Food abundance and weather modify reproduction of two arboreal squirrel species

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The importance of weather in relation to food resources, in determining reproduction, remains poorly understood for mammals, particularly for species that do not depend on food resources limited by spring weather conditions. We studied the effects that weather and food supply had on timing of spring reproduction and observed litter size in 2 squirrel species, the Siberian flying squirrel and the European red squirrel, using long-term data sets spanning 20–30 years. Both species subsist on foods from tree masting, and these are available for squirrels from autumn until early spring. Good food conditions in winter and spring before reproduction had positive effects on spring reproduction in both species by advancing the onset of reproduction, and in flying squirrels, slightly increasing litter size. Higher temperature in late winter and, surprisingly, increased precipitation in late winter resulted in early reproduction in flying squirrels and red squirrels, respectively. In addition, higher early spring temperature was positively related to litter size in red squirrels, likely reflecting low survival of small juveniles in cold weather. Our study supports the view that spring reproduction in these species is determined by food supply before breeding. Our results also highlight the fact that reproduction is also dependent on weather.

Key words: climate change, demographic responses, masting, resource pulse

Despite wide interest in effects of weather on reproduction (Van Vuren and Armitage 1991; Sheriff et al. 2011; Lane et al. 2012; Gaillard et al. 2013; Boutin and Lane 2014), the importance of weather conditions in relation to food resources in determining reproduction remains poorly understood (Bronson 2009; Lehikoinen et al. 2011; Millon et al. 2014; Terraube et al. 2014). It can be predicted that species that fuel reproduction using food limited by recent weather conditions, such as grazers depending on spring plant growth (Post and Forchhammer 2008) or insectivorous birds (Eeva et al. 2000), are greatly affected by spring weather conditions. Alternatively, species that use food that is not dependent on current weather conditions may be less affected by weather during breeding attempts (Stephens et al. 2009; Lehikoinen et al. 2011; Millon et al. 2014; Terraube et al. 2014).

Effects of food on reproduction have been studied intensively in European and North American red squirrels (Wauters and Lens 1995; Boutin et al. 2006; Wauters et al. 2008 Williams et al. 2014; Selonen et al. 2015). Red squirrel population size tracks seed production by trees (Gurnell 1983; Boutin et al. 2006; Selonen et al. 2015) and both current and future food

levels affect reproduction (Boutin et al. 2006; Wauters et al. 2008; Selonen et al. 2015). Future food levels are observed to correlate with juvenile production in summers preceding mast, as mother squirrels may anticipate the autumn's seed production (Boutin et al. 2006; Wauters et al. 2008; Williams et al. 2014). However, in European red squirrels, production of spring litters is dependent only on current and past, and not future, resource levels (Wauters and Lens 1995; Wauters et al. 2008; Selonen et al. 2015, but for North American red squirrels, see Boutin et al. 2006). Effects of weather are less studied than effects of food on reproduction by squirrels. For North American red squirrels, Williams et al. (2014) concluded that the effect of food supersedes the effect of spring weather in explaining reproduction by North American red squirrels (*Tamiasciurus hudsonicus*). However, warmer spring temperatures may increase juvenile survival in North American red squirrels (Studd et al. 2015).

In this study, we focused on spring reproduction of the Siberian flying squirrel (*Pteromys volans*) and the European red squirrel (*Sciurus vulgaris*). For both species, the masting of trees used as food creates resource pulses in the forest (Ranta

et al. 2005; Pukkala et al. 2010; Selonen et al. 2015). Both flying and red squirrels use these food resources from winter until the beginning of spring before reproduction (Hanski et al. 2000; Selonen et al. 2015). Thus, we predicted that flying squirrels and red squirrels would respond similarly to variation in food levels before reproduction. The Siberian flying squirrel feeds on birch (*Betula* sp.), alder (*Alnus* sp.), and aspen (*Populus tremula*) in our study areas (Hanski et al. 2000; V. Selonen and R. Wistbacka, pers. obs.). During winter and early spring, birch and alder catkins are the main food (Mäkelä 1996; Hanski et al. 2000). Birch catkins form the main part of the winter diet (80% of food consumed, based on diet analysis of fecal samples—Mäkelä 1996, for possible biases in fecal samples, see Flaherty et al. 2010), whereas alder catkins are preferred over birch based on analysis of use versus availability (Sulkava and Sulkava 1993; Mäkelä 1996). In addition, flying squirrels store alder catkins in cavities, nest-boxes, and on tree branches (Sulkava and Sulkava 1993; Mäkelä 1996; Hanski et al. 2000). Catkins develop in summer, and flying squirrels start to consume them in autumn. Catkins remain in trees, and flying squirrels continue eating the catkins during the following winter and early spring when the catkins flower. Catkin production varies considerably between years (Hokkanen 2000; Ranta et al. 2005, 2008; Supporting Information S1) and increases when the previous summer has been warm, but trees seldom manage to produce mast for 2 successive years (Ranta et al. 2005). After the opening of leaves in the beginning of May, leaves form the main diet of flying squirrels in late spring and summer (Mäkelä 1996). However, during pregnancy and parturition, females are still dependent on catkin production and stores, because mating season starts in mid-March and first litters are born in late April.

