

Reproductive decisions of boreal three-toed woodpeckers (*Picoides tridactylus*) in a warming world: from local responses to global population dynamics

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Here, I examine whether both nestling prey abundance and profitability affect the timing of reproduction and hence the number of fledglings of three-toed woodpeckers, *Picoides tridactylus*. Individuals living in eastern Finland reproduced earlier and reared larger broods in habitat patches where the bark-beetle community developed earlier and/or faster and where the wood-boring beetles, whose larvae account for the bulk of the nestlings' diet, were more abundant. As expected, mean breeding success increased with spring temperature, if laying date was related to prey phenology, which is temperature-dependent. However, using a larger data set with more years, adults seemed to face increasing difficulties in optimising their reproductive effort above certain spring temperature threshold, with a dramatic reduction in natal dispersal and winter population size over Finland following the warmest springs. I suggest climate-mediated phenological disjunction between the predator and its prey to be a likely cause of further decline in the insect specialist three-toed woodpecker.

Introduction

Annual changes in nestling food supply are known to affect breeding initiation and limit productivity in birds (Lack 1968). Besides the overall abundance of food in the environment, there is now considerable evidence that prey availability acts as main selection pressure on the timing of the breeding season (Nager & van Noordwijk 1995). For most forest insectivorous bird populations, initiation of egg-laying is determined by a synchronisation of the peak energy demand of nestlings with maximum food supply (van Balen

1973, Zandt *et al.* 1990, Blondel *et al.* 1992). Such a pattern seems to be especially prevalent in populations in natural habitats, where the range of environmental conditions is similar to those experienced in the past (i.e., in the environment of selection).

Therefore, it is predicted that a sudden change in the environment would promote a mismatch between offspring needs and food abundance and should negatively affect reproductive success and perhaps population size (Winkler *et al.* 2002). Accordingly, in habitats recently modified by human activities, or in years with unusual

spring weather conditions, evidence suggests the timing of laying may be maladaptive, caused by phenological disjunction between predator and prey. Local mismatch between nestling requirements and food supply may result from regular asymmetric dispersal in the breeding habitat of individuals that are genetically programmed to breed at different times in their natal habitats, preventing adapted response mechanisms from evolving (Dhondt *et al.* 1990, Blondel *et al.* 1992, 1993, Dias & Blondel 1996, Dias *et al.* 1996, Lambrechts *et al.* 1997). Global change in spring temperature, an important constraint on laying date (Stevenson & Bryant 2000), may also promote mistimed phenotypic responses in relation to a temperature-dependent food peak. In warmer springs, ectothermic insect prey tend to hatch earlier and develop faster, tracking earlier blooming and leafing of host plants (Penuelas & Filella 2001). This, in turn, tends to disrupt the evolved phenological synchrony between predatory birds and prey, with implications for population dynamics (Visser *et al.* 1998, Both & Visser 2001). In general, mismatched breeding individuals suffer higher fitness costs than optimally adjusted birds, whether directly in terms of adult survival (Thomas *et al.* 2001) or indirectly following a reduction in likelihood of double brooding (Visser *et al.* 2003), nestling condition and fledging recruitment (Buse *et al.* 1999, Sanz *et al.* 2003).

The dietary preferences of the three-toed woodpecker *Picoides tridactylus* change seasonally, but throughout the year it eats insects that colonise dying and recently dead trees (Imbeau & Desrochers 2002). From late summer to early spring, the woodpecker relies almost exclusively on bark beetles (Col., Scolytidae), with a marked preference for the species that colonise spruce (*Picea* spp.) (Hogstad 1970, Fayt 1999). During the late spring–summer months, wood-boring beetle larvae, and in particular longhorn beetle larvae (Col., Cerambycidae), contribute significantly to the diet of individuals, including nestlings (Dement'ev 1966, Hogstad 1970, Pechacek & Krištín 1996). Pechacek and Krištín (2004) found that three-toed woodpeckers reduced their bark beetle consumption with the onset of reproduction, despite no apparent changes in beetle availability. Meanwhile, they observed a con-

comitant increase in the consumption of energetically more profitable longhorn-beetle larvae. Among controlling factors, ambient temperature has a major effect upon the duration and timing of the different phases of development of the woodpecker insect prey (Annala 1969, Salonen 1973, Post 1984). As a general pattern, beetles begin to move and develop again after hibernation at a temperature threshold of 3–6 °C (Chararas 1962, Annala 1969). Insect emergence or timing of natal dispersal depends on the time of reproduction (Annala 1969). The length of the life cycle depends also on the species of beetle and factors such as moisture content of tree tissues and density of conspecifics (Post 1984).

