



HAL
open science

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

Katrine S. Hoset, Alexandre Villers, Ralf Wistbacka, Vesa Selonen

► **To cite this version:**

Katrine S. Hoset, Alexandre Villers, Ralf Wistbacka, Vesa Selonen. Pulsed food resources, but not forest cover, determines lifetime reproductive success in a forest-dwelling rodent. *Journal of Animal Ecology*, 2017, 86 (5), pp.1235-1245. 10.1111/1365-2656.12715 . hal-01595206

HAL Id: hal-01595206

<https://hal.science/hal-01595206v1>

Submitted on 25 May 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

DR KATRINE S. S. HOSET (Orcid ID : 0000-0002-1371-012X)

Article type : Standard Paper

Handling Editor: Jean-Michel Gaillard

Section heading: Behavioural Ecology

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

Katrine S. Hoset^{*1}, Alexandre Villers^{2,3}, Ralf Wistbacka⁴, Vesa Selonen¹

¹ Section of Ecology, Department of Biology, University of Turku, FI-20014 Turku, Finland.

² Centre d'Etudes Biologiques de Chizé, UMR 7372, CNRS & Université de La Rochelle, 79360 Villiers-en-Bois, France

³ Biostatistics and Spatial Processes Unit, INRA, Domaine Saint-Paul, Site Agroparc 84914 Avignon Cedex 9

⁴ Department of Biology, FI-90014 University of Oulu, Finland

* Corresponding author: katrine.hoset@nord.no, Current address: Science section, Nord University, 7600 Levanger, Norway

Running title: LRS in Siberian flying squirrels

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/1365-2656.12715

This article is protected by copyright. All rights reserved.

SUMMARY

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 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 data set 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 smaller role. The path analysis indicated that lifetime food availability had direct effect on longevity and fecundity, and these had equal effect on LRS at both study sites.
5. Our results on LRS shows that the occurrence of tree masting events during a flying squirrel female's lifetime have profoundly larger effect on lifetime reproductive success 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 of female flying squirrels.

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

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 (Van Horne 1983; Gaillard *et al.* 2010). 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 *et al.* 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 (Clutton-Brock 1988; Newton 1989; Brommer *et al.* 2004). 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 (Wauters, Suhonen & Dhondt 1995;

Bérubé, Festa-Bianchet & Jorgenson 1999; Bieber & Ruf 2009). Habitat quality or habitat use are often important determinants of LRS in both birds (Herman & Colwell 2015) and mammals (McLoughlin *et al.* 2006; Bieber & Ruf 2009; Regan *et al.* 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., Clutton-Brock 1988; Newton 1989; Bérubé *et al.* 1999, but see Gaillard *et al.* 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 (Hokkanen, Törmälä & Vuorinen 1982; Hanski 2006; Selonen *et al.* 2010) and possible role as umbrella species potentially indicating biodiversity values in old growth forests (Hurme *et al.* 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 *et al.* 2013b). Understanding how habitat characteristics and food availability contribute to the variation in LRS, lifespan 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 suitable habitat, but species also seem to cope well with fragmentation (Selonen & Hanski 2004; Santangeli, Hanski & Mäkelä 2013a).

In this paper, we take advantage of a 22 year-long longitudinal data set 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 lifetime reproductive success (LRS) of this forest specialist. Further, 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 (Selonen, Hanski & Stevens 2001; Hurme *et al.* 2008; Santangeli *et al.* 2013a; 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. Further, 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 e.g. Bérubé *et al.* (1999).

MATERIAL AND METHODS

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 at both sites is about 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: $72 \pm 130\text{m}$, average natal dispersal distance: $1830 \pm 1390\text{m}$, 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 *et al.* 2001, 2013). Annual local apparent survival in our populations is about 0.43-0.53 (Lampila *et al.* 2009), and although most females disappear from the population after their first breeding season (probably from death, and not breeding dispersal, Selonen & Wistbacka 2017; Brommer, Wistbacka & Selonen 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).

Study sites and CMR 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, $63^{\circ}3'\text{N}$, $21^{\circ}41'\text{E}$). The marking of flying squirrels started in 1992 in Vaasa within an area of 400ha, after 2000 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 ($63^{\circ}49'\text{N}$, $22^{\circ}49'\text{E}$; 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 (CMR) data has 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 2–4 nest-boxes per site, with an average of 2 nest-boxes per mature spruce forest hectare. Box occupancy percentage by the flying squirrel was low (~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 per hectare 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 presence of breeding females 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 1 breeding season, 1 female skipped 2 seasons, and 17 individuals (3.6%) were not observed breeding until second year after birth. Many of these females were likely not breeding as radio-tracking 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 *et al.* 2016; Selonen & Wistbacka 2016).

