

Effects of food abundance, density and climate change on reproduction in the sparrowhawk *Accipiter nisus*

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Abstract The reproductive success of predators depends on abiotic environmental conditions, food abundance and population density, and food abundance, density and their interactions may respond to changes in climatic conditions. Timing of reproduction by five of the eight numerically most common prey of the sparrowhawk *Accipiter nisus* advanced significantly since 1971, during a period of temperature increase. There was no evidence that mean laying date or any other reproductive parameter of sparrowhawks changed consistently during the study period 1977–1997. Laying date advanced and percentage of unsuccessful female sparrowhawks decreased with beech mast in the current year, an index of food abundance for avian prey. Mean laying date of sparrowhawks was advanced in warmer springs, and although mean clutch size was not larger in warm than in cold springs, mean brood size of successful pairs and breeding success increased in such springs, showing that sparrowhawks enjoyed a fitness gain when reproducing early. The timing of sparrowhawk reproduction with respect to

the peak in abundance of fledgling prey increased, from a good match between mean timing of fledging by prey and maximum demand for food by the predator in 1977, to reproduction occurring later than the peak in fledging prey availability in 1997. The size of the breeding population of sparrowhawks was not predicted by mean spring temperature, the size of the breeding population the previous year or beech mast crop. The size of the post-breeding population was predicted by size of the breeding and post-breeding population the previous year and by the proportion of unsuccessful females the current year. These findings imply that sparrowhawks did not respond to change in climate, although climate changed the timing of reproduction by the main prey species.

Keywords Beech mast · Fecundity · Laying date · Reproductive success · Variance in reproductive success

Introduction

Climate change is currently occurring at an unprecedented rate, with global temperatures having risen by 0.6°C during the last century, with even greater increases predicted for the current century (Houghton et al. 2001). Locally, such as in parts of the temperate and arctic zones, temperatures have increased even more dramatically, with increases in mean temperatures during spring exceeding 3°C in certain areas. Not surprisingly, abundance, distribution and phenology of numerous organisms have shown evidence of consistent response to climate change across the globe (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003;

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Böhning-Gaese and Lemoine 2004; Sæther et al. 2004). Likewise, many studies have investigated effects of climate change on timing of reproduction, clutch size and reproductive success, with significant effects being reported in many different organisms (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Dunn 2004). Several studies have shown that the start of reproduction has advanced considerably during recent decades (Crick and Sparks 1999; Dunn and Winkler 1999; Przybylo et al. 2000; Sanz et al. 2003; Sheldon et al. 2003; Pulido and Berthold 2004; review in Dunn 2004). Such changes can be linked directly to geographic patterns of change in climatic conditions (Dunn and Winkler 1999; Sanz 2002, 2003; Sæther et al. 2003; Visser et al. 2003; Both et al. 2004), providing evidence of fine scale patterns of phenology being determined by fine scale patterns of climate change. Likewise, clutch size, egg size and body size have been shown to change (Järvinen 1989; Winkel and Hudde 1997; Yom-Tov 2001; Møller 2002; Yom-Tov et al. 2002; Dunn 2004; Tryjanowski et al. 2004). While most studies have addressed questions about the effects of climate on mean estimates of phenology or reproductive variables, only a couple of studies have addressed how climate may impact on variance in such variables. Winkler et al. (2002) suggested that changes in laying date during global warming may affect the variance and the mean date of reproduction, and they showed that the variance in laying date of a passerine bird was smaller in the warmest and hence the earliest years.

Studies of the effects of climate change have only just begin to investigate how effects on lower trophic levels affect higher levels (Walther et al. 2002). Few studies have investigated how climate change affects predator–prey and parasite–host interactions, although such effects are widely predicted to be key for understanding community level effects of climate change (Kareiva et al. 1993; Møller and Erritzøe 2002; Mouritsen and Poulin 2002). Theoretical studies suggest that predators and parasites may be particularly susceptible to the effects of climate change due to the direct effects of climate on the distribution and the abundance of prey and host populations, respectively (Kareiva et al. 1993). However, there are only few empirical studies indicating that the ability of hosts to defend themselves against parasites is strongly influenced by environmental conditions (Møller 2002; Møller and Erritzøe 2002). The North Atlantic Oscillation has been shown to affect predator–prey cycles in the Canadian arctic (Rueness et al. 2003). Studies of the great tit *Parus major* and its caterpillar prey have shown increasing mal-adaptation of timing of breeding to maximum availability of prey, providing a cause for concern for

the future of such mis-timed populations (Visser et al. 1998, 2003; Visser and Holleman 2001). Similar effects have been reported for other species (Visser et al. 2004). There is, to the best of our knowledge, no other published information on how raptors respond to climate change in terms of timing of reproduction and reproductive performance relative to timing of availability of prey, although we would a priori expect raptors to track prey both in space and time.

Here, we provide a study of the relationships between climate change and timing of breeding, reproductive success and population size of a small avian predator, which preys on small passerine birds that have been shown to advance their breeding dates considerably during recent decades. The sparrowhawk *Accipiter nisus* is the most common avian predator in forested regions of the Palaearctic. The main prey of this sexually size dimorphic predator is tits, thrushes, finches, buntings and sparrows (Newton 1986). Male sparrowhawks defend breeding territories where they, with the female, build a large nest in early spring (Newton 1986). Females lay a clutch of 3–7 eggs, most frequently 4–5, that are incubated by the female alone (Newton 1986). Males bring all food for the egg laying, incubating and brooding female until the nestlings are 3 weeks old, and most food for older nestlings (Newton 1986). Timing of breeding is determined by food availability during early spring, as suggested by indices of food availability, resulting in an advancement of laying and experimental addition of food advancing laying date (Newton and Marquiss 1981b; Newton 1986). Timing of breeding by the sparrowhawk coincides with the first summer peak in abundance of fledgling prey (Newton 1986), and rates of recruitment by sparrowhawks decreases during the breeding season. Therefore, an advancement of timing in the occurrence of fledgling passerine prey should allow sparrowhawks to advance their reproduction to gain benefits from early reproduction.

The aims of this study were to quantify: (1) how timing of breeding changed in prey of the sparrowhawk and in the sparrowhawk itself; (2) how timing of breeding was related to recent climatic change during spring; (3) how changes in timing of breeding affected reproductive success; (4) how the effects of climate interacted with population density and food abundance to affect reproductive variables; and (5) how these phenomena affected the size of the breeding and the post-breeding population. We did not directly measure the abundance of prey for the sparrowhawk, but used the beech mast index the previous autumn as an estimate of food abundance for finches, tits and other birds that constitute important prey for the sparrowhawk

(Bejer and Rudemo 1985; Jacobsen 1994; Jenni 1987; Källander 1981; Perdeck et al. 2000; Verhulst 1992).