The main food source for European red squirrels in European boreal forests is the seeds of the Norway spruce (*Picea abies*—Rajala and Lampio 1963; Gurnell 1983; Selonen et al. 2015). In Finland, red squirrels may start to consume developing cones in July–August (Rajala and Lampio 1963; V. Selonen, pers. obs.), and they continue to do so during the following winter and early spring, when the seeds fall to the ground. Red squirrels are known to store cones of coniferous trees (Wauters et al. 1995), although the significance of this behavior is unclear in our study areas, where squirrels mostly consume cones directly in trees. In boreal forests in Finland, red squirrels also eat seeds of pine, *Pinus sylvestris* (spruce and pine are the only trees used by red squirrels in Finnish boreal forests), but they are less preferred than spruce seeds. Spruce mast every few years, where peak years are followed by years with low cone production (see Pukkala et al. 2010; Selonen et al. 2015). The flowering of spruce, similar to the aforementioned case of birch, is determined by weather conditions in the previous summer (Pukkala et al. 2010). However, cone production is also related to other factors, such as spring weather conditions, which influence pollination. The first litters of the red squirrels observed in the current analysis are usually born in March–April.

We studied the roles that weather conditions and food resources, before and during reproduction, played in spring reproduction (the effect of future resource levels were omitted because they do not affect spring reproduction in our species and are analyzed elsewhere—Selonen et al. 2015; V. Selonen and R. Wistbacka, pers. obs.). That is, we observed litter size and estimated parturition based on the size of juveniles at the point of capture. We used long-term data sets spanning 20–30 years and data on yearly variation in main resource levels in winter and early spring. In an earlier study, we reported that high cone production in the previous winter advances timing of reproduction of red squirrels (Selonen et al. 2015; see also Wauters et al. 2008). Our hypothesis is that the same is true for flying squirrels. We predict that 1) increased food supply in winter to early spring advances timing of reproduction and increases observed litter size in the subsequent spring. For both study species, we further predict 2) that cold temperatures in winter and spring lower body condition of mothers and, thus, decrease the observed litter size and delay the timing of reproduction. In addition, decreasing precipitation in winter (snow cover) may affect squirrel reproduction, e.g., by affecting food quality of squirrels.

MATERIALS AND METHODS

Study Areas and Data Collection

Our studies on flying squirrels and red squirrels involved individuals living in nest-boxes in study areas located in western Finland. Flying squirrels nest in tree cavities, nest-boxes, and dreys in spruce-dominated boreal forests. We know of no obvious behavioral or reproductive differences between individuals living in nest-boxes and those living in natural cavities (Selonen et al. 2014; V. Selonen, pers. obs.), nor are we aware of significant differences in predator communities between study areas. The observed flying squirrels lived in nest-boxes with entrance-hole diameters of 4.5 cm. This entrance-hole size prevents the main predators (pine martens, *Martes martes*, and large owls) from entering the nest-box. The entrance-hole diameter of red squirrel boxes was 8–10 cm, which does not prevent pine martens from entering the box.

Flying squirrels.—Studies involving flying squirrels were carried out in 2 areas: Luoto (63°49′N, 22°49′E) and Vaasa (63°3′N, 22°41′E). In Luoto, flying squirrels were studied from 1993 to 2014 within an area of 44 km². The main forest types in Luoto are shoreline spruce-dominated mixed forests, clear-cuts, and cultivated Scots pine forests. The Vaasa study area is located about 90 km southwest of Luoto. We marked flying squirrels starting in 1992 in Vaasa within an area of 400 ha; after 2000, the area was 25 km². Vaasa is covered by spruce forest patches, clear-cuts, and agricultural fields (for more information, see Lampila et al. 2009; Selonen et al. 2014).

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 hectare of mature spruce forest. Natural cavities were rare in our study areas (R. Wistbacka, pers. obs.). Flying squirrels are known to frequently change nest sites (individuals can use 8–10 different nests yearly). In our case, box occupancy by the flying squirrel was low (25%, i.e., in 15,596 nest-box checks, occupancy by a flying squirrel was noted 3,946 times); that is, in most cases, a nest-box was empty when

checked. Thus, we assert that the number of nest-boxes was not so large that it affected the social structure of the flying squirrel population, because density of individuals remained low. Flying squirrels were captured by hand from nest-boxes, sexed, weighed, and marked with ear-tags (Hauptner 73850, Hauptner, Germany). The nest-boxes were checked systematically during 2 sessions, once in June and once in August. During June sessions, 1st litter juveniles were on average 59 ± 11 g. Juveniles of this size are still strictly dependent on the natal nest and do not generally move outside the natal nest (V. Selonen, pers. obs.).

