring, birch and alder catkins are the main food of flying squirrels with birch constituting the main part of the winter diet (80% of used food, based on faecal diet analysis; Mäkelä, 1996), although they eat pine buds and other food items when catkins are not available (Mäkelä, 1996). However, only alder catkins are stored and are preferred over birch (Mäkelä, 1996; Sulkava & Sulkava, 1993). A recent study indicates that the availability of catkins before initiation of breeding was important for flying squirrel reproduction in our study area by increasing the likelihood of second litters (Selonen & Wistbacka, 2016). However, catkin production varies considerably between years, and forms a highly pulsed resource in the forest (Hokkanen, 2000; Ranta, Oksanen, Hokkanen, Bondstam, & Heino, 2005; Ranta et al., 2008; Selonen et al., 2016). Weather conditions during the previous summer determine birch mast; catkin production increases when the previous summer has been warm, but trees seldom manage to produce mast for two successive years (Ranta et al., 2005). After the opening of leaves, in the beginning of May in our study areas, leaves form the main diet of flying squirrels in late spring and summer (Mäkelä, 1996).

Following Selonen et al. (2016), we used two estimates of landscape-level food availability in this study. First, we used estimates from an annual birch catkin survey conducted by the Finnish Forest Research Institute (Hokkanen, 2000). These data are collected to describe nation-wide pollen situation in Finland. Birch catkins were counted in winter from seed-crop observation stands. The catkin data originated from 15 permanent research stands in different parts of Finland (Hokkanen, 2000). We used indices for western Finland that are sampled in Vaasa. Catkin production of deciduous trees is spatially correlated at scales of up to several hundred kilometres in Finland (Ranta et al., 2008). Thus, although the food availability index is less accurate for Luoto than Vaasa, both study sites are located in coastal areas with very similar weather conditions and the spatial correlation in birch catkin production between two sampling sites at similar distance is around $r \approx .7$. Consequently, this index is able to properly describe the yearly variation in catkin production in the area.

There were no catkin count data for alder, but we used aerial pollen estimates that correlate with catkin production as a proxy (Ranta et al., 2008; Selonen et al., 2016). Pollen data were collected by the aerobiology unit at University of Turku with samples collected from 10 different locations in Finland using EU standard methods and Burkard samplers. The data consisted of accumulated sums of average daily counts of airborne pollen in 1 m^3 of air during spring (Ranta et al., 2008). Similarly as for the birch catkin data, we used the estimates for western Finland, sampled in Vaasa for both of our study areas.

2.4 | Land cover data

Yearly maps of habitat classes for each site from 1997 to 2012 were compiled from the SLICE dataset (Mikkola, Jaakkola, & Sucksdorff, 1999), and combined with two forest classifications available for 1997 (National Land Survey 1997) and 2009 (METLA 2009, <http://www.maanmittauslaitos.fi/en/e-services/>). To determine the extent of clear-cutting of forest patches between years, we estimated an index of vegetation cover (the Normal Difference Moisture Index) based on an analysis of Landsat images (<http://landsat.usgs.gov/>). This index allows identifying areas with and without vegetation by measuring the variation in the moisture level due to the degree of vegetation cover (Jin & Sader, 2005), which can thus be used to reveal the moment vegetation has been removed from a plot. We were thus able to produce accurate landscapes (on a 25×25 m pixels grid) on a yearly basis (see method details in Morosinotto, Villers, Thomson, Varjonen, & Korpimäki, 2017).

We defined buffer zones around each nest box at 100 and 500 m distances and calculated the total area of each land cover class within each buffer of active nest boxes for each study year. The 100 m buffer (3.14 ha) represent the core area available for daily use (average distance moved per night: 111 ± 33 m, Hanski, Stevens, Ihalempiä, & Selonen, 2000), with a size about half of an average annual female home range (c. 7 ha, Selonen et al., 2001). The 500 m buffer covers 78.5 ha and represents the availability of habitats on a larger landscape level, but likely to impact settlement decisions. All GIS analyses were done in R version 3.3.0 (R Core Team, 2016).