Materials and methods

Study areas

J.T.N. studied sparrowhawks in a 68-km² area around Sindal (57°28'N, 10°10'E) and a 436-km² study area west of Hjørring (57°28'N, 10°00'E), Northern Jutland, Denmark. The first area is open farmland with scattered forests, often connected with hedges. Plantations and forests constitute 16.2% of the area. A total of 95% of plantations and forests are covered with intensively managed conifers. The second study area is mainly intensely cultivated farmland with small plantations sized 2–40 ha. Only 1.9% of the area is covered with forest. The two areas are separated by 8 km.

A total of 937 breeding events of sparrowhawks were followed during the years 1977–1997, with no detailed data available for 1987. The number of breeding pairs varied between 33 and 66, with a decreasing trend due to predation by goshawks *Accipiter gentilis* on the sparrowhawks (J.T. Nielsen and A.P. Møller, unpublished data), while the number of breeding pairs of goshawks varied between 5 and 16.

Estimating laying date of prey

We analysed temporal trends in laying dates of three passerines that represent three different life history strategies. Laying date of the barn swallow *Hirundo rustica*, representing a long distance migrant, was recorded annually from 1971 to 2004 at Kraghede (57°12'N, 10°00'E), Denmark. Details about procedures are described by Møller (2002). The total number of laying dates for first clutches was 1,886.

Laying date for the great tit, representing a resident hole nesting species that is a common prey item of sparrowhawks, was determined for a nest box breeding population at Rødhus (57°12'N, 9°40'E), Denmark, during 1970–2004 by K. Klarborg. Over 100 nest boxes were checked regularly for contents during the period May–June each year, and nestlings were ringed when 5–10 days old. Laying date was estimated as ringing date minus age of nestlings (8 days), duration of the incubation period (14 days) and clutch size (the sum of the number of nestlings and eggs, assuming that one egg is laid daily). We excluded second clutches from these calculations. The total number of laying dates for first clutches was 460.

Laying date for the blackbird *Turdus merula*, representing an open nesting species that is a common prey item for sparrowhawks, was recorded in the same farms where barn swallows were studied. Blackbirds breed commonly inside barns and other farm buildings, and nest contents at Kraghede were checked regularly by A.P.M. (at least weekly) when nests of barn swallows were being checked. We only included nests that were known to be first clutch nests by using the criterion that only the first nest found in a barn each year was included in the data. We have only ever found a single pair breeding in each building, and the same pair often breed for several years in the same building as determined from banding of adults. The total number of laying dates for first clutches was 462.

Finally, laying dates were gathered for the house sparrow *Passer domesticus* and tree sparrow *P. montanus*, which are both gregarious passerines associated with human habitat and both common prey species of the sparrowhawk. Both species breed in farm buildings, and A.P.M. recorded breeding events at Kraghede in the same buildings as those used by barn swallows. Only nests from the first clutch were included. The total number of laying dates were 884 and 681, respectively.

Population size estimates

J.T.N. visited all possible nest sites 1–5 times each year during the period May–June, searching the forests for sparrowhawks or sparrowhawk nests. The number of breeding pairs of sparrowhawks was estimated based on the presence of new nests with or without nest content or the presence of a pair of birds during the breeding season. Thus, any territory that held sparrowhawks during the breeding season was considered to represent a breeding pair when a pair was present or a new nest was recorded, independent of whether the nest was successful. Pairs that built replacement nests in the same territory due to early nest failure were not considered new pairs.

The same forests were searched systematically for the presence of goshawks or nests of goshawks. Playback and observations were used to determine whether birds were present in a given forest during the breeding season (March–June).

The number of territories that had been used for more than 10 years during the period 1977–1997 was estimated for each year using information on the distribution of breeding pairs. A territory was considered to be re-used if the distance between nests in two consecutive years was less than 1 km (see Nielsen 2004a for further details).

The size of the post-breeding population in number of individuals was estimated as twice the number of breeding pairs plus mean brood size multiplied by the number of breeding pairs.

Recording reproductive variables

We determined laying date as the date when the first egg was laid. This was estimated from the age of nestlings when nest contents were inspected in May–June each year, using the growth curve in Moss (1979). Hatching takes place over a period of 1–6 days, depending on clutch size and the start of incubation (Newton 1986). For clutches of 4 eggs, incubation period (defined as the period from laying of the first egg until the mean date of hatching) has been set to 38 days. For clutches of 5 eggs we used 40 days, for clutches of 6 eggs 41 days, and for clutches of 7 eggs 42 days. Broods of 1–3 young usually originate from clutches of at least 4 eggs, since clutches of 1–3 eggs are usually deserted before hatching (Newton 1986). Therefore, nests with 1–3 infertile or crushed eggs and/or nestlings were assumed to have an incubation period of 38 days like clutches of 4 eggs. The error rate in estimating laying date was maximally 1–3 days according to our data on nests that were visited regularly. Laying date was expressed relative to 1 April = 1.

Clutch size was estimated as the number of nestlings plus the number of unhatched or broken eggs and the number of dead nestlings. Since unhatched eggs usually remain in the nest, this provides an unbiased estimate of clutch size, although some broken eggs or dead nestlings may disappear when eaten (Newton and Marquiss 1984; Newton 1986). Clutch size estimates are thus minima. We assumed that adult females had a minimum clutch size of 4 eggs and yearling females a minimum clutch size of 3 eggs, since smaller clutches are usually caused by egg loss (Newton and Marquiss 1984; Newton 1986). Smaller clutches were only included if we were sure due to regular visits that egg loss did not cause reduction in clutch size (i.e., that clutch size did not decrease from one visit to the next).

Brood size was estimated when nestlings were ringed at an age of 12–24 days, and was further estimated after fledging. Brood size was separately estimated for all pairs that had at least 1 nestling. Breeding success was estimated as brood size divided by clutch size. The proportion of nests without any breeding success was the number of pairs with no fledglings divided by the total number of pairs.

We determined age of breeding females from characteristics of primaries moulted in the territory near the nest, using the age criteria reported by Opdam and

Müskens (1976) and Newton and Marquiss (1981a). See Nielsen (2004a) for details.

Recording beech mast abundance

The crop of beech mast was scored on a scale of 0, 1, 2, or 3 each year by professional forestry personnel in Denmark working for the Plant Breeding Unit of Danish State Forests (Jacobsen 1994; J.T. Laursen, personal communication). This index varied from no beech mast (0) to an extremely large production of beech mast (3).