Red squirrels.—The red squirrel study was carried out in the Kauhava region in western Finland (63°5′N, 23°4′E) in a study area of ca. 1,300 km². The landscape consisted of forests (70%), agricultural land (20%), and peatland bogs (10%) (Korpimäki and Hakkarainen 1991, 2012). Forests were either pine-dominated or spruce-dominated, although many forest sites were mixed to some extent, containing pine, spruce, and some deciduous trees. The red squirrels were observed in nest-boxes between 1982 and 2014. Red squirrels frequently occupy nest-boxes when they are available for roosting and nesting (Shuttleworth 1999; Korpimäki and Hakkarainen 2012; Bosch and Lurz 2013; Selonen et al. 2015). Nest-boxes were evenly distributed in forests across the study area, including both pine-dominated and spruce-dominated forests, at an average density of about 1 box per 200 ha. They were checked during late March through April and again in mid-May through June each year (for more information, see Korpimäki and Hakkarainen 1991, 2012; Selonen et al. 2015).

Food Abundance Indices

For flying squirrels, we used estimates from an annual birch catkin survey conducted by the Finnish Forest Research Institute (Hokkanen 2000). These data were collected to describe nationwide pollen conditions in Finland. Birch catkins were assessed in winter using 15 permanent research observation stands, where catkins from 30 to 50 birches per stand were counted. Observations were made repeatedly from the same individual trees (Hokkanen 2000). For the Vaasa study area, the closest sampling site (Vaasa) was located within our study area. There was no sampling site within the Luoto study area. The closest sampling site was in Vaasa, 90 km from Luoto. Thus, we used Vaasa indices for both study areas. Previous analyses of these catkin data revealed a strong correlation between 2 sampling sites at this distance ($r \approx 0.7$). Catkin production of deciduous trees is spatially correlated at scales of up to a few hundred kilometers in Finland (Ranta et al. 2008). Thus, although the food index is less accurate for Luoto than it is for Vaasa, it still adequately describes the yearly variation in catkin production in the area. Both study areas were located in the same larger coastal area and had very similar weather conditions (Supporting Information S1).

There was no catkin count data for alder and aspen, but as a proxy, we used aerial pollen estimates, which correlate with catkin production (Ranta et al. 2008). Pollen data were collected by the aerobiology unit at University of Turku. Pollen samples were collected from 10 different locations 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). As with the birch catkin data, we used the Vaasa sampling site for both study areas.

For red squirrels, we used spruce cone production estimates based on annual cone surveys conducted by the Finnish Forest Research Institute (Hokkanen 2000). The cones were counted annually in late summer from as many as 37 seed crop observation stands in different areas of Finland. Cones were counted for 50 spruce trees with dominant crowns near each stand (Hokkanen 2000). The same trees were used each year and were classified into 7 groups according to cone abundance (I: no cones, II: 1–20 cones, III: 21–50 cones, IV: 51–100 cones, V: 101–200 cones, VI: 201–500 cones, VII: more than 500 cones). The annual cone abundance indices were calculated by taking the arithmetic mean of all trees (Hokkanen 2000; Pukkala et al. 2010). We used a cone production estimate for the south Ostrobothnia region, where the Kauhava study area is located. Spruce cone production is spatially correlated at scales of up to a few hundred kilometers in Finland (Ranta et al. 2010).

Weather Indices

We used weather information from the weather station (maintained by the Finnish Meteorological Institute) nearest each study area. For Kauhava and Vaasa, the closest weather station was located within our study area, and for Luoto, it was 10 km southeast of the study area. Weather recording stations were at the same elevation as the study areas. Monthly average weather indices from the previous November thorough May was used to explain squirrel reproduction. Based on the biology of the study species (mating occurs in late winter and reproduction in spring), we selected the following time periods for our analysis: early winter, late winter, and spring (Table 1). For spring weather, instead of monthly average temperatures, we used 1) the starting date of the growing season and 2) effective temperature sum (sum of temperatures above +5°C) in April and May (see Table 1). These indices were assumed to describe spring conditions better than average temperatures, although we also tested the effect of temperature in April–May. Temperatures consistently above +5°C indicate the beginning of growing season (Finnish Meteorological Institute; http://en.ilmatieteenlaitos.fi/seasons-in-finland) and have also been shown to correlate with birch bud burst in Finland (Rousi and Heinonen 2007).

Estimate of Parturition and Litter Size

We did not observe litter size at birth, thus the observed litter size reflects that at birth and mortality of juveniles before capture. Similarly, the exact parturition date was not known, as juveniles were observed at ages of approximately 3–4 weeks.