The original land cover classes were combined to represent biological relevant classes for flying squirrels (Table S1 and Santangeli et al., 2013a), including mature forest (all mature and old growth forests), young forest, open habitat (clear-cuts and peat bogs), agricultural fields, human impacted habitats (roads and buildings) and water (see full description of classes in Table S1). The cover of each habitat type within the 100 and 500 m buffers was averaged across breeding years for each female to obtain a relevant measure of habitat use to compare with LRS for a territorial species. Exchanging average cover with maximum cover barely changed the values as flying squirrel females are site tenacious (Hanski & Selonen, 2009; Selonen & Wistbacka, 2017) and moved between breeding attempts only over very short distances (see Study species description above). Extensive occupancy analyses of flying squirrels indicate that spruce-dominated mixed old growth and mature forests are important habitats for the species (e.g. Reunanen, Mönkkönen, & Nikula, 2002; Santangeli et al., 2013a), and also the

presence of agricultural fields, likely due to the preference for edge habitat in fertile soil, are an important determinant of landscape-level occupancy (Santangeli et al., 2013a). Our study areas are characterised by a large degree of mixed forest structure where mature pine forests (less preferred forest type) often are small fragments surrounded by spruce/birch forests (preferred mature forest type), where flying squirrels in our study are known to forage (R. Wistbacka, pers. obs.). Several studies also indicate that young forest is not used for nesting, feeding or moving (Reunanen et al., 2002; Santangeli et al., 2013a). Therefore, we decided to use cover of all mature forest (hereafter, suitable forest habitat) in our analyses (our results were robust for different definitions of suitable habitat, for example, including patch size measured from aerial photographs, see Appendix S1).

2.5 | Statistical analyses

All statistical calculations were conducted using R version 3.3.0 (R Core Team, 2016). Data exploration was applied following Zuur, Ieno, and Elphick (2010). The presence of outliers was investigated using Cleveland dotplots, collinearity was assessed using multi-panel scatterplots, Pearson correlation coefficients and variance inflation factors.

The importance of suitable habitat, agricultural fields and landscape-level food availability measures (cumulative lifetime birch catkin availability = the sum of average birch catkins per tree and cumulative lifetime alder pollen availability = the sum of Alder pollen/ m^3 of air during the lifetime of each female) for determining LRS of each individual ($n = 500$) was modelled with Generalised Additive Mixed Models (GAMM) using the `GAMM4` package (Wood & Scheipl, 2014) in R. Cover of suitable habitat and of agricultural fields within each buffer zone were centred according to site-specific means to take into account the difference in the site-specific availability of each habitat class (see Table S2). We used the lifetime sum of food availability (number of birch catkins and pollen density) for each female to capture the variability in annual food availability experienced by each female. Annual food availability ranged from 31 to 1857 catkins per birch tree and 47–3,000 alder pollen per m^3 air. Although the dataset is not optimal for detecting possible silver spoon effects (sensu Grafen, 1988), we also tested the importance of food availability during year of birth of each female since food availability early in life can have important consequences for future reproductive success (Descamps, Boutin, Berteaux, McAdam, & Gaillard, 2008; Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toigo, 2000b). However, food availability in the year of birth did not have any effects on LRS, longevity or fecundity (see Table S6 in Appendix S4) and was not considered further. In addition to habitat and food variables, we included study site as a fixed factor to control for site-specific variation in LRS. Year of birth of females was entered as a random effect to take into account for any cohort effects on LRS. The model was fitted assuming Poisson distributed error terms as LRS represent a count of offspring. Alternative error terms, such as Generalized Poisson distribution, are found to potentially describe the distribution of variables such as LRS (Kendall & Wittmann, 2010). However, current implementation of Generalized Poisson distribution

in regressions do not allow for fitting models including random effects. Therefore, we compared model estimates from the GAMM assuming Poisson distribution with model estimates from a GAM model fitted with the `vgam`-function in R-package `VGAM` (Yee, 2017). Model estimates were similar (Table S3 in Appendix S2) and we report results from the GAMM.

The same model structure as for LRS above was used to test the importance of habitat and food in determining average fecundity and longevity ($n = 500$). In the model for fecundity, we assumed errors to be Gaussian distributed, while errors were assumed to be Poisson distributed in the model for longevity. For a smaller subset of females, we included an average winter body mass (measured at captures from September until March) of females as an explanatory factor in addition to the above-mentioned covariates (results presented in Appendix S3), as body mass may influence reproductive success in this species (Selonen et al., 2013). As most females were trapped during the breeding season, only a portion of females had body mass measures not confounded by pregnancy ($n = 213$).