Like other insectivorous woodpeckers, female three-toed woodpeckers that lay later in a breeding season tend to produce smaller broods (Fayt 2003). This decline in breeding output parallels a seasonal decrease in the amount of wood-boring beetle larvae delivered to offspring (Fayt 2003), supporting the view that, similar to birds in general (e.g., Siikamäki 1995), breeding time and productivity in woodpeckers is largely determined by the amount of food available to nestlings. Nevertheless, at a smaller spatial scale, it is unknown whether variation in reproductive traits are causally related to the timing and abundance of wood-boring beetles, especially the longhorn beetle. Earlier observations, that woodpeckers in habitats where spruce bark-beetles develop earlier had larger broods, suggest an additional role for prey phenology as a cue in fine-tuning reproductive decisions (Fayt 2003). On the other hand, given its particularly narrow diet during egg-laying and chick rearing, the three-toed woodpecker is likely to be limited in its ability to cope with unusual changes in prey phenology (Winkler *et al.* 2002).

In this paper, I test general predictions for the working hypothesis that the availability of profitable longhorn-beetle larvae, the main food of the three-toed woodpecker nestlings, at the time of egg-laying is a key factor in explaining intraspecific variation in reproductive success.

1. Brood size and laying (here fledging) date, two fitness-related traits (Fayt 2003), will be related to local longhorn-beetle abundance and timing of development.
2. Annual mean brood size will increase with

spring (April–May) temperature if laying date is related to prey phenology, which is temperature-dependent.

3. As a result, the annual number of dispersing juveniles and the subsequent number of wintering individuals should increase following warmer springs (and so with an early nestling prey development), assuming a positive relationship between the population density prior to dispersal and dispersal rate.

Material and methods

Prediction 1: Nestling prey supply and breeding performance

The woodpecker population study was conducted from 1996 to 1999 in North Karelia, easternmost Finland (63°N, 31°E). The study area consisted of a Norway spruce (*Picea abies*) dominated patchwork of seven old-growth and one recently burnt forests, spatially isolated from the others by a surrounding matrix of younger, managed Scots pine (*Pinus sylvestris*) dominated stands. Each habitat patch (65–90 ha) was yearly inhabited by a single pair of three-toed woodpeckers. Nests were located by nest-excavation noises, by fresh woodchips, by noisy vocalisations of offspring or by accident. Determining woodpecker brood

size required climbing the nest tree and using a small mirror and flashlight to investigate the cavity. In case the nestling count was uncertain, tree cavities were revisited during the following days. The initiation of laying was estimated from the fledging date. Nests were visited daily once a nestling was seen extending its head from the cavity to beg; fledging was considered to have occurred when the first nestling left the nest. In this study, brood size referred to a single measure for an individual female in a given year. To avoid repeated brood size measurements from the same females, woodpeckers were individually colour-ringed whenever possible. To catch birds a plastic tunnel prolonged with a hoop net was placed in front of the nest hole. The birds were captured upon entering the nest cavity to feed the offspring. In addition, un-trapped males and females were considered as different birds when observed in forest stands a year before the capture of the second calendar year individuals or after the occurrence of colour-ringed residents.

Overall, a total of 27 woodpecker pairs were found breeding in the study area. Among them, 19 females were individually colour-ringed. I tested whether their brood size and fledging date were related to (i) prey abundance and (ii) number of coexisting great spotted woodpeckers *Dendrocopos major*, a larger and more numerous potential competitor for food resources (Table 1).

Table 1. Summary of variables related to habitat quality and reproductive traits (fledging date, brood size) of the three-toed woodpecker. Number of individuals per habitat patch (mean ± standard deviation) and total sample size (n) among categories of variables are given.

Variable	Description	Mean ± S.D. (n)
Prey abundance (19 broods)		
Total	Total no. of individual beetles	965.526 ± 307.631 (18 345)
Bb	No. of individual bark beetles of all the species	721.895 ± 296.350 (13 716)
Sbb	No. of individual bark beetles of the species that specifically live on spruce ^a	284.789 ± 154.074 (5411)
Wbb	No. of individual wood-boring beetles	42.158 ± 17.573 (801)
Lhb	No. of individual longhorn beetles	9.158 ± 11.187 (174)
Interspecific pressure (19 broods)		
Gsw	Total no. of coexisting ^b great spotted woodpeckers (adults and nestlings)	10.632 ± 6.121 (202)
Prey phenology (10 broods)		
Bbdev	Ratio in the no. of adults to larvae of spruce bark beetles per bark sample	3.313 ± 3.621 (300)

^a Classification based on the species assemblage sampled from the bark of spruce trees (Fayt 1999, 2003).

^b No. of Gsw individuals in the same habitat patch as a pair of three-toed woodpeckers.