Food availability data

The flying squirrel feeds in 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 (Sulkava & Sulkava 1993; Mäkelä 1996). 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 *et al.* 2005, 2008; Selonen *et al.* 2016). Weather conditions during previous summer determine birch mast; catkin production increase 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 $r \approx 0.7$. Consequently, this index is able to properly describe the yearly variation in catkin production in the area.

There was 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 was 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 m³ 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.

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/opendata>). 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 x 25m pixels grid) on a yearly basis (see method details in Morosinotto *et al.* 2017).

We defined buffer zones around each nest box at 100m and 500m distances and calculated the total area of each land cover class within each buffer of active nest boxes for each study year. The 100m buffer (3.14 ha) represent the core area available for daily use (average distance moved per night: 111 ± 33 m, Hanski *et al.* 2000), with a size about half of an average annual female home range (ca 7 ha, Selonen *et al.* 2001). The 500m 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 Development Core Team, 2016).

The original land cover classes were combined to represent biological relevant classes for flying squirrels (Table S1 in Supporting Information 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 100m and 500m 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 habitat for the species (e.g., Reunanen, Mönkkönen & Nikula 2002; Santangeli *et al.* 2013a), and also presence of agricultural fields, likely due to 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, e.g. including patch size measured from aerial photographs, see Appendix S1).

Statistical analyses

All statistical calculations were conducted using R version 3.3.0 (R Development Core Team, 2016). Data exploration was applied following Zuur *et al.* (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/m³ 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 31-1857 catkins per birch tree and 47-3000 alder pollen per m³ 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 females since food availability early in life can have important consequences for future reproductive success (Gaillard *et al.* 2000b; Descamps *et al.* 2008). 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 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 lifetime reproductive success (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-models 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-model.

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 average winter body mass (measured at captures from September until March) of females as an explanatory factor in addition to the above mentioned co-variables (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, i.e. 6 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 versus fitted values to assess homogeneity of variance, and the residuals versus 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 non-linear effects. However, none of the best models obtained included non-linear terms. We followed a hierarchal approach where we tested, 1) whether food and habitat variables explained winter body mass, 2) how food and habitat variables and winter body mass explained fecundity and longevity, and finally 3) 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.

RESULTS

LRS

Lifetime reproductive success (LRS, 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 < 0.001) and fecundity ($r_p = 0.594$ [0.535, 0.648], $t_{498} = 16.49$, p -value < 0.001). Average longevity (number of breeding seasons) was 1.82 ± 0.08 (\pm standard error) 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 non-linear 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 $R^2 = 0.517$).

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 $R^2 = 0.06$).

Longevity was best explained by a non-linear 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 100m buffer (Table 1). The model explained about 55% of the variation in longevity (adjusted $R^2 = 0.545$).

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 100m buffer had negative effects on female winter body mass, while suitable forest within the 500m buffer and alder availability had positive effects on winter body mass. However, body mass had only weak effect on longevity, and no effects on fecundity or LRS (Table S5). Longevity was positively affected by availability of birch catkins and alder pollen, as well as the amount of suitable forest within the 500m 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 100m 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 500m 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).

DISCUSSION

Lifetime mast availability mainly determined fecundity, longevity and lifetime reproductive success of female Siberian flying squirrels. Cover of suitable habitat did not have strong effects, but at landscape scale (cover within the 500m buffer) suitable habitat had positive effects on body mass, longevity or fecundity, and at local scale (100m 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 lifetime reproductive success and habitat, and these studies concentrate on birds (e.g., Newton 1985; Laaksonen, Hakkarainen & Korpimäki 2004) 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., Wauters *et al.* 1995; Bieber & Ruf 2009; Millon *et al.* 2010), and often the effect of food is mediated through longevity (Wauters & Dhondt 1995; Bérubé *et al.* 1999; Bieber & Ruf 2009). 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 *et al.* 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 500m radius of nest boxes on longevity and negative effects of cover within 100m 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 *et al.* 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 (500m buffer) relative to local habitat cover (100m 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 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 (Imbeau, Mönkkönen & Desrochers 2001; Holloway & Malcolm 2006; Bai & Mühlenberg 2008). The availability of natural nesting sites in our study populations is low (ca 0.1 cavities per hectare based on 742 spruce forest hectares surveyed within our study areas), partially due to forest management practices 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 (Selonen & Hanski 2004; Santangeli *et al.* 2013a), 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 10-15m 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 (Santangeli *et al.* 2013b; Jokinen, Mäkeläinen &

Ovaskainen 2015). 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 & Dhondt 1989; Wauters, Bijmens & Dhondt 1993; Wauters & Dhondt 1995), had only minor effect in 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 profoundly larger effect on lifetime reproductive success 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.