We determined the optimal model for each model set (LRS, fecundity and longevity, with and without body mass, that is, six model sets) implementing the `dredge`-function in the R-package `MuMIn` (Bartoń, 2016). We first fitted a full model, for which we tested nested models. Full models and model selection tables are available in Appendix S4. In addition, model validation was applied on the optimal model to verify the underlying assumptions. Specifically, we plotted residuals vs. fitted values to assess homogeneity of variance, and the residuals vs. each covariate to investigate model misfit.

Finally, we used the smaller dataset including body mass in a piecewise path analysis (Shipley, 2009) to get better understanding on how the different variables interacted and were linked with LRS. Each path in the model was fitted with function `gamm4` using the same random structure and error terms as outlined above to allow for nonlinear effects. However, none of the best models obtained included nonlinear terms. We followed a hierarchical approach where we tested, (i) whether food and habitat variables explained winter body mass, (ii) how food and habitat variables and winter body mass explained fecundity and longevity, and finally (iii) whether all of the above-mentioned variables explained LRS (see hypothetical paths in Figure S1). At each step, we optimised fit as for previous models. However, many of the final models included not statistically significant terms. For these models, we manually simplified models until only significant terms were left in the model. For each path, we extracted standardised path coefficients and R^2 values. The path analysis was conducted for the sites combined and for each site separately.

3 | RESULTS

3.1 | Lifetime reproductive success

Lifetime reproductive success (number of offspring produced during a lifetime) of female flying squirrels ranged from 0 to 16 offspring, and LRS correlated highly with both breeding longevity ($r_p = 0.648$ [0.594, 0.696], $t_{498} = 18.99$, p -value $< .001$) and fecundity ($r_p = 0.594$ [0.535,

TABLE 1 Statistical details of models of Lifetime reproductive success (LRS), fecundity and longevity. Coefficients (coeff) are reported with their associated standard errors (SE). Variables marked with * are represented with nonlinear terms and coefficients are not reported

	Coeff ± SE	Statistic	p-value
LRS			
Intercept	1.070 ± 0.055	Z = 19.451	<.001
Site	0.122 ± 0.053	z = 2.317	.021
Fields 500 m	0.009 ± 0.005	z = 1.874	.061
Fields 500 m:site	-0.012 ± 0.005	z = -2.223	.026
Sum birch catkins*		$\chi^2_{2.8} = 121.28$	<.001
Sum alder pollen*		$\chi^2_{3.2} = 33.99$	<.001
Fecundity			
Intercept	1.868 ± 0.083	t = 22.471	<.001
Site	0.453 ± 0.111	t = 4.085	<.001
Sum alder pollen	0.214 ± 0.055	t = 3.877	<.001
Longevity			
Intercept	0.504 ± 0.040	z = 12.708	<.001
Fields 100 m	-0.125 ± 0.066	z = -1.889	.059
Sum birch catkins*		$\chi^2_{2.6} = 21.36$	<.001
Sum alder pollen*		$\chi^2_{1.8} = 41.85$	<.001

0.648], $t_{498} = 16.49$, p -value <.001). Average longevity (number of breeding seasons) was 1.82 ± 0.08 (\pm SE) in Luoto and 1.75 ± 0.07 in Vaasa and ranged from 1 to 7 years while fecundity (LRS/longevity) ranged from 0 to 6 offspring per year.

The best model explaining variation in LRS of female flying squirrels included nonlinear terms for the lifetime sum of alder pollen concentration and the lifetime sum of birch catkins (Table 1). LRS

increased with increasing alder pollen concentrations and increasing number of birch catkins, but levelled off at intermediate birch catkin availability (Figure 2). LRS was, on average, higher in Vaasa than Luoto and showed a positive linear relationship with cover of agricultural fields within the 500 m buffer around the nest site that tended to be steeper in Luoto than in Vaasa (Table 1). The model explained about 52% of the variation in LRS (adjusted $R^2 = .517$).

3.2 | Fecundity and longevity

The best model describing variation in average fecundity included a positive linear relationship with the lifetime sum of alder pollen for each female and was higher in Vaasa than in Luoto (Table 1). However, the covariates of interest poorly described fecundity and showed poor explanation power (adjusted $R^2 = .06$).