Temperature and precipitation

We deliberately chose to use information on precipitation and temperature from the study area as indicators of climatic conditions. The reason for doing so was: (1) to only use a very restricted number of variables to avoid problems of randomly arising statistical associations, (2) to analyse variables that are known that have shown temporal change, and (3) to use variables that are easily interpretable. While numerous studies have relied on climatic indicators such as the North Atlantic Oscillation Index, this index has shown no clear recent temporal trend, suggesting that there is no a priori reason to expect that this composite variable can account for the changes recorded in our study. We obtained mean monthly temperatures from the meteorological stations at Hjørring between the two study areas and at Tylstrup just south of the study areas for the months December–June 1977–1997. Likewise, we obtained monthly level of precipitation (in mm) from the same months and the same period.

Estimating mistiming of reproduction

We estimated the timing of fledging for the five prey species that constituted rank number 2, 3, and 6–8 in terms of numbers of prey for the start and the end of the study (1977 and 1997). The abundance of the prey species in the diet based on 34,923 prey items of 117 species was 4,086 *Passer montanus* (rank number 2 among prey species), 2,688 *Turdus merula* (rank number 3), 2,031 *Hirundo rustica* (rank number 6), 1,930 *Passer domesticus* (rank number 7) and 1,914 *Parus major* (rank number 8). The skylark *Alauda arvensis* was the most common prey species for the sparrowhawk ($n=4,804$). We used information on mean laying date in 1977 and 1997, mean clutch size, and incubation period and nestling period to calculate mean fledging date (*Hirundo rustica*: 13 June and 9 June, 5 eggs, 15 days, 20 days; *Parus major*: 22 May and 1 May, 9

eggs, 14 days, 19 days; *Turdus merula*: 29 May and 20 May, 5 eggs, 13 days, 14 days; *Passer domesticus*: 6 May and 25 April, 5 eggs, 12 days, 14 days; *Passer montanus*: 10 May and 2 May, 5 eggs, 13 days, 18 days). These estimated dates were weighted by the abundance of prey listed above to estimate mean date of fledging of all the prey species. For the sparrowhawk in 1977 and 1997, we estimated age of nestlings based on the mean laying date (2 May and 1 May, respectively), mean clutch size (5.20 and 4.76, respectively), an incubation period of 34 days (Newton 1986) and a nestling period of 27 days (Newton 1986).

Statistical analyses

The proportion of females without success, the proportion of territories occupied more than 10 years and the proportion of adult females were square-root arcsine-transformed to obtain distributions that did not differ significantly from normal distributions (Sokal and Rohlf 1995).

Sample sizes differed between analyses because only a fraction of all nests were used for determining laying date and clutch size. Early nest failure due to a number of different causes prevented us from estimating laying date or clutch size for all pairs. See Nielsen (2004a) for further details.

For laying date, clutch size and brood size, we calculated annual means and standard deviations. We used the coefficient of variation as an estimate of variability in these three reproductive parameters.

We used the proportion of unsuccessful pairs as a covariate in the statistical analyses because mean and standard deviation in laying date, clutch size and brood size could have been biased due to variation in the proportion of unsuccessful pairs among years. This procedure is justified by the fact that we know for the study population that unsuccessful pairs differed in reproductive parameters from the overall population (Nielsen 2004a).

We used means and standard deviation for each year as statistically independent observations in the analyses. This procedure assumes that there is little or no temporal auto-correlation in the data (Chatfield 1999), and therefore we specifically tested for temporal auto-correlation in our annual estimates, using JMP (2000). These analyses showed evidence of temporal auto-correlation with significant correlations for population size, post-breeding population size and proportion of territories used more than 10 years with a time lag of 1 year and population size of breeding goshawks with time lags of 1 and 2 years. These significant correlations were small to intermediate, accounting for a

maximum of 72% of the variance (population size of goshawks). To avoid these problems of auto-correlation we repeated all analyses based on variables with temporal autocorrelation by using detrended variables, subtracting the value in year ($i+1$) from the value in year (i) and then basing the analyses on these differences (e.g. Chatfield 1999).

We developed the best-fit statistical models of reproductive variables, the size of the breeding population and the size of the post-breeding population, respectively, by using a stepwise procedure (JMP 2000; Sokal and Rohlf 1995). We tested for the fit of both linear and curvilinear models because linear regression models assume linearity, and because several relationships clearly were non-linear with polynomial regressions providing a significantly better fit than a linear regression. Models were tested for robustness by using both forward and backward procedures (Sokal and Rohlf 1995). None of the models showed differences in variables included using these procedures. Model selection was based on Akaike's information criterion as an estimate of the improvement in fit for addition of variables (Burnham and Anderson 1998). Collinearity between variables can cause problems in model selection, but when $r < 0.70$ as in the present study, this is generally not considered problematic (Green 1979).

We tested for delayed effects of beech mast and population density by including values for the previous year as well as the current year in the analyses. This was done because we could expect to see delayed effects in a relatively long-lived species like the sparrowhawk.

We only included two-way interactions between population size, beech mast, temperature and proportion of territories used more than 10 years because the study only included data for 20 years and inclusion of higher order interactions was thus not possible.

Results

Temporal trends in climate

Spring temperature for the months February–April increased dramatically during the period 1971–2004 (Fig. 1). The increase in mean temperature for February–April was on average 2.65°C for 1977–1997, which is the period during which we conducted our study. In contrast, there was no evidence of change in temperature for the months December–January or May–June or for change in level of precipitation for any month ($F < 2.85$, $df = 1,33$, $r^2 < 0.08$, $P > 0.10$). This provides evidence for rapid change in temperature at the start of

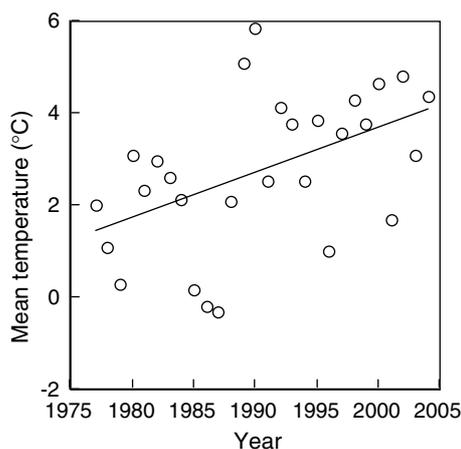


Fig. 1 Mean temperature during February–April 1977–2004 in Tylstrup, Denmark. The line is the linear regression line with the equation $F = 8.18$, $df = 1,26$, $r^2 = 0.24$, $P = 0.0082$, slope (SE) = 0.098 (0.034)

the growing season. Temporal change in breeding date could thus only be accounted for by the effects of temperature, but not be precipitation.