Authors' contributions. VS conceived ideas for the study; RW collected the data; KH and AV analysed the data; KH and VS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements. We thank all of the field workers Pasi Reunanen, Rune Jakobsson, Antero Mäkelä and Markus Sundell, who have assisted during data gathering. Research adhered to all applicable international, national, and/or institutional guidelines for the care and use of animals under several project licences issued by the Finnish Animal Experiment Board (project licence no., 2002-2006: Dnr LSU-2002-L-265(254), 2007-2011: Dnr LSU-2007-L-573(254), 2012-2016: Dnr EPOELY/412/07.01/2012). The study was financially supported by Academy of Finland (grant number 259562 to VS), Oskar Öflunds Stiftelse (to RW), Societas Pro Fauna et Flora Fennica (to RW), Svensk-Österbottniska Samfundet (to RW), and Vuokon luonnonsuojelusäätiö (to RW).

Data accessibility

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.mr11t> (Hoset *et al.* 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.

REFERENCES

- Bai, M.-L. & Mühlenberg, M. (2008) Sequential use of holes by birds breeding in a natural boreal forest in Mongolia. *Bird Study*, **55**, 161–168.
- Bartoń, K.A. (2016) *MuMIn: Multi-Model Inference*.
- Bérubé, C.H., Festa-Bianchet, M. & Jorgenson, J.T. (1999) Individual Differences, Longevity, and Reproductive Senescence in Bighorn Ewes. *Ecology*, **80**, 2555–2565.
- Bieber, C. & Ruf, T. (2009) Habitat differences affect life history tactics of a pulsed resource consumer, the edible dormouse (*Glis glis*). *Population Ecology*, **51**, 481–492.
- Boutin, S., Wauters, L.A., McAdam, A.G., Humphries, M.M., Tosi, G. & Dhondt, A.A. (2006) Anticipatory Reproduction and Population Growth in Seed Predators. *Science*, **314**, 1928–1930.
- Brommer, J.E., Gustafsson, L., Pietiäinen, H. & Merilä, J. (2004) Single-Generation Estimates of Individual Fitness as Proxies for Long-Term Genetic Contribution. *The American Naturalist*, **163**, 505–517.
- Brommer, J.E., Wistbacka, R. & Selonen, V. (2017) Immigration ensures population survival in the Siberian flying squirrel. *Ecology and Evolution*, **7**, 1858–1868.
- Clutton-Brock, T.H. (ed). (1988) *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*. University of Chicago Press.
- Colwell, M.A., Burrell, N.S., Hardy, M.A., Kayano, K., Muir, J.J., Pearson, W.J., Peterson, S.A. & Sesser, K.A. (2010) Arrival times, laying dates, and reproductive success of Snowy Plovers in two habitats in coastal northern California. *Journal of Field Ornithology*, **81**, 349–360.
- Delibes, M., Gaona, P., Ferreras, P. & Doak, A.E.D.F. (2001) Effects of an Attractive Sink Leading into Maladaptive Habitat Selection. *The American Naturalist*, **158**, 277–285.
- Descamps, S., Boutin, S., Berteaux, D., McAdam, A.G. & Gaillard, J.-M. (2008) Cohort effects in red squirrels: the influence of density, food abundance and temperature on future survival and reproductive success. *Journal of Animal Ecology*, **77**, 305–314.