Longevity was best explained by a nonlinear relationship with lifetime sum of birch catkin availability and with lifetime sum of alder pollen availability (Table 1). As for LRS, longevity increased with increasing birch catkin and alder pollen availability. The best model after model selection also included a negative effect of cover of agricultural fields within the 100 m buffer (Table 1). The model explained about 55% of the variation in longevity (adjusted $R^2 = .545$).

3.3 | Path analysis

The path model (based on the smaller dataset including body mass) for Luoto and Vaasa combined (Figure 3) showed that the amount of agricultural fields and suitable forest within the 100 m buffer had negative effects on female winter body mass, while suitable forest within the 500 m buffer and alder availability had positive effects on winter body mass. However, body mass had only a weak effect on longevity, and no effects on fecundity or LRS (Table S5). Longevity was

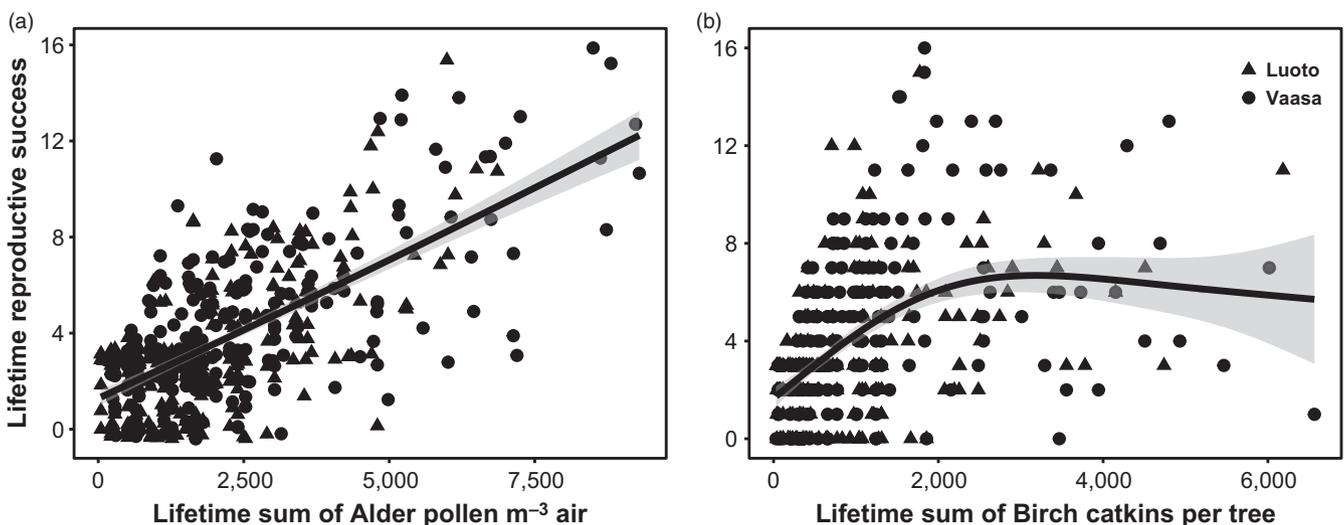


FIGURE 2 Observed lifetime reproductive success (LRS) as a function of (a) lifetime sum of alder (*Alnus* spp.) pollen concentration per m^3 air and (b) lifetime sum of number of birch (*Betula* spp.) catkins per tree experienced by each female flying squirrel (*Pteromys volans*). The fitted lines represent smooth functions based on the function $LRS \sim \exp(s(\text{cumulative food availability measure}, k = 3))$ that mirrors the results obtained in the GAMM models where estimated degree of freedom (edf -value) was 2.8 and 3.2 for alder pollen and birch catkins respectively