Temporal trends in breeding date for common prey

Barn swallows showed a trend towards earlier laying in recent years, with a highly significant polynomial regression (Fig. 2a). Laying date advanced on average by a week since the maximum estimated for 1983. Blackbirds also showed a significant advance in laying date during 1971–2004 (Fig. 2b). Mean laying date advanced by 10.7 days according to the linear regression model in Fig. 2b. Great tits showed a polynomial relationship between laying date and year (Fig. 2c). Mean laying date advanced by 25 days since the estimated maximum in 1983. House sparrow and tree sparrow showed a polynomial relationship between laying date and year (Fig. 2d, e). Mean laying dates advanced by 18 and 20 days, respectively, since their maximum in the early 1970s. Therefore, there was evidence of considerable advances in laying date for five common passerine birds that constitute common prey for the sparrowhawk.

These five species constituted five of the top eight prey species in terms of abundance. The fraction of these five species for the entire diet did not change significantly during the years 1977–1997 [mean (SE) = 35.9% (1.0), linear regression: $F = 1.50$, $df = 1,17$, $r^2 = 0.08$, $P = 0.24$].

Temporal trends in reproductive variables

Laying date of the sparrowhawk was on average 2 May (SE = 0.4, $n = 525$). There was no evidence of mean

laying date advancing during the study ($F = 0.95$, $df = 1,18$, $r^2 = 0.05$, $P = 0.34$). Likewise, there was no evidence that the coefficient of variation in laying date changed ($F = 2.90$, $df = 1,18$, $r^2 = 0.14$, $P = 0.11$). Clutch size was on average 4.73 (SE = 0.03, $n = 487$). Brood size was on average 2.60 (SE = 0.10, $n = 823$). Brood size of successful pairs was on average 3.91 (SE = 0.06, $n = 541$). Breeding success was on average 54.8% (SE = 1.8, $n = 487$). Mean and coefficient of variation in clutch size, brood size or brood size for successful broods did not change significantly during 1977–1997 ($F < 3.06$, $df = 1,18$, $r^2 < 0.15$, $P > 0.10$). The mean percentage of unsuccessful females per year was 31.2% (SE = 1.9, $n = 20$ years). The percentage of females with no success did not change ($F = 0.06$, $df = 1,17$, $r^2 = 0.003$, $P = 0.81$). The percentage of adult females was on average 82.7% (SE = 2.0, $n = 18$ years). The age composition measured as the percentage of adult females decreased during the study [$F = 5.19$, $df = 1,16$, $r^2 = 0.25$, $P = 0.04$, slope (SE) = -0.010 (0.004)].

The size of the breeding population showed a U-shaped relationship with year during 1977–1997, reaching a maximum during the last years of the study (Fig. 3a). The size of the breeding population of sparrowhawks was not predicted by the size of the breeding population of goshawks (analyses based on detrended data: $F = 0.24$, $df = 1,17$, $r^2 = 0.01$, $P = 0.63$). The size of the post-breeding population increased significantly in a linear fashion (Fig. 3b). The proportion of pairs breeding on territories that had been occupied for more than 10 years initially increased to reach a maximum in 1986 followed by a significant decrease to reach a minimum in 1997 (Fig. 3c).

Effects of food abundance and density on reproduction

There was no evidence of density-dependent or delayed density-dependent effects for any of the nine reproductive variables (all $F < 2.69$, $df = 1,17$, $r^2 < 0.10$, $P > 0.19$).

The beech mast index did not change during the study ($F = 0.42$, $df = 1,19$, $r^2 = 0.02$, $P = 0.53$). Food abundance as estimated from beech mast had a significant effect on reproduction by the sparrowhawk the following year. Brood size was larger following years with high beech mast (Fig. 4a). This effect was independent of clutch size [partial regression: $F = 9.63$, $df = 1,17$, $r^2 = 0.36$, $P = 0.007$, slope (SE) = 0.179 (0.058)]. Furthermore, variation in brood size estimated as the coefficient of variation decreased with increasing beech mast the previous year (Fig. 4b). Therefore, reproductive success increased with increasing beech mast the previous year (Fig. 4c). Brood size for successful broods