In addition, 10 of those females had their brood size and fledging date related to (iii) the development time of local spruce bark beetle communities, a phenological indicator of the bark-living insect fauna.

Window flight traps, a reliable sampling device for bark beetles (Martikainen *et al.* 1996, 1999), were used to estimate local food abundance within patches. The traps were made of two perpendicular intercepting 20×40 cm transparent plastic planes, and a plastic funnel leading into a container attached below the panes. A solution of water, salt and detergent was used in the container to preserve the insects. A sampling effort of 1 trap per 7 ha was assumed to allow representative sampling of the patchily distributed forest beetles. Accordingly, woodpecker habitats were divided into 7 ha plots (200×350 m) on maps with scales of 1:10 000 to 1:20 000. Within each plot, 1 tree was randomly chosen in which 1 trap was hung near the trunk on a solid branch 1.5 m above the ground, measured from the lower margin of the panes. Traps were placed after choosing the direction and distance from the centre of each plot from random number combinations. The yearly sampling period was 1 May–20 July, covering the main flying season for the beetles. Overall, ten traps were distributed throughout each woodpecker habitat patch and were emptied twice during the summer. Beetles were sampled in habitat patches in the same season that the brood size of the woodpecker was determined. However, due to trap damage caused by accidental breaking of trees or branches or by encounters with moose (*Alces alces*), the information collected from 1 trap in 1996, 4 traps in 1997, and 1 trap in 1998 could not be included in the final analyses. To overcome this problem, insect counts were standardised among years and patches by adjusting the number of captures to the number of traps.

Catches from window traps yielded altogether 18 345 individual beetles, which included 13 716 bark beetles (75%) from 31 species. Estimates of prey abundance included the number of individual bark beetles, spruce bark-beetles, wood-boring beetles, and the total number of individual beetles. Among wood-boring beetles, I counted the number of individuals that belonged to families known to develop large

larvae (i.e., Elateridae, Anobidae, Oedemeridae, Cerambycidae and Curculionidae). Bark beetles were classified as species living on spruce according to the species assemblage previously found from the bark of spruce trees selected by the woodpecker (Fayt 1999, 2003).

To see whether interspecific pressure may contribute to explaining some variation in reproductive performances of resident three-toed woodpeckers, I counted the total number of great spotted woodpecker individuals (adults and nestlings) living in the same habitat patches as three-toed woodpeckers. Methods to find nests and count nestlings were similar to those used for three-toed woodpeckers. A total of 37 great spotted woodpecker nests were sighted, producing 128 offspring.

To relate individual variation in brood size with local prey phenology, bark samples were collected in 1998 and 1999 in 5 and 5 habitat patches, respectively, simultaneously with determination of brood size in the same patch. Bark samples were removed from spruce trees with recent evidence of three-toed woodpecker foraging. In order to minimise multiple effects of tree host conditions on the spatial distribution of trunk beetle communities, bark samples (10×15 cm) were collected at breast height exclusively from standing trees. Insect fauna was investigated from a total of 300 bark samples collected on four sampling days (3 in 1998 and 1 in 1999) in June, in July–August, and in September. Five samples were taken per visit to be stored at -16°C . Bark samples produced 7207 bark beetles from 16 species in various stages of development.

Based on the sequential order of development stages of beetles (egg–larva–pupa–adult), I built an index of development for the spruce bark-beetle community of individual patches that developed from eggs laid the year before. This was done by dividing the number of adult beetles of the different species, whose respective development was found synchronous (Fayt 2003), by the number of larvae from bark samples collected from June to September. Accordingly, it was assumed that the earlier and/or faster the prey community reproduction and/or development was, the more adults and fewer larvae should be collected and the higher the index should be.

This method also assumed that the development time of the bark beetle community should reflect the timing of development and thereby the size-dependent profitability of alternative prey, such as longhorn beetle larvae.

Prediction 2: Temperature and breeding performance

Using the population data from eastern Finland (1996–1999), the woodpecker annual brood size and fledging date from the same five habitat patches were related to the yearly air temperature recorded during the preceding winter (November–March) and spring (April–May). Winter and spring temperatures in the study area were estimated by taking an average of the monthly mean temperatures measured from the nearby weather station of Licksa Lampela (63°19'N, 30°02'E). Temperature measurements were available from the meteorological yearbooks of Finland (Finnish Meteorol. Inst.).