For flying squirrels, estimating parturition date from body mass was complicated, because the exact growth curve is unknown. Thus, we used body mass at capture to estimate body mass on the 15th of June (time-corrected body mass; Table 2). The time-corrected body mass was calculated as an average for

Table 1.—Description of all variables used for explaining reproduction in flying squirrels (*Pteromys volans*) and red squirrels (*Sciurus vulgaris*).

Variable	Unit	Average ± SD, min, max	Description
Food data			
Flying squirrel			
Birch catkins	Catkins per tree	434 ± 450, 30, 1,860	Estimate from an annual birch catkin survey for Vaasa region
Alder pollen	Pollen in 1 m³ of air	950 ± 820, 40, 3,500	Aerial pollen estimate for Vaasa region (correlates with catkin production)
Aspen pollen	Pollen in 1 m³ of air	146 ± 163, 6, 630	Same as above
Red squirrel			
Spruce cones	Cones per tree	21 ± 26, 0, 70	The annual cone abundance index for Ostrobothnia region
Weather data			
Early winter temperature	°C	−4 ± 3.3, −11, 4	Mean temperature in December–January
Late winter temperature	°C	−4.7 ± 2.8, −9.3, 0	Mean temperature in February–March
Start date of the growing season	Day	26th of April ± 7 days, 16th of April, 12th of May	Date after which the average daily temperature in spring was permanently above +5°C
Effective temperature sum in April and May (spring)	Sum of degrees °C	April: 16 ± 11, 0, 39; May: 115 ± 50, 44, 246	The sum of degrees that in daily average temperature were above 5°C in a given month
Early winter precipitation	mm/month	42 ± 13, 15, 71	Mean rain in December–January
Late winter precipitation	mm/month	28 ± 11, 10, 44	Mean rain in February–March
Spring precipitation	mm/month	29 ± 12, 4, 62	Mean rain in April–May

Table 2.—Descriptive data for red squirrels (*Sciurus vulgaris*) and flying squirrels (*Pteromys volans*) litters.

	Years	No. of nest-boxes	Number of litters per year[a]	Average litter size[a]	Parturition index	SD in parturition index[b]
Flying squirrel					Time-corrected body mass	
Vaasa	1992–2014	200–400[c]	17.7 ± 9.9	2.5 ± 0.7	58.8 ± 10.8 g, n = 403	Within years = 8.4, between years = 5.3
Luoto	1993–2014	300–400	14.1 ± 5.2	2.4 ± 0.7	61.8 ± 9.4 g, n = 292	Within years = 9.0, between years = 4.9
Red squirrel					Estimated parturition	
Kauhava	1982–2014[d]	400–500	14 ± 12	4.0 ± 1.3	20th of March ± 11 days, n = 288	Within years = 21.4, between years = 11.0

[a] Average and SD for yearly values.
[b] Average SD within years and SD calculated between years.
[c] 200 before 2002, 400 after 2002.
[d] We lacked data for red squirrels for years 1983, 1985, 1988, 1991, 1995, 1996, 1998, 1999, 2000, and 2004.

each litter and was used as an index of parturition date. This calculation was based on an average daily growth of 0.8 g, observed in body mass measurements for 176 juvenile flying squirrels in this study (the same average daily growth was observed in Selonen and Hanski 2010). For these data, year had no significant effect on growth (176 observations over 19 years: $F_{18,175} = 1.14$, $P = 0.32$). In these data, there was no significant relationship between growth of juveniles and food resources available in the preceding winter/spring (general linear model with year as random variable and number of days between observations, sex, birch, and alder as explanatory variables; effect of alder on observed growth: estimate $−0.03 ± 0.04$, $F_{21,27} = 0.59$, $P = 0.45$; birch: estimate $−0.04 ± 0.04$, $F_{21,27} = 1.15$, $P = 0.29$). Thus, our parturition index reflects birth date of individuals rather than growth differences due to food availability.

The red squirrels in this study were not weighed, but the developmental stage of juveniles was evaluated visually and categorized using the following descriptions: newborn, hairless, fur but eyes not open, eyes open, small juvenile (< 100 g), and large juvenile (> 100 g). We estimated average parturition date (Table 2) for each red squirrel litter using these descriptors. Newborn red squirrels are covered with pelage at 21 days, their eyes open at 28–32 days, juveniles start moving out of the nest at 40–45 days, and they are weaned at 8–10 weeks (Lurz et al. 2005). We believe this approach allowed a comparison of parturition dates between red squirrel litters born in different years. It is known that timing of parturition in squirrels can vary considerably between years, even over 1 month (Williams et al. 2014). We omitted years without sufficient data to estimate developmental stage of juveniles (1983, 1985, 1988, 1991, 1995, 1996, 1998, 1999, 2000, and 2004). Sample size differs from that used in Selonen et al. (2015), because possible second litter juveniles were omitted from the current analysis. Second litter juveniles were apparent after the initial juveniles that were found were already large (> 100 g), and these started to appear in mid-May (Selonen et al. 2015). Variation in parturition index within a year was not related to food levels that preceded reproduction (estimate $0.003 ± 0.003$, $F_{21,27} = 1.1$, $P = 0.29$; or with weather variables, analysis not shown), indicating that birth dates of individuals used in the analysis were comparable between years.