- Desrochers, A., Hanski, I.K. & Selonen, V. (2003) Siberian flying squirrel responses to high- and low-contrast forest edges. *Landscape Ecology*, **18**, 543–552.
- Gaillard, J.-M., Festa-Bianchet, M., Delorme, D. & Jorgenson, J. (2000a) Body mass and individual fitness in female ungulates: bigger is not always better. *Proceedings of the Royal Society of London B: Biological Sciences*, **267**, 471–477.
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. (2000b) Temporal Variation in Fitness Components and Population Dynamics of Large Herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–393.
- Gaillard, J.-M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M. & Moorter, B.V. (2010) Habitat–performance relationships: finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2255–2265.
- Grafen, A. (1988) On the uses of data on lifetime reproductive success. *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (ed T.H. Clutton-Brock), pp. 454–463. University of Chicago Press.
- Hanski, I.K. (2006) *Liito-Oravan Pteromys Volans Suomen Kannan Koon Arviointi. Loppuraportti*. Luonnontieteellinen Keskusmuseo, Helsingin yliopisto.
- Hanski, I.K. & Selonen, V. (2009) Female-biased natal dispersal in the Siberian flying squirrel. *Behavioral Ecology*, **20**, 60–67.
- Hanski, I.K., Stevens, P.C., Ihalempiä, P. & Selonen, V. (2000) Home-Range Size, Movements, and Nest-Site Use in the Siberian Flying Squirrel, *Pteromys volans*. *Journal of Mammalogy*, **81**, 798–809.
- Herman, D.M. & Colwell, M.A. (2015) Lifetime reproductive success of Snowy Plovers in coastal northern California. *The Condor*, **117**, 473–481.
- Hokkanen, T. (2000) Seed crops and seed crop forecasts for a number of tree species. *Forest regeneration in the northern parts of Europe. Proceedings of the Finnish-Russian Forest Regeneration Seminar in Vuokatti, Finland, 28 Sept.–2nd Oct. 1998* (eds E. Mälkönen, N.A. Babich, V.I. Krutov & I.A. Markova), p. Metsäntutkimuslaitoksen tiedonantoja - The Finnish Forest Research Institute, Research Papers 790.
- Hokkanen, H., Törmälä, T. & Vuorinen, H. (1982) Decline of the flying squirrel *Pteromys volans* l. populations in Finland. *Biological Conservation*, **23**, 273–284.
- Holloway, G.L. & Malcolm, J.R. (2006) Sciurid Habitat Relationships in Forests Managed Under Selection and Shelterwood Silviculture in Ontario. *The Journal of Wildlife Management*, **70**, 1735–1745.
- Holloway, G.L. & Smith, W.P. (2011) A meta-analysis of forest age and structure effects on northern flying squirrel densities. *The Journal of Wildlife Management*, **75**, 668–674.
- Hoset, K.S., Villers, A., Wistbacka, R. & Selonen, V. (2017) Data from: Pulsed food resources, but not forest cover, determines lifetime reproductive success in a forest-dwelling rodent. *Dryad Digital Repository*. doi:10.5061/dryad.mr11t

- Hurme, E., Mönkkönen, M., Sippola, A.-L., Ylinen, H. & Pentinsaari, M. (2008) Role of the Siberian flying squirrel as an umbrella species for biodiversity in northern boreal forests. *Ecological Indicators*, **8**, 246–255.
- Imbeau, L., Mönkkönen, M. & Desrochers, A. (2001) Long-Term Effects of Forestry on Birds of the Eastern Canadian Boreal Forests: a Comparison with Fennoscandia. *Conservation Biology*, **15**, 1151–1162.
- Jin, S. & Sader, S.A. (2005) Comparison of time series tasseled cap wetness and the normalized difference moisture index in detecting forest disturbances. *Remote Sensing of Environment*, **94**, 364–372.
- Jokinen, M., Mäkeläinen, S. & Ovaskainen, O. (2015) ‘Strict’, yet ineffective: legal protection of breeding sites and resting places fails with the Siberian flying squirrel. *Animal Conservation*, **18**, 167–175.
- Kendall, B.E. & Wittmann, M.E. (2010) A Stochastic Model for Annual Reproductive Success. *The American Naturalist*, **175**, 461–468.
- Laaksonen, T., Hakkarainen, H. & Korpimäki, E. (2004) Lifetime reproduction of a forest-dwelling owl increases with age and area of forests. *Proceedings of the Royal Society of London B: Biological Sciences*, **271**, S461–S464.
- Lampila, S., Wistbacka, R., Mäkelä, A. & Orell, M. (2009) Survival and Population Growth Rate of the Threatened Siberian Flying Squirrel (*Pteromys volans*) in a Fragmented Forest Landscape. *Écoscience*, **16**, 66–74.
- Mäkelä, A. (1996) Liito-oravan (*Pteromys volans* L.) ravintokohteet eri vuodenaikoina ulosteanalyysin perusteella. *WWF Finland Reports*, **8**, 54–58.
- McAdam, A.G., Boutin, S., Sykes, A.K. & Humphries, M.M. (2007) Life histories of female red squirrels and their contributions to population growth and lifetime fitness. *Écoscience*, **14**, 362–369.
- McLoughlin, P.D., Boyce, M.S., Coulson, T. & Clutton-Brock, T. (2006) Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1449–1454.
- Mikkola, A., Jaakkola, O. & Sucksdorff, Y. (1999) The Slices-project: National classification of land use, land cover and soil, and the production of databases. *The Finnish Environment*, **342**, 1–86.
- Millon, A., Petty, S.J. & Lambin, X. (2010) Pulsed resources affect the timing of first breeding and lifetime reproductive success of tawny owls. *Journal of Animal Ecology*, **79**, 426–435.
- Mönkkönen, M., Reunanen, P., Nikula, A., Inkeröinen, J. & Forsman, J. (1997) Landscape Characteristics Associated with the Occurrence of the Flying Squirrel *Pteromys volans* in Old-Growth Forests of Northern Finland. *Ecography*, **20**, 634–642.