Prediction 3: Spring temperature, autumn dispersal and winter population size

I correlated the spring temperature (April–May) in Finland with number of dispersing juveniles the following autumn and the winter population size. Spring temperature throughout the country was estimated by taking an average of the monthly mean temperatures measured from six weather stations; two stations were situated in southern Finland (61°N, 22°–28°E), two in central Finland (63°N, 23°–30°E) and two in northern Finland (65°N, 26°–29°E). Yearly spring air temperature was calculated by taking an average of the monthly mean temperatures recorded from the six weather stations (1973–2004). Temperature measurements were available from the national weather statistics (Finnish Meteorol. Inst.). The annual number of dispersing woodpeckers was estimated from the ringing data records of the Finnish Museum of Natural History (1973–2004). Woodpeckers were only considered as dispersing individuals when captured from localities known to be outside the breeding habi-

tat (e.g., ringing stations located by the seaside) (J. Haapala pers. comm.). Because the number of woodpeckers captured every autumn might be connected with the ringing activity effort, counts were also made comparable by adjusting them to the total number of fully grown birds ringed each year and expressed as the number of woodpeckers per 10 000 birds ringed. Winter density was estimated by dividing the yearly number of individuals observed during the early- (1–14 Nov.), mid- (25 Dec.–07 Jan.) and late- (21 Feb.–06 Mar.) census periods of the national winter bird count (1975–2004) with the total length of census routes and transformed into a population index (R. A. Väisänen pers. comm.).

Statistical analyses

All the analyses were carried out with the SPSS 11.0 statistical software package. All tested variables were checked for the distribution of the data using one-sample Kolmogorov-Smirnov test, and standard transformations ($\log_{10}x + 1$) were used if necessary.

I first used partial Pearson correlation test to quantify the level of association between the woodpecker reproductive traits (brood size and fledging date) and environmental variables while controlling for year effect. I then performed stepwise multiple regression analyses to identify which among these prey abundance, prey phenology and interspecific pressure variables explained significant variation in brood size and fledging date (prediction 1). Since brood size may also be classified as a categorical variable (small (2–3) vs. large (4–5)), I also used a logistic approach following a stepwise forward procedure. Variables were removed from the model using the likelihood ratio test. The significance of predictor variables was tested using the change in deviance and degrees of freedom when the variable was removed from the model.

The influence of nestling prey phenology on reproductive decisions was further indirectly studied by relating to ambient temperature either annual changes in breeding time and brood size over the same five territories or annual means over the population (prediction 2). In the first case, I carried out analyses of covariance (ANCOVA)

to study the effect of winter (November–March) and spring (April–May) temperatures on woodpecker reproductive parameters, with monthly mean temperature as covariate and territory as a random factor (being a random sample of territories available in the landscape). Only one observation per female was included.

One-way ANOVA allowed me to examine the potential impact of spring temperature on subsequent natal dispersal movements and winter density, by comparing bird numbers following usually warm (average monthly mean temperature $T < 6\text{ }^{\circ}\text{C}$) and abnormally hot springs ($T > 6\text{ }^{\circ}\text{C}$) (April–May). Spearman correlations were used

to assess long-term trends in monthly mean temperature, annual number of dispersing juveniles and winter population size over Finland.

Results

Prediction 1: Nestling prey supply and breeding performance

As revealed from partial correlations, among food variables only prey phenology had a significant effect on the woodpecker breeding time, with earlier fledging in habitat patches where

Table 2. Pearson's partial correlation table of measured environmental variables with size and fledging date of 19 three-toed woodpecker broods (only the line of correlations for the prey phenology variable (Bbdev) is based on 10 females), after controlling for annual effect. Variables were log-transformed +1 for normality. Significant associations are: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. See Table 1 for explanation of acronyms.

	Brood	Fldate	Total	Bb	Sbb	Wbb	Lhb	Gsw	Bbdev
Brood	1								
Fldate	−0.815***	1							
Total	−0.054	−0.081	1						
Bb	−0.141	−0.017	0.975***	1					
Sbb	−0.297	0.103	0.734**	0.767***	1				
Wbb	0.533*	−0.424	0.027	−0.141	−0.296	1			
Lhb	0.332	−0.136	−0.121	−0.291	−0.313	0.796***	1		
Gsw	0.328	−0.488*	0.020	0.016	−0.187	−0.004	−0.224	1	
Bbdev	0.670*	−0.699*	−0.148	−0.277	−0.382	0.517	0.393	−0.420	1

Table 3. Results of stepwise multiple regression analyses showing the sets of environmental variables that explain variation in three-toed woodpecker breeding time (fledging date) and productivity (brood size), with and without information on prey development time (Bbdev). See Table 1 for explanation of acronyms.

Step	Variables entered	Partial R^{2a}	Model R^{2b}	F	p
Fledging date					
+ Bbdev (10 broods)					
1	Bbdev	0.607	0.607	12.38	0.008
2	Gsw	0.184	0.791	6.17	0.042
− Bbdev (