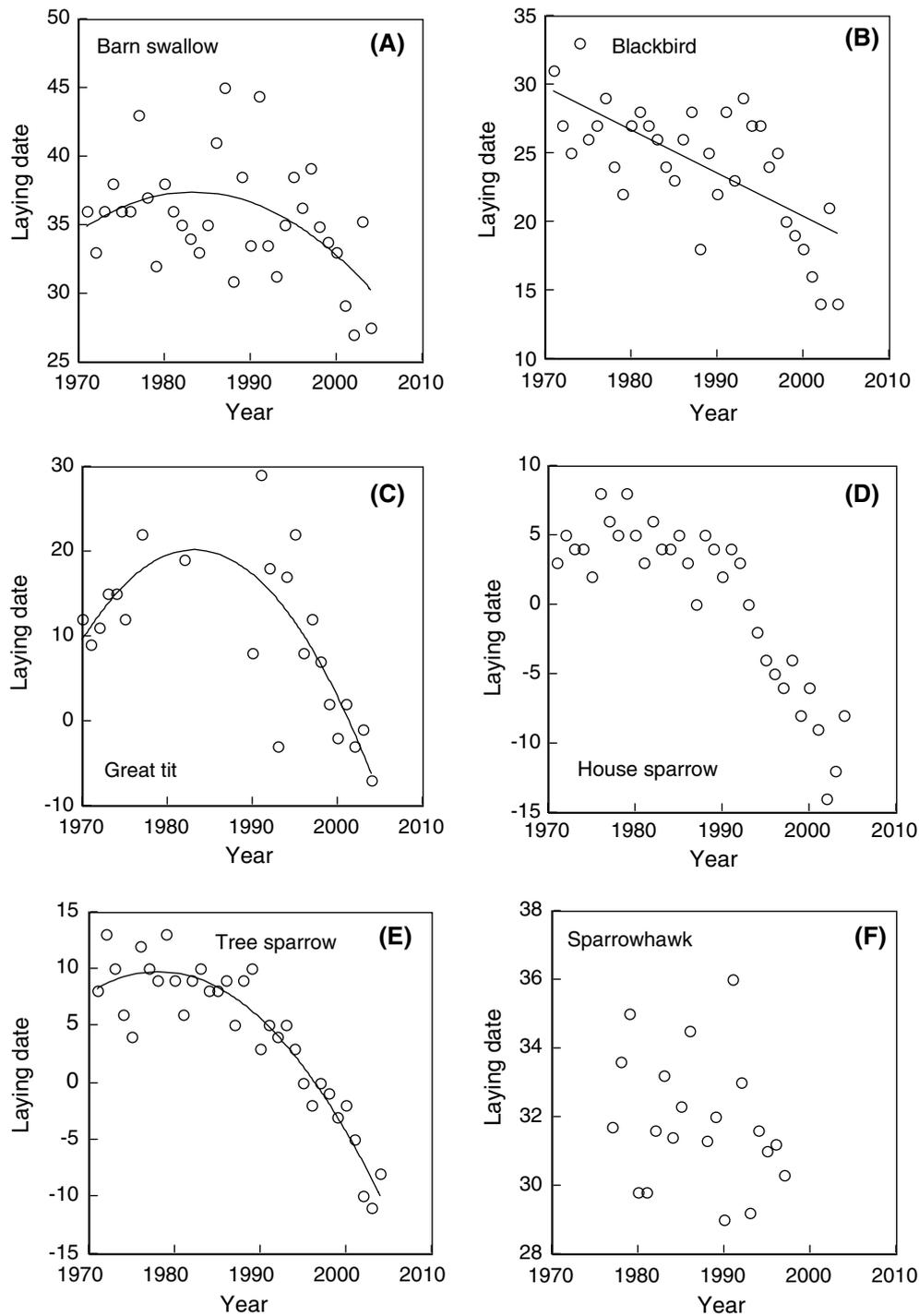


Fig. 2 Mean laying date of **a** barn swallows *Hirundo rustica*, **b** blackbird *Turdus merula*, **c** great tit *Parus major*, **d** house sparrow *Parus domesticus*, **e** tree sparrow *P. montana* and **f** sparrowhawk *Accipiter nisus* during the period 1971–2004 (sparrowhawk only 1977–1997). Dates are relative to 1 May = 1. The lines are the best fit regression lines. The models have the following statistics: **a** $F = 4.77$, $df = 2,31$, $r^2 = 0.24$, $P = 0.016$, linear term slope (SE) = 66.32 (29.60) $t = 2.24$, $P = 0.03$, quadratic term slope (SE) = -0.017 (0.007), $t = -2.25$, $P = 0.03$; **b** $F = 30.71$, $df = 1,32$, $r^2 = 0.49$, $P < 0.001$, slope (SE) = -0.31 (0.06); **c** $F = 13.79$,

$df = 2,20$, $r^2 = 0.58$, $P = 0.0002$, linear term slope (SE) = 231.27 (60.84), $t = 3.80$, $P = 0.001$, quadratic term slope (SE) = -0.058 (0.015), $t = -3.80$, $P = 0.001$; **d** $F = 119.34$, $df = 2,31$, $r^2 = 0.89$, $P < 0.0001$, linear term slope (SE) = 112.40 (16.22), $t = 6.93$, $P < 0.001$, quadratic term slope (SE) = -0.028 (0.004), $t = -6.96$, $P < 0.001$; **e** $F = 111.03$, $df = 2,31$, $r^2 = 0.88$, $P < 0.0001$, linear term slope (SE) = 119.87 (17.82), $t = 6.73$, $P < 0.001$, quadratic term slope (SE) = -0.030 (0.004), $t = -6.76$, $P < 0.001$; **f** $F = 0.95$, $df = 1,18$, $r^2 = 0.05$, $P = 0.34$

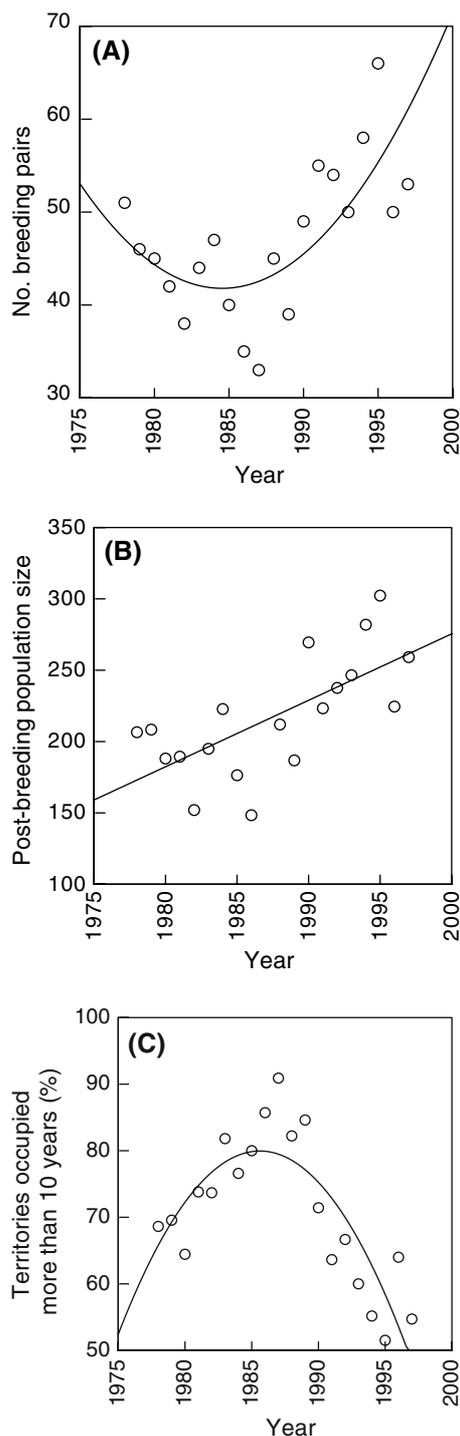


Fig. 3 **a** Breeding population size, **b** post-breeding population size, and **c** percentage of pair breeding in territories occupied for more than 10 years during the period 1977–1997. The lines are the regression lines with the statistics **a** $F = 8.62$, $df = 2, 17$, $r^2 = 0.50$, $P = 0.003$, linear term slope (SE) = -491.50 (180.98), quadratic term slope (SE) = 0.12 (0.05), **b** $F = 14.58$, $df = 1, 17$, $r^2 = 0.46$, $P = 0.001$, slope (SE) = 4.66 (1.22), and **c** based on square-root arcsine-transformed proportions $F = 16.38$, $df = 2, 17$, $r^2 = 0.66$, $P < 0.0001$, linear term slope (SE) = 11.17 (2.37), quadratic term slope (SE) = -0.003 (0.001)

only also increased with beech mast the previous year, although the relationship was not significant [$F = 3.76$, $df = 1, 18$, $r^2 = 0.17$, $P = 0.07$, slope (SE) = 0.094 (0.049)].

Effects of spring temperature on reproduction

Despite laying dates not having advanced significantly, there was evidence suggesting that laying advanced during warm springs. Laying date advanced significantly in years with high mean temperatures during February–April [$F = 7.74$, $df = 1, 18$, $r^2 = 0.30$, $P = 0.01$, slope (SE) = -0.65 (0.23)]. Although the regression explained 29% of the variance, the 2.65°C increase in temperature during 1977–1997 only accounted for an advancement in laying date by 1.7 days. Although mean clutch size was not larger in warm springs ($F = 0.05$, $df = 1, 18$, $r^2 = 0.00$, $P = 0.83$), mean brood size was slightly larger [$F = 6.14$, $df = 1, 17$, $r^2 = 0.27$, $P = 0.02$, slope (SE) = 0.12 (0.05)], as was breeding success [$F = 7.02$, $df = 1, 17$, $r^2 = 0.29$, $P = 0.02$, slope (SE) = 0.024 (0.009)].