Analyses

Despite obvious correlations between weather variables, the explanatory variables were relatively independent of each other. To minimize collinearity between variables, we did not include both the birch and start of growing season variables in the same flying squirrel model or both the rain in early winter and temperature in late winter variables in the same red squirrel model. Inclusion of these variables resulted in a variance inflation factor (VIF) > 4 (Proc Reg, SAS 9.3; SAS Institute, Cary, North Carolina). Removal of these correlated variables produced VIF values < 2. We checked for temporal trends by assessing correlations between weather and reproduction variables and year (analyzed with linear models using GLIMMIX, SAS). We found no significant temporal effects in our reproduction data (see "Results"). Thus, we did not consider possible spurious correlations arising when trends occurred both in the response and the explanatory variables (Grosbois et al. 2008).

To analyze effects on reproduction we used multimodel inference based on Akaike's information criterion (AIC). If there was no single clear best fit model or parameter, we used model averaging (using cutoff ΔAIC of 10 and including all models where the term of interest appeared—Burnham and Anderson 2002). We considered a parameter to be statistically significant in explaining squirrel reproduction if its coefficient and associated 95% confidence interval (*CI*) did not include zero (Burnham and Anderson 2002).

We built generalized linear mixed models using Procedure GLIMMIX (SAS). Explanatory variables were the resource and weather variables described above (Table 1). The study areas (Luoto and Vaasa) were always included as a class variable in the flying squirrel models. We tested interaction effects and quadratic terms, but if no significant improvement in model fit (ΔAIC > 2) was observed, they were omitted from the final models. We tested the effect of maternal age for flying squirrels, but we did not have these data for all individuals (298 out of 506 mothers). In the model for these 298 individuals, maternal age was not significant and was omitted from further analysis (effects of age on flying squirrel reproduction will be analyzed elsewhere).

Parturition index.—Analyses for time-corrected body mass (flying squirrel) or parturition index (red squirrel) of litters as a dependent variable were done assuming log-normal distributions and with year as a random factor using Kenward–Roger estimated degrees of freedom (Kenward and Roger 1997). In addition to year, maternal id (flying squirrel) or nest-box id (to control for repeated measures from 1 nest-box site for red squirrel) was included as a random factor in the analysis. We tested the effect of litter size in the models, but the litter size was omitted from final models because it was not litter size at birth (see above) and did not affect results obtained for other studied variables.

Litter size.—For analyses with litter size as a dependent variable, we used a Poisson distribution and the year and maternal id (flying squirrel) or nest-box id (red squirrel; we did not have knowledge on mother id for red squirrel) as a random factor using the Laplace approximation (see Stroup 2012). Because

age of juveniles potentially affects observed litter size, we included body mass (flying squirrel) or developmental stage (red squirrel) at the time of capture in the model for litter size analysis.

Our research conformed to the guidelines for research on wild mammals of the American Society of Mammalogists (Sikes et al. 2011).

RESULTS

Over the years of our study, there was a trend of increasing temperature in May in the Vaasa/Luoto study area (year correlated against effective temperature sum in May; Supporting Information S1), but not for the Kauhava study area. Otherwise, no positive or negative temporal trends could be observed in our weather data (Supporting Information S1). Neither litter size nor parturition index was related to year for either flying squirrels (litter size estimate = −0.0002 ± 0.005, $F_{1,41} = 0.01$, $P = 0.96$; parturition index estimate = 0.003 ± 0.002, $F_{1,41} = 2.29$, $P = 0.14$) or red squirrels (litter size estimate = 0.0053 ± 0.0043, $F_{1,23} = 1.5$, $P = 0.23$; parturition index estimate = 0.026 ± 0.02, $F_{1,20} = 1.68$, $P = 0.21$). Variation in parturition index was larger within years than between years (Fig. 1; Table 2). For flying squirrels, time-corrected body mass was correlated between Luoto and Vaasa study areas ($r^2 = 0.26$, $P = 0.01$).