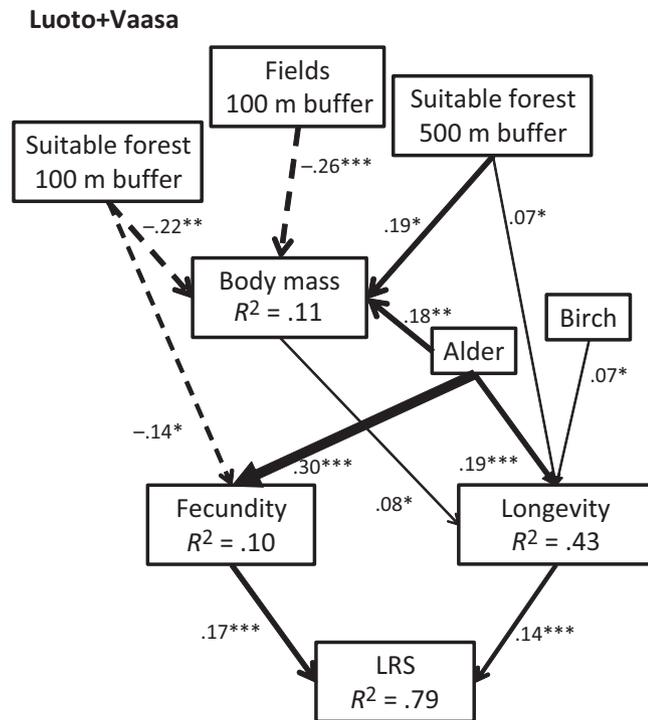


FIGURE 3 Path model of the relationship between habitat variables (suitable forest habitat and agricultural fields within 500 m buffers), food variables (lifetime availability of alder *Alnus* spp. pollen and birch *Betula* spp. catkins), female flying squirrel winter body mass, fecundity, longevity and lifetime reproductive success (LRS) for Luoto and Vaasa study sites combined. For statistically significant paths, line thickness indicates the strength of the relationship with thick lines representing stronger effects. Solid lines indicate positive relationships while dashed lines indicate negative relationships. Note that this analysis was done for the reduced dataset ($n = 213$) for individuals with data for winter body mass. Numeric values show the standardised path coefficients and R^2 -values are reported for each path, • indicate significance at $p < .1$, * indicate significance at $p < .05$, ** indicate significance at $p < .01$, *** indicate significance at $p < .001$

positively affected by availability of birch catkins and alder pollen, as well as the amount of suitable forest within the 500 m buffer. These variables together explained about 43% of the variation in longevity. Fecundity, on the other hand, was explained by a strong positive effect of alder availability and a negative effect of amount of suitable forest within the 100 m buffer. However, only 10% of the variability in fecundity was explained. LRS was only directly affected by fecundity and longevity, which explained about 79% of the variation in LRS.

When study areas were analysed separately body mass did not have detectable effects, but was weakly affected by alder in Luoto and negatively by fields in Vaasa (Table S5, Figure 4). Suitable forest within the 500 m buffer had a positive effect on longevity in Luoto, but no effects in Vaasa (Table S5, Figure 4). Of the food availability variables, lifetime availability of alder was the main determinant of fecundity and longevity at both study sites, although model fit for fecundity in Vaasa was poor (Figure 4). Instead, birch availability had no detectable effects (Table S5, Figure 4). LRS was equally explained by variation in fecundity and longevity at both sites (Table S5, Figure 4).

4 | DISCUSSION

Lifetime mast availability mainly determined fecundity, longevity and LRS of female Siberian flying squirrels. Cover of suitable habitat did not have strong effects, but at landscape scale (cover within the 500 m buffer) suitable habitat had positive effects on body mass, longevity or fecundity, and at local scale (100 m buffer) no or negative effects. This discrepancy may reflect the preference for edge habitat at the local scale, whereas at the landscape scale the amount of forests may be important for the settlement process of female flying squirrels.

Only a few long-term studies have assessed the direct link between LRS and habitat, and these studies concentrate on birds (e.g. Laaksonen, Hakkarainen, & Korpimäki, 2004; Newton, 1985) and large ungulates (reviewed in Gaillard et al., 2010). Our study supports the view that determining habitat quality requires careful evaluation of individual performance, in particular, for species that rely on pulsed resources. The rare mast events have an obvious importance for lifetime fitness (e.g. Bieber & Ruf, 2009; Millon et al., 2010; Wauters et al., 1995), and often the effect of food is mediated through longevity (Bérubé et al., 1999; Bieber & Ruf, 2009; Wauters & Dhondt, 1995). In our case, availability of alder had a strong effect on both fecundity and longevity at both study sites while availability of birch catkins only affected longevity when considering both sites together. This partial difference in response paths and effect strength for birch and alder is logical since birch is the main winter food of flying squirrels possibly affecting winter survival (Mäkelä, 1996), whereas alder is cached and is important for fuelling production of second litters (Selonen & Wistbacka, 2016). Our results are in partial contrast to our initial expectations for the importance of longevity for reproductive success. For example, in North American red squirrels (McAdam, Boutin, Sykes, & Humphries, 2007) longevity of females was the major factor behind population growth rate. In our case, the equal contribution of fecundity and longevity on LRS may be related to the fact that most individuals seem to be short-lived, and short-lived individuals breeding in a mast year may still have a high fecundity. However, survival probabilities for flying squirrels may be smaller than for some other tree squirrels (Lampila et al., 2009), which may explain some of the differences between flying squirrels and North American tree squirrels.