- Morosinotto, C., Villers, A., Thomson, R.L., Varjonen, R. & Korpimäki, E. (2017) Competitors and predators alter settlement patterns and reproductive success of an intraguild prey. *Ecological Monographs*, **87**, 4–20.
- Newton, I. (1985) Lifetime Reproductive Output of Female Sparrowhawks. *Journal of Animal Ecology*, **54**, 241–253.
- Newton, I. (1989) *Lifetime Reproduction in Birds*. Academic.
- Ostfeld, R.S. & Keesing, F. (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology & Evolution*, **15**, 232–237.
- Pulliam, H.R. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652–661.
- Ranta, H., Hokkanen, T., Linkosalo, T., Laukkanen, L., Bondestam, K. & Oksanen, A. (2008) Male flowering of birch: Spatial synchronization, year-to-year variation and relation of catkin numbers and airborne pollen counts. *Forest Ecology and Management*, **255**, 643–650.
- Ranta, H., Oksanen, A., Hokkanen, T., Bondestam, K. & Heino, S. (2005) Masting by *Betula*-species; applying the resource budget model to north European data sets. *International Journal of Biometeorology*, **49**, 146–151.
- Regan, C.E., Pilkington, J.G., Pemberton, J.M. & Crawley, M.J. (2016) Sex differences in relationships between habitat use and reproductive performance in Soay sheep (*Ovis aries*). *Ecology Letters*, **19**, 171–179.
- Reunanen, P., Mönkkönen, M. & Nikula, A. (2000) Managing Boreal Forest Landscapes for Flying Squirrels. *Conservation Biology*, **14**, 218–226.
- Reunanen, P., Mönkkönen, M. & Nikula, A. (2002) Habitat requirements of the Siberian flying squirrel in northern Finland: comparing field survey and remote sensing data. *Annales Zoologici Fennici*, **39**, 7–20.
- Robertson, B.A. & Hutto, R.L. (2006) A Framework for Understanding Ecological Traps and an Evaluation of Existing Evidence. *Ecology*, **87**, 1075–1085.
- Santangeli, A., Hanski, I.K. & Mäkelä, H. (2013a) Integrating multi-source forest inventory and animal survey data to assess nationwide distribution and habitat correlates of the Siberian flying squirrel. *Biological Conservation*, **157**, 31–38.
- Santangeli, A., Wistbacka, R., Hanski, I.K. & Laaksonen, T. (2013b) Ineffective enforced legislation for nature conservation: A case study with Siberian flying squirrel and forestry in a boreal landscape. *Biological Conservation*, **157**, 237–244.
- Selonen, V. & Hanski, I.K. (2004) Young flying squirrels (*Pteromys volans*) dispersing in fragmented forests. *Behavioral Ecology*, **15**, 564–571.
- Selonen, V., Hanski, I.K. & Stevens, P.C. (2001) Space use of the Siberian flying squirrel *Pteromys volans* in fragmented forest landscapes. *Ecography*, **24**, 588–600.

- Selonen, V., Hanski, I.K. & Wistbacka, R. (2014) Communal nesting is explained by subsequent mating rather than kinship or thermoregulation in the Siberian flying squirrel. *Behavioral Ecology and Sociobiology*, **68**, 971–980.
- Selonen, V., Painter, J.N., Rantala, S. & Hanski, I.K. (2013) Mating system and reproductive success in the Siberian flying squirrel. *Journal of Mammalogy*, **94**, 1266–1273.
- Selonen, V., Sulkava, P., Sulkava, R., Sulkava, S. & Korpimäki, E. (2010) Decline of flying and red squirrels in boreal forests revealed by long-term diet analyses of avian predators. *Animal Conservation*, **13**, 579–585.
- Selonen, V. & Wistbacka, R. (2016) Siberian flying squirrels do not anticipate future resource abundance. *BMC Ecology*, **16**, 51.
- Selonen, V. & Wistbacka, R. (2017) Role of breeding and natal movements in lifetime dispersal of a forest-dwelling rodent. *Ecology and Evolution*, **7**, 2204–2213.
- Selonen, V., Wistbacka, R. & Korpimäki, E. (2016) Food abundance and weather modify reproduction of two arboreal squirrel species. *Journal of Mammalogy*, **97**, 1376–1384.
- Shaffer, M.L. (1981) Minimum Population Sizes for Species Conservation. *BioScience*, **31**, 131–134.
- Shipley, B. (2009) Confirmatory path analysis in a generalized multilevel context. *Ecology*, **90**, 363–368.
- Sulkava, P. & Sulkava, R. (1993) Liito-oravan ravinnosta ja ruokailutavoista Keski-Suomessa [Feeding habits of flying squirrels; in Finnish]. *Luonnon tutkija*, **97**, 136–138.
- Van Horne, B. (1983) Density as a Misleading Indicator of Habitat Quality. *The Journal of Wildlife Management*, **47**, 893–901.
- Wauters, L., Bijmens, L. & Dhondt, A.A. (1993) Body Mass at Weaning and Juvenile Recruitment in the Red Squirrel. *Journal of Animal Ecology*, **62**, 280–286.
- Wauters, L. & Dhondt, A.A. (1989) Body Weight, Longevity and Reproductive Success in Red Squirrels (*Sciurus vulgaris*). *Journal of Animal Ecology*, **58**, 637–651.
- Wauters, L.A. & Dhondt, A.A. (1995) Lifetime Reproductive Success and Its Correlates in Female Eurasian Red Squirrels. *Oikos*, **72**, 402–410.
- Wauters, L.A., Githiru, M., Bertolino, S., Molinari, A., Tosi, G. & Lens, L. (2008) Demography of alpine red squirrel populations in relation to fluctuations in seed crop size. *Ecography*, **31**, 104–114.
- Wauters, L.A., Suhonen, J. & Dhondt, A.A. (1995) Fitness Consequences of Hoarding Behaviour in the Eurasian Red Squirrel. *Proceedings of the Royal Society of London B: Biological Sciences*, **262**, 277–281.
- Wood, S. & Scheipl, F. (2014) *Gamm4: Generalized Additive Mixed Models Using Mgcvm and Lme4*.