Effects of Food

In both studied squirrel species, food availability before reproduction was related to the parturition index of litters (Fig. 2). The best supported models explaining time-corrected body mass (index for parturition) of juvenile flying squirrels included alder pollen (estimated in spring, reflecting catkins available during the previous winter; Supporting Information S2) and, based on model averaging, alder pollen had a significant positive relationship to time-corrected body mass (Fig. 2A; coefficient 0.035, 95% *CI* = 0.01–0.062). When time-corrected body mass is considered as the difference in time of parturition (assuming 0.8 g daily growth, see "Materials and Methods"), there was an average increase of 12 days from the poorest to the richest catkin production years (Fig. 2A). Similarly for red squirrels, spruce cones (measured during the previous fall and available for squirrels until spring; Supporting Information S2) were in the best supported model and, based on model averaging, had a significant positive effect on parturition estimates (Fig. 2D; coefficient −0.09, 95% *CI* = −0.03 to −0.16). The average advancement in parturition time from the poorest to the richest cone production years was around 17 days (Fig. 2D).

Food availability before reproduction was related to litter size of flying squirrels, but this was not the case with red squirrels (Supporting Information S2). The top ranked models explaining litter size for flying squirrels included both birch catkins and alder pollen (Supporting Information S2). Based on model averaging, birch catkins had a positive effect on litter size (Fig. 2C; coefficient 0.044, 95% *CI* = 0.003–0.086), but the relationship of alder was not statistically significant (coefficient 0.038, 95% *CI* = −0.01 to 0.087).
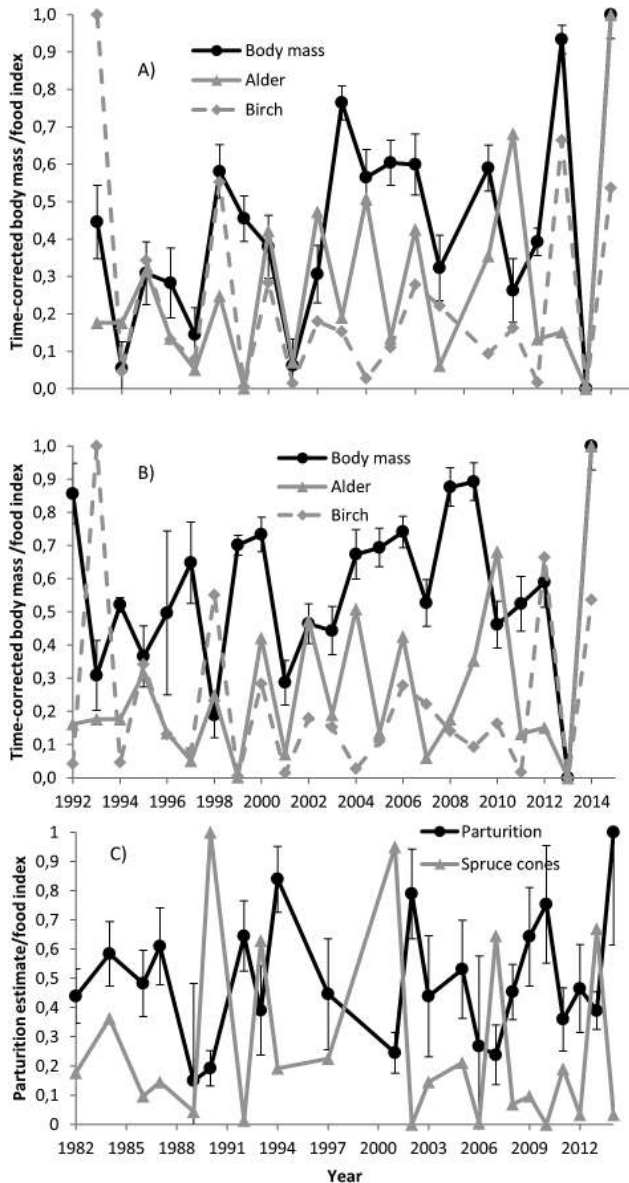
Figure 1.—Yearly variation in juvenile flying squirrel (*Pteromys volans*) time-corrected body mass (average for a litter on 15 June; yearly average and 95% confidence interval), alder pollen estimate (a proxy for catkin production) and birch catkin production estimate in the A) Luoto and B) Vaasa study areas. C) Red squirrels' (*Sciurus vulgaris*) estimated parturition in the Kauhava study area and spruce cone production estimate. Note that in the data for red squirrels, there are several missing years, see Table 2. All data are scaled to values between 0 and 1.

Effects of Weather

For flying squirrels, late winter temperature and early winter precipitation were included in the best supported models for time-corrected body mass (Supporting Information S2). Based on model averaging, increasing temperatures in late winter had a slight positive effect (advanced parturition at maximum 9 days; Fig. 2B; coefficient 0.12, 95% *CI* = 0.001–0.24; early winter rain: coefficient 0.13, 95% *CI* = −0.13 to 0.38). For red squirrels, the best supported models in explaining estimated parturition included late winter rain (Supporting Information S2) that,

based on model averaging, had a significant effect (coefficient −0.18, 95% *CI* = −0.03 to −0.33). That is, greater precipitation in late winter (snow; Fig. 2E) indicated earlier parturition in red squirrels (advanced parturition to at most 22 days in Fig. 2E).