Interestingly, the cover of suitable forest habitat did not explain variation in LRS directly, with non-conclusive positive effects of cover within a 500-m radius of nest boxes on longevity and negative effects of cover within a 100-m radius on fecundity (Table 1, Figure 3, and Figure 4). This is quite surprising for an arboreal forest species (e.g. Reunanen et al., 2002; Santangeli et al., 2013a; see also, Holloway & Smith, 2011) that is expected to experience better shelter and higher food availability in mature spruce-dominated forests (Mönkkönen, Reunanen, Nikula, Inkeröinen, & Forsman, 1997; Reunanen, Mönkkönen, & Nikula, 2000). Our results were also robust against alternative definitions of suitable habitat. As indicated by the positive effect of large-scale habitat cover (500 m buffer) relative to local habitat cover (100 m buffer), the cover of forests might be more important for the initial acceptance of a site as female flying squirrels settle for breeding. We did not test for habitat selection in this study, and

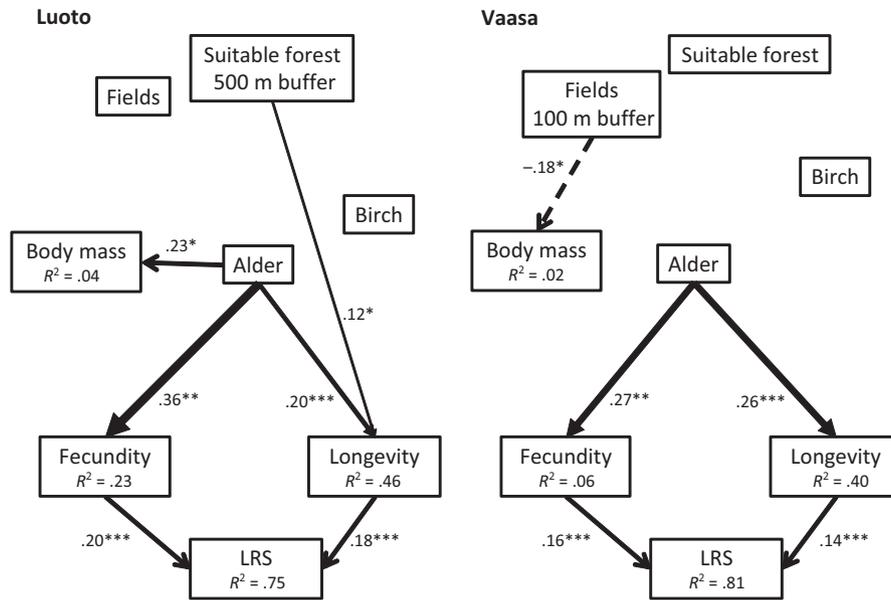


FIGURE 4 Path models of the relationship between habitat variables (suitable forest habitat and agricultural fields within 500 m buffers), food variables (lifetime availability of alder *Alnus* spp. pollen and birch *Betula* spp. catkins), female flying squirrel winter body mass, fecundity, longevity and lifetime reproductive success (LRS) for the Luoto and Vaasa study sites separately. For statistically significant paths, line thickness indicates the strength of the relationship with thicker lines representing stronger effects. Solid lines indicate positive relationships while dashed lines indicate negative relationships. Note that this analysis was done for the reduced dataset ($n = 213$) for individuals with data for winter body mass. Numeric values show the standardised path coefficients and R^2 -values are reported for each path, • indicate significance at $p < .1$, * indicate significance at $p < .05$, ** indicate significance at $p < .01$, *** indicate significance at $p < .001$

all nesting sites were located within suitable habitats, although with varying amount (on average 4 ha forest patches, see Appendix S1). This being the case, the local forest cover did not affect individual breeding parameters. An important resource provided by mature and old growth forests for birds and other species of flying squirrels is the availability of cavities (Bai & Mühlenberg, 2008; Holloway & Malcolm, 2006; Imbeau, Mönkkönen, & Desrochers, 2001). The availability of natural nesting sites in our study populations is low (c. 0.1 cavities/ha based on 742 spruce forest hectares surveyed within our study areas), partially due to forest management practises removing, for example, aspen, and have been replaced by nest boxes. Thus, we had decoupled the availability of nesting sites from other habitat characteristics. These features of the physical habitat, availability of tall trees for gliding and shelter, probably reflect variation in perceived predation risk.