Consequences of early laying dates for reproduction

Mean brood size was larger in years with early laying (Fig. 5a). Likewise, mean breeding success was larger in years with early mean laying [$F = 5.27$, $df = 1, 18$, $r^2 = 0.23$, $P = 0.03$, slope (SE) = -0.020 (0.009)]. Even when only considering pairs with at least one nestling, brood size was larger in years with early laying (Fig. 5b). Therefore, sparrowhawks would have benefited from advancing their laying date.

Interactions between climate, population density and beech mast on reproduction

We can only expect to determine the effects of climate change after controlling statistically for potentially confounding variables. Because reproduction of the sparrowhawk population is potentially related to beech mast, climate and population density and their interactions, we predicted reproductive variables from these variables and their two-way interactions. In addition, we included delayed effects of beech mast and population density from the previous year because sparrowhawks may be influenced by long-term effects. Finally, we also included the proportion of unsuccessful females as a predictor variable, since variation in this proportion could potentially bias estimates. These analyses were made by using detrended variables to remove problems of temporal autocorrelation.

Laying date was earlier in years with a large beech mast and in years with warm springs (Table 1). The

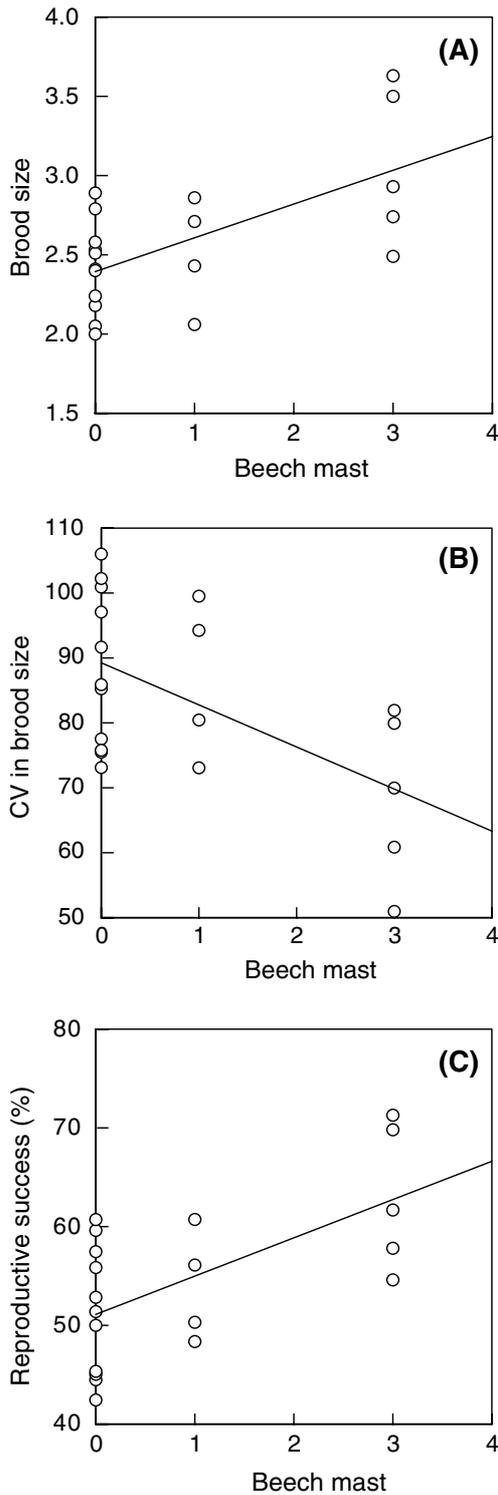


Fig. 4 Effect of food abundance as estimated from beech mast the previous autumn on **a** brood size, **b** coefficient of variation in brood size, and **c** reproductive success (%). The lines are the linear regression lines with the statistics: **a** $F = 11.59$, $df = 1,18$, $r^2 = 0.39$, $P = 0.003$, slope (SE) = 0.213 (0.063); **b** $F = 8.85$, $df = 1,18$, $r^2 = 0.33$, $P = 0.008$, slope (SE) = -0.065 (0.022); **c** $F = 11.53$, $df = 1,18$, $r^2 = 0.39$, $P = 0.003$, slope (SE) = 0.040 (0.012)

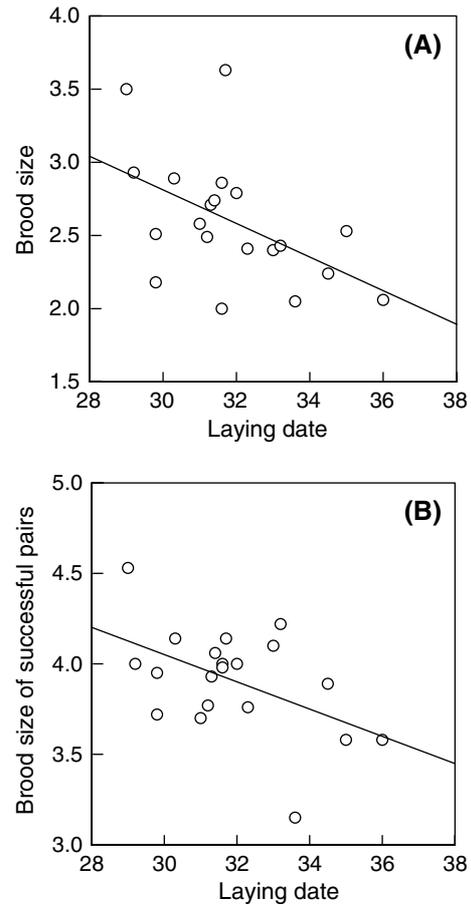


Fig. 5 **a** Mean brood size and **b** mean brood size of successful pairs in relation to mean laying date in different years. The lines are the linear regression lines with the statistics: **a** $F = 6.02$, $df = 1,18$, $r^2 = 0.25$, $P = 0.02$, slope (SE) = -0.115 (0.047); **b** $F = 5.78$, $df = 1,18$, $r^2 = 0.24$, $P = 0.03$, slope (SE) = -0.075 (0.031)

variation in laying date was not predicted by any of the variables (Table 1).

Mean clutch size was significantly predicted by four variables that explained 95% of the variance (Table 1). Mean clutch size decreased with the proportion of unsuccessful females, and also decreased with population size, the proportion of adult females and increasing size of the goshawk population. The variation in clutch size was larger when the population size was large and when spring temperature was low (Table 1). In addition, there was a significant interaction between population size and temperature, implying that clutch size was more variable for a given temperature when population size was large.