Yee, T.W. (2017) *VGAM: Vector Generalized Linear and Additive Models*.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, **1**, 3–14.

The following Supporting Information is available for this article online:

Table S1. Habitat classification.

Table S2. Availability of habitat classes within buffer zones.

Table S5. Standardized coefficients and statistics for path analysis

Figure S1. Habitat classification.

Appendix A1. Analysis of patch size effects on LRS

Appendix A2. Analysis of LRS assuming Generalized Poisson distributed error terms

Appendix A3. Analysis of LRS, fecundity and longevity on data including body mass, including path analysis

Appendix A4. Model selection tables

TABLES

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 non-linear terms and coefficients are not reported.

	coeff ± se	Statistic	p-value
LRS			
Intercept	1.070 ± 0.055	z = 19.451	P < 0.001
Site	0.122 ± 0.053	z = 2.317	P = 0.021
Fields 500m	0.009 ± 0.005	z = 1.874	P = 0.061
Fields 500m:site	-0.012 ± 0.005	z = -2.223	P = 0.026
Sum birch catkins*		$\chi^2_{2.8} = 121.28$	P < 0.001
Sum alder pollen*		$\chi^2_{3.2} = 33.99$	P < 0.001
Fecundity			
Intercept	1.868 ± 0.083	t = 22.471	P < 0.001
Site	0.453 ± 0.111	t = 4.085	P < 0.001
Sum alder pollen	0.214 ± 0.055	t = 3.877	P < 0.001
Longevity			
Intercept	0.504 ± 0.040	z = 12.708	P < 0.001
Fields 100m	-0.125 ± 0.066	z = -1.889	P = 0.059
Sum birch catkins*		$\chi^2_{2.6} = 21.36$	P < 0.001
Sum alder pollen*		$\chi^2_{1.8} = 41.85$	P < 0.001

FIGURE LEGENDS

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 yellow = agricultural land, green tones = forests) where red points indicate the approximate spread and location of nest boxes available for flying squirrels during the study period.

Figure 2. Observed lifetime reproductive success (LRS) as a function of A) lifetime sum of alder (*Alnus* spp.) pollen concentration in 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 $LRS \sim \exp(s(\text{maximum food availability measure}, k=3))$ 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 500m 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 data set (n= 213) for individuals with data for winter body mass. Numeric values show the standardised path coefficients and R²-values are reported for each path, • indicate significance at p < 0.1, * indicate significance at p < 0.05, ** indicate significance at p < 0.01, *** indicate significance at p < 0.001.

Figure 4. Path models of the relationship between habitat variables (suitable forest habitat and agricultural fields within 500m 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 data set (n= 213) for individuals with data for winter body mass. Numeric values show the standardised path coefficients and R²-values are reported for each path, • indicate significance at p < 0.1, * indicate significance at p < 0.05, ** indicate significance at p < 0.01, *** indicate significance at p < 0.001.

FIGURES

Figure 1.