Characteristics of the physical habitat of a species are often highly coupled with food availability, which is evident from the niche-based definition of habitat which includes the resources and environmental factors that define the presence and persistence of a species in a given locality (reviewed in Gaillard et al., 2010). In our study, however, we were able to compare the relative importance of the physical habitat and food availability separately. The important food sources, alder and other deciduous trees, are known pioneer species that often occur at forest edges, which may explain the affinity of flying squirrels to forest/field edges (Desrochers, Hanski, & Selonen, 2003) and shoreline forests (R. Wistbacka, unpublished data). These results support the notion that flying squirrels cope well with forest fragmentation (Santangeli et al., 2013a; Selonen & Hanski, 2004), and do not necessarily need large forest areas for breeding. However, it is clear that

the area of 0.03–0.07 ha of forest (corresponding to 10–15 m radius) that recent Finnish guidelines require to be preserved around breeding or resting flying squirrel locations is not sufficient to ensure a viable and breeding population of flying squirrels (Jokinen, Mäkeläinen, & Ovaskainen, 2015; Santangeli et al., 2013b). Our study supports the view that the currently inefficient management rules might quite easily be improved with a little bit more planning and preserving larger uncut areas around flying squirrel nest sites. The total area of forest cover needed cannot be evaluated from this study, or the above mentioned studies, and needs further investigation.

Our results indicate a possibly regional difference in fitness response to landscape structure. At Vaasa, landscape scale cover of agricultural fields negatively affected winter body mass according to the path analysis, but not in Luoto (Figure 4). In Luoto, where the cover of fields are lowest, the addition of field edges may act as a resource and predictor of suitable habitat for food where the likelihood of finding birch, aspen and alder are higher. In Vaasa, where the cover of fields within buffers is more extensive, fields may act more as a feature that increases fragmentation, and therefore reduces the long-term body condition of female flying squirrels. The positive effect of fields on flying squirrels was not as clear in our study as the association with occupancy reported previously (Santangeli et al., 2013a). However, the positive association between field edges and flying squirrel occupation is likely related with food availability (Santangeli et al., 2013a), which we analysed separately from fields, and suggests fields may be an indicator of general food availability on a larger scale. Interestingly, the effect of body mass, which is correlated with reproductive success in our data (see Appendix S3) and in other arboreal squirrels (Wauters, Bijmens, &

Dhondt, 1993; Wauters & Dhondt, 1989, 1995), had only a minor effect on our path analysis. This perhaps indicates that body mass correlation with reproduction is mainly mediated through food availability.

Conclusively, we show that the occurrence of masting events of tree species during a flying squirrel female's lifetime, affecting lifetime availability of food, have a profoundly larger effect on LRS than the cover of suitable forest habitat. The importance of mast for LRS may have far reaching consequences for population dynamics (Ostfeld & Keesing, 2000), source-sink dynamics (Pulliam, 1988), habitat selection (Wauters et al., 2008) and optimal foraging (Boutin et al., 2006) of the species. Identifying the cause of variation in life-history traits linked with lifetime fitness is important for guiding and improving conservation of this species as fitness is tightly coupled with population growth and viability through stochastic events (Shaffer, 1981). Our study emphasises the importance of both fecundity and longevity, and the indirect effects of food availability via those components, as determinants of lifetime fitness of female flying squirrels.

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AUTHORS' CONTRIBUTIONS

V.S. conceived ideas for the study; R.W. collected the data; K.H. and A.V. analysed the data; K.H. and V.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.mr11t> (Hoset, Villers, Wistbacka, & Selonen, 2017). Since Siberian flying squirrels are of conservation value, any data that potentially reveals exact locations of breeding individuals are omitted from the data package.

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