Mean brood size was predicted by two variables that explained 88% of the variance (Table 1). Brood size decreased with the proportion of unsuccessful

Table 1 Best fit models of reproductive variables of sparrowhawks *Accipiter nisus* in relation to population size, temperature, beech mast, reproductive variables and their two-way interactions

Variable	<i>F</i>	<i>r</i> ²	<i>P</i>	Slope (SE)
Laying date	11.60	0.61	0.0009	
Beech mast year (<i>i</i>)	9.00		0.009	-0.683 (0.227)
Temperature	15.69		0.0013	-0.960 (0.242)
Clutch size	41.90	0.95	<0.0001	
Unsuccessful females (%)	131.13		<0.0001	-2.561 (0.224)
Population size	10.48		0.01	-0.010 (0.003)
Adult females (%)	23.44		<0.0001	-3.194 (0.660)
Goshawk population size	39.54		<0.0001	-0.070 (0.011)
SD in clutch size	5.35	0.55	0.01	
Population size	12.05		0.0004	0.018 (0.005)
Temperature	3.31		0.09	-0.031 (0.017)
Population size × temperature	5.07		0.042	0.006 (0.003)
Brood size	39.34	0.88	<0.0001	
Unsuccessful females (%)	78.55		<0.0001	-5.156 (0.582)
Goshawk population size	5.57		0.02	-0.068 (0.029)
SD in brood size	11.26	0.48	0.0057	
Unsuccessful females (%)	11.26		0.0057	-0.043 (0.013)
Brood size successful broods	7.29	0.38	0.02	
Temperature	7.29		0.02	0.126 (0.047)
Breeding success	46.18	0.89	<0.0001	
Unsuccessful females (%)	59.51		<0.0001	-0.744 (0.096)
Temperature	6.05		0.01	0.013 (0.005)
Unsuccessful females (%)	4.00	0.25	0.07	
Beech mast year (<i>i</i>)	4.00		0.07	-0.024 (0.012)

Temperature is mean temperature during February–April

females and the size of the goshawk population (Table 1). The variation in brood size was predicted by a single variable that accounted for 48% of the variance (Table 1). When the proportion of unsuccessful females was large, the variation in brood size was obviously large (Table 1). Brood size of successful pairs was explained by a single variable that accounted for 38% of the variance (Table 1). Mean brood size was larger in years with a warm spring (Table 1).

Breeding success was explained by two variables that accounted for 89% of the variance (Table 1). Breeding success was obviously lower when the proportion of females that were unsuccessful was large (Table 1); a variable that was included to control statistically for variance in success due to differences in the proportion of pairs included in the estimates. In addition, breeding success was larger in years with a warm

spring (Table 1). The percentage of unsuccessful females was explained by one variable that accounted for 25% of the variance (Table 1). Since the model did not reach significance, the findings should be interpreted with caution. There was a negative relationship between the proportion of unsuccessful females and beech mast the current year (Table 1).

Population size in relation to population density, climate and beech mast

We investigated the population consequences of variation in climate by predicting the size of the breeding population and the post-breeding population from beech mast, climate and population density and their two-way interactions. In addition, we included delayed effects of beech mast and population density from the previous year since it was possible that there were long-term effects dating back more than a year. Finally, we included the proportion of unsuccessful females as a predictor, since variation in this proportion could potentially bias estimates of reproductive success. These analyses were made by using detrended variables to remove problems of temporal autocorrelation.

The stepwise regression model for population size did not include any of the variables

The stepwise regression model predicting the size of the post-breeding population included three variables that explained 97% of the variance (Table 2). The size of the post-breeding population was mainly explained by population size the current year, with a larger post-breeding population when the size of the breeding population was large (Table 2). The second-most important predictor was the proportion of unsuccessful females, which had a negative effect on the size of the post-breeding population (Table 2). Finally, there was a weak negative effect of the size of the post-breeding population the previous year on the size of the post-breeding population the current year (Table 2).

Timing of reproduction by the sparrowhawk in relation to prey availability

We estimated the discrepancy of timing of reproduction by the sparrowhawk and availability of prey from information on timing of breeding by the five prey species investigated and the predator (Table 3). While the mean date of fledging by prey occurred when the nestlings of the sparrowhawk in 1977 were 14 days old on average, and hence just before the peak in food

Table 2 Best fit models of post-breeding population size of sparrowhawks in relation to population size, temperature, beech mast, reproductive variables and their two-way interactions

Variable	<i>F</i>	<i>r</i> ²	<i>P</i>	Slope (SE)
Post-breeding population	85.52	0.97	<0.0001	
Population size year (<i>i</i>)	160.57		<0.0001	4.730 (0.373)
Unsuccessful females (%)	48.72		<0.0001	-198.799 (28.480)
Post-breeding population size year (<i>i</i> -1)	13.71		<0.001	-0.250 (0.067)

requirements by nestlings (Newton 1986), this age had dropped to only 6 days in 1997, at an age when sparrowhawk nestlings only need very limited amounts of food (Newton 1986).

Discussion

The main findings of this study were that five species of passerine prey for sparrowhawks significantly advanced their laying dates during the last 34 years, apparently in response to an increase in spring temperature by over 3.2°C. However, sparrowhawks barely advanced laying date during 1977–1997, although mean laying date was earlier in warm than in cold springs. Brood size and reproductive success were mainly predicted by the percentage of successful pairs, population size of the goshawk, and spring temperature. Size of the post-breeding population was predicted by size of the breeding population the current year, post-breeding population the previous year and the percentage of unsuccessful females. We will briefly discuss these findings.

Table 3 Timing of fledging of the main prey species (weighted by their abundance as prey) and timing of reproduction by the sparrowhawk

Variable	1977	1997
Mean fledging date of prey (weighted by abundance)	25 June (13)	17 June (12)
Mean laying date of sparrowhawk	2 May (7)	1 May (7)
Mean fledging date of sparrowhawk	7 July (7)	6 July (7)
Mean age of nestling sparrowhawks at mean fledging date of prey	14 days	6 days

Values are means (SD). See [Materials and methods](#) for further information

Effects of climate change on reproduction

We found consistent evidence of advancement in timing of breeding by five common passerine prey of sparrowhawks. Barn swallows, blackbirds, great tits, house sparrows and tree sparrows comprise 6.4, 8.5, 6.0, 6.1 and 7.8%, respectively, of the avian prey during the breeding season in our population of sparrowhawks, according to 34,923 prey remains that were systematically collected near and in sparrowhawk nests during 1977–1997 (Nielsen 2004b). These species are five of the eight most common prey species of the sparrowhawk. The proportion of prey constituted by these five species of passerines did not change significantly during our study, and we can therefore dismiss the possibility that the sparrowhawks simply switched prey as climate changed. Because mean laying date of these five species of passerines advanced by 7–25 days during recent years (Fig. 2), we would expect sparrowhawks also to advance their laying date to a similar extent to track the earlier availability of prey provided by inexperienced fledglings. However, there was no evidence of advancement of mean laying date by the sparrowhawk during 1977–1997, even though we could show that there was a fitness advantage to be gained from early reproduction, not only in terms of larger brood size, but also in terms of recruitment rate per offspring produced. This suggests that timing of reproduction in the sparrowhawk is becoming mismatched with timing of reproduction in prey, as reported for some populations of small passerines (Visser et al. 1998, 2004; Visser and Holleman 2001).