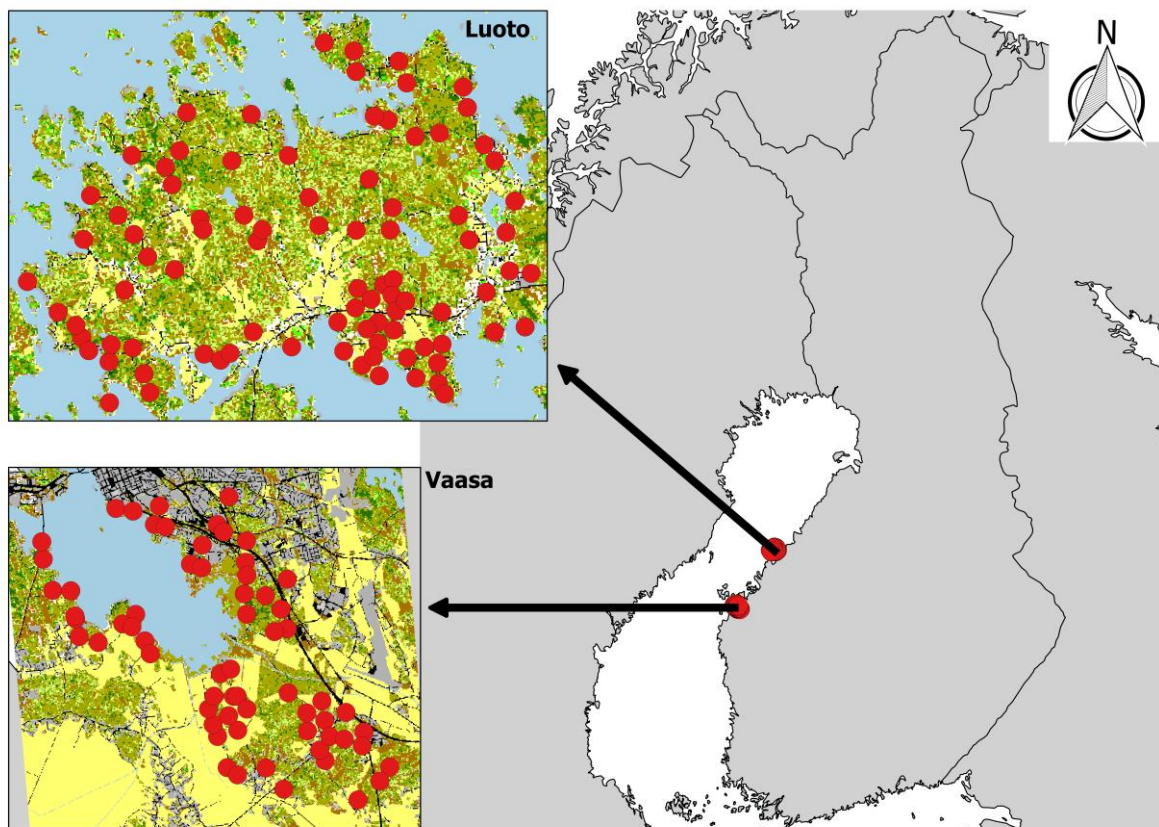


Figure 2.