Weather had no obvious effect on flying squirrel litter size (Supporting Information S2), but all best supported models for red squirrel litter size included temperature in April (effective temperature sum; Supporting Information S2) that, based on model averaging, had a positive effect on red squirrel litter size (Fig. 2F; coefficient 0.09, 95% *CI* = 0.02–0.15).

DISCUSSION

We found that both food resources before reproduction and winter and early spring weather affected spring reproduction by Siberian flying squirrels and European red squirrels. Siberian flying squirrels responded similar to observed patterns for squirrels in other studies (Boutin et al. 2006; Wauters et al. 2008; Williams et al. 2014; Selonen et al. 2015), advancing the timing of spring reproduction when food abundance before reproduction was high. Early parturition may be positively related to fitness advantages later in life, as observed in North American red squirrels (Williams et al. 2014). For flying squirrels, we also found a slight increase in spring litter sizes when food was abundant before reproduction. This may indicate either decreased survival of very small juveniles (before we observed them) or smaller litter sizes in spring with low food abundance. Spruce cone production was not related to litter size of red squirrels in spring of the same year. However, based on our earlier analysis, the proportion of nests with litters is higher after spruce cone mast (Selonen et al. 2015), and it is known that low resource abundance situations may result in lower rates of reproduction for both European and North American red squirrels (Gurnell 1983; Boutin et al. 2006).

Our results are consistent with the patterns for ground squirrels (Sheriff et al. 2011, 2013), grazers dependent on spring plant growth (Post and Forchhammer 2008), and insectivorous birds (Eeva et al. 2000) that weather conditions before and during breeding have clear effects on reproduction. In our study, early spring weather affected only red squirrels, but winter weather correlated with reproduction in both species. This was surprising because we expected spring weather to have some effect on flying squirrels. This species eats leaf material (Sulkava and Sulkava 1993; Mäkelä 1996) that develops relative to spring temperatures (Rousi and Heinonen 2007) and thus a pattern was expected. However, only temperatures in late winter influenced parturition indices of flying squirrels. Mating season begins in late winter (average starting March 15 in our study areas; V. Selonen and R. Wistbacka, pers. obs.) and advanced timing of the mating season in warm weather might explain the relationship between parturition index and late winter temperature. It should be noted that during our study of flying squirrels, cold winters were not very common (Supporting Information S1). In addition, the only observed weather trend during our study was that of warming spring temperatures, which is consistent with earlier reports for climate change in Finland during the period of our study (Mikkonen et al. 2015).
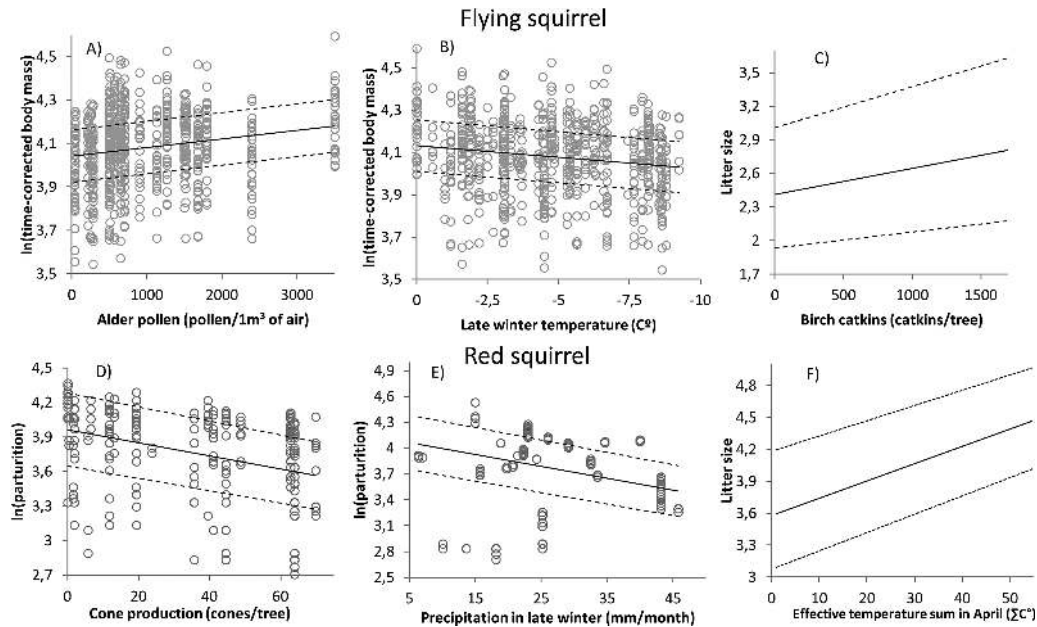
Figure 2.—Predicted effects of A) alder pollen and B) late winter temperature on time-corrected body mass (high values indicating earlier parturition) in flying squirrels (*Pteromys volans*). C) Effect of birch catkins on the size of spring born litters in flying squirrels. D) Effect of spruce cones and E) rain in late winter on estimated parturition in red squirrels (*Sciurus vulgaris*). F) Effect of temperature in April on the size of spring born litters in red squirrels. Line based on predicted values, upper and lower lines for confidence interval, from best fit model based on multimodel inference (Supporting Information S2). Gray dots for raw data (lacking for C and F, because litter size was not a continuous variable).