We found empirical evidence of an increase in the degree of reproductive mistiming by the sparrowhawk from 1977 to 1997. While sparrowhawk nestlings were on average 14 days old in 1977 when the average prey nestling fledged, they were only 6 days old in 1997. Because the food requirements of sparrowhawk nestlings peak around the middle of the nestling period (Newton 1986), there was a good agreement between timing of breeding by the sparrowhawk, food demand for the sparrowhawk and maximum food availability in 1977. That was clearly not the case in 1997 because sparrowhawk nestlings were only 6 days old when the average prey nestling fledged. Fledgling birds have very high mortality rates just after leaving the nest. For example, great tits suffer large mortality during the first week after fledging (Perrins 1979). This implies that most individuals of common prey species like the ones studied here have already suffered most of their excessive post-fledging mortality when sparrowhawk nestlings reached a peak in food demand in 1997, but not in 1977. Food demand for young sparrowhawks remain

high until weeks after fledging (Newton 1986), and the first difficult attempts by fledglings to catch their own prey are often directed towards inexperienced young prey individuals (Newton 1986). Given that nestlings of common prey species were generally older and more experienced when young sparrowhawks started hunting in 1997 than in 1977, this should have resulted in higher post-fledging mortality among sparrowhawks in 1997 than in 1977. This prediction could readily be tested based on data from some of the large ringing schemes.

Because our sparrowhawk population is resident, this lack of response in laying date to change in timing of reproduction by prey cannot be due to the lack of possibility of assessing phenology in the breeding area, as suggested for long distance migrants (Both and Visser 2001). This raises the possibilities that either it was not advantageous to advance laying, or that changes in timing of reproduction by the sparrowhawk were constrained. Although mean clutch size did not increase with mean early laying, mean brood size and mean breeding success was larger in years with early laying (Fig. 5). Likewise Newton and Marquiss (1986) showed that cold and wet springs resulted in small breeding populations, apparently because this is the time of the year when prey numbers reach their minimum. Thus, there was evidence in our study suggesting that it was beneficial for sparrowhawks to lay early, thereby refuting the first explanation.

The second possibility is that constraints may have prevented sparrowhawks from responding to climate change (Møller and Merilä 2004; Pulido and Berthold 2004). For example, individual sparrowhawks may have been unable to show a phenotypic plastic response in laying date to changes in climate. This seems unlikely given experimental evidence suggesting that sparrowhawks advance their laying date in response to experimental manipulation of food abundance (Newton and Marquiss 1981b). A second possible constraint related to the inability of species with multiple broods to time their reproduction to coincide with the annual food peak (Crick et al. 1993) cannot apply to the single-brooded sparrowhawk. A third possible constraint is that lack of additive genetic variation in laying date, or negative genetic correlations between laying date and other life history traits, may have prevented a response to selection for earlier laying date. There is no information available on heritability of laying date in sparrowhawks, and information on the additive genetic variance-covariance matrix is likewise missing. Given that laying date generally has a small, but significant, heritability in a range of different bird species (Merilä and Sheldon 2001), it seems unlikely

that such a constraint would prevent a response to selection. However, sparrowhawks went through an extreme bottleneck during the 1950s and 1960s due to organic chemical pollution (Newton 1986), and bottlenecks are known to reduce the amount of genetic variation and constrain adaptation to novel environmental conditions (Roff 1997). We can estimate generation time T as $T = A + P/(1 - P)$, where A is age at first reproduction and P is adult annual survival rate. If we set $A = 1$ year and $P = 77.7\%$, we obtain $T = 4.48$, implying that the study period constituted 21 years/4.48 years/generation or 4.69 generations. Many selection experiments on birds have already recorded a response to selection after two to three generations, suggesting that the absence of a response is unlikely to be due to an evolutionary lag.

We found evidence of effects of food abundance on reproduction. Using the beech mast index as an index of food availability we found that laying date and the percentage of unsuccessful females were strongly affected by food availability (Fig. 4). We found evidence of density-dependence for clutch size and variation in clutch size (Table 1). Furthermore, spring temperature had a significant effect on laying date, brood size of successful pairs and breeding success. Finally, our analyses suggested that the population of goshawks that has increased from five pairs in 1977 to 14–17 pairs in 1993–1997 affected clutch size and brood size of sparrowhawks. Goshawks are common predators on sparrowhawks, therefore potentially affecting their brood size and breeding success through differential predation. Such effects of interspecific competition among predators are common, although rarely described for birds (e.g. Spiller and Schoener 1994). Since all evidence discussed in this section is entirely correlational, we cannot rule out the possibility that the effects act through mechanisms other than those suggested here. An experimental approach would be needed to test these alternatives.

Effects of climate change on population size

Population consequences of climate change have been studied on many occasions. Sæther et al. (2004) summarised the extensive literature by listing different studies determining how population size or change in population size was related to local climate factors or large-scale climate phenomena such as the North Atlantic Oscillation. While altricial species were generally regulated outside the breeding season, precocial species were generally regulated during breeding. Here, we showed evidence of delayed density-dependence affecting the size of the post-breeding breeding

population (Table 1). There was no evidence suggesting that the size of the breeding or the post-breeding population was affected by spring temperature.

The size of the post-breeding population was mainly determined by population size the current year, the proportion of unsuccessful females, and the size of the post-breeding population the previous year (Table 2). The proportion of unsuccessful females was weakly affected by beech mast index the current year (Table 1). Thus, post-breeding population size was determined by density-dependence and perhaps food availability (Table 2).

Only the size of the post-breeding population could be explained by the variables considered, while that was not the case for the size of the breeding population (Table 2). The best-fit model explained 97% of the variance in post-breeding population size. Density-dependence was an important predictor of post-breeding population (Table 2). This is in accordance with studies by Newton (1988) and Newton and Marquiss (1986) suggesting that density-dependent recruitment is the single most important determinant of the size of the breeding population. Newton (1988) also found no evidence of density-dependent reproduction in sparrowhawks, as we have reported here. These findings are consistent with the general pattern described by Sæther et al. (2004) suggesting that populations of altricial species such as the sparrowhawk are regulated by density-dependence outside the breeding season.

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