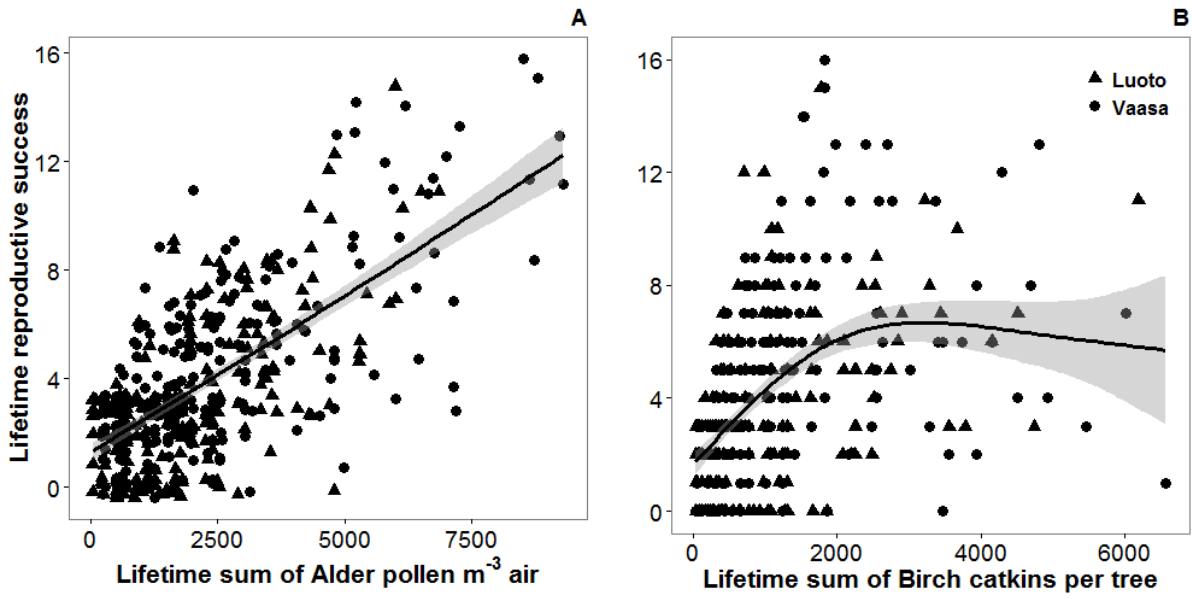


Figure 3.

Luoto + Vaasa

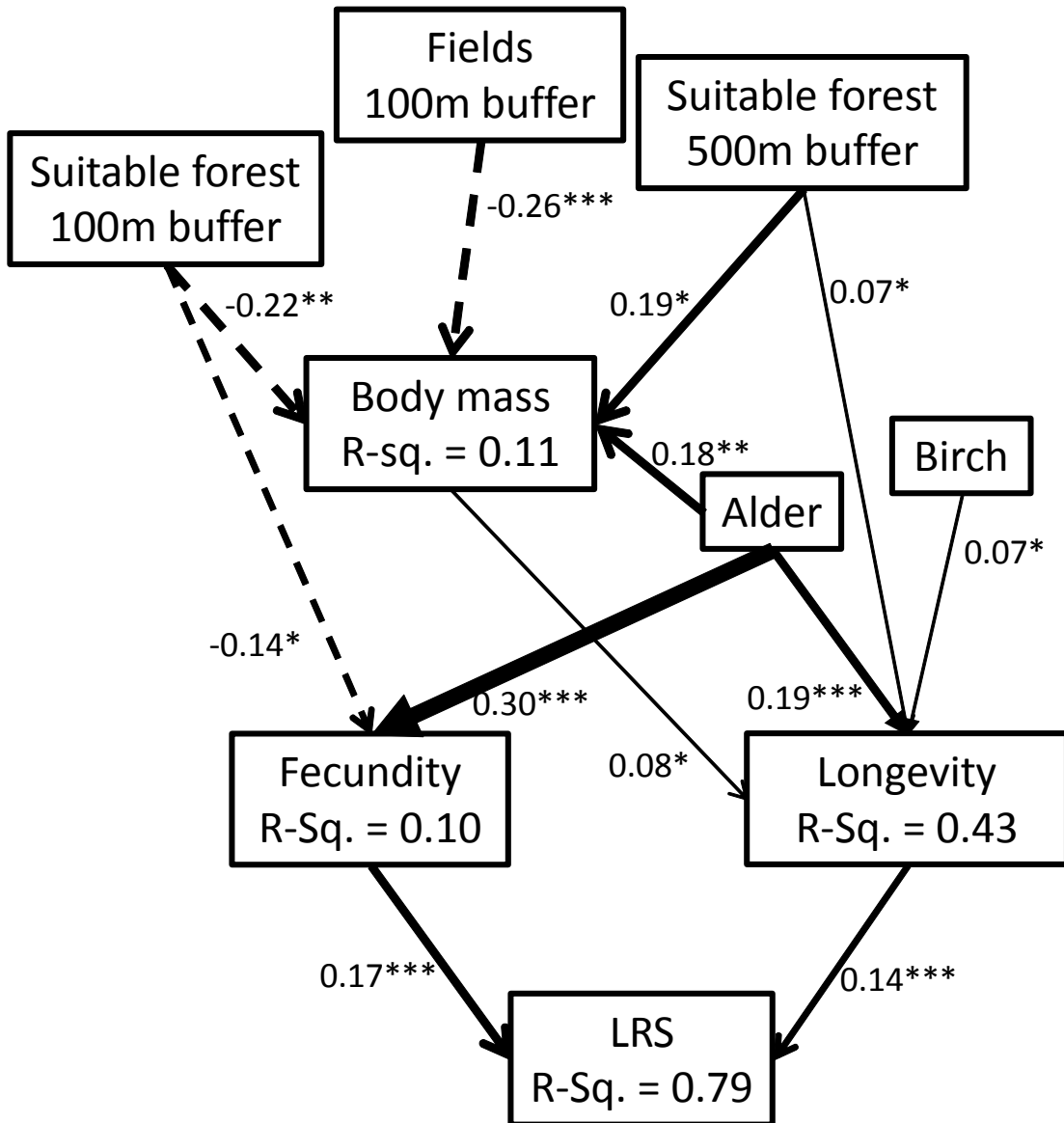


Figure 4.