Interestingly, in the case of red squirrels, increased precipitation (snow) in late winter had a positive effect on the parturition index. Parturition advanced even slightly more in response to changes in late winter precipitation than in response to changes in spruce cone production (22 versus 17 days). However, based on AIC values, spruce cone production was the parameter best explaining parturition in red squirrels. The mechanism underlying the correlation between late winter rain and parturition is unclear for red squirrels. One explanation could be that when winter snow melts, it enhances moisture conditions in early spring, which influences plant growth in the beginning of spring. That is the period between the end of pregnancy and parturition for red squirrels. Juvenile mammals are most sensitive to variations in environmental conditions just after birth (Gaillard et al. 2000), and red squirrels must supplement their diets with food items other than seeds in spring, after seeds have fallen from the cones in late winter/early spring. Indeed, differences in snow cover have been observed to influence growth of vegetative buds and shoots in spruce trees (Sutinen et al. 2015), which are an important food item for red squirrels in boreal forests (Rajala and Lampio 1963; Gurnell 1983; Wauters et al. 1992). Finally, our results for red squirrels are consistent with observations for North American red squirrels: Studd et al. (2015) observed that cold spring temperatures increased litter loss. Similarly, our observation of smaller litter sizes in cold springs could be related to reduced survival of small juveniles. Juveniles are likely to be vulnerable to cold before their pelage is fully developed.

Observed relationships in our analyses were modest, particularly for flying squirrels. For example, the correspondence between resource levels and parturition index are less clear for flying squirrels (Figs. 1A and 1B), than for red squirrels (Fig. 1C). This might indicate that red squirrels are greater food specialists than flying squirrels, although as predicted, both species responded to food levels that preceded reproduction. The parturition of red squirrels advanced on average 17 days during ideal food conditions compared to periods when spruce cones were sparse. However, we had no data for the 2 greatest mast years (Supporting Information S1), and it seems likely that the observed response would have been larger if these years had been included. Our parturition indices may not perfectly predict parturition dates, because growth rates of young may vary in response to food supply or weather in the previous year. This may create bias in our parturition date estimates. However, for flying squirrels, food levels that preceded birth did not affect growth (see "Materials and Methods"). This supports the conclusion that observed variation in body mass between individuals was more strongly related to birth date than growth differences between individuals. In any case, data for both species were characterized by a larger intra-annual variance than inter-annual variance (Fig. 2; Table 2). For example, the parturition indices for flying squirrels in both the Luoto and Vaasa study areas were correlated, but only weakly, despite a distance of only 90 km between the 2 areas. This indicates that individual characteristics and local effects on mothers may have a greater effect on production of spring litters than large-scale changes in resource levels and weather. One factor that increases the role of local effects on female reproductive success is the territoriality of females, because territory quality affects breeding success: body condition, body size, and territory quality are factors that affect breeding success of female red squirrels (Wauters and Dhondt 1995). Similarly, in flying squirrels, larger female

body mass has been observed to increase breeding success (Selonen et al. 2013).

In conclusion, our study supports the view that squirrel reproduction in spring is determined largely by food supply before breeding (for other species, see Kerby and Post 2013; Millon et al. 2014; Terraube et al. 2014; Williams et al. 2014). However, squirrel reproduction was dependent not only on food abundance, but also on temperature and precipitation, particularly in winter but also in early spring. In addition, when we consider that summer weather conditions in the year prior to squirrel reproduction influences both catkin and cone production of tree species used (Ranta et al. 2005; Pukkala et al. 2010), we conclude that weather has a major influence on squirrel reproduction. Clearly, our results support the idea that the effects of climate change are more extensive than simple changes in temperature (Ozgul et al. 2010; Regehr et al. 2010; Lane et al. 2012).

Acknowledgments

Supporting Information

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Figures for variation in food levels for the studied squirrels and figures for trends in weather data during the study period.

Supporting Information S2.—Tables for the ranking of the best candidate models in explaining reproduction in flying squirrels and red squirrels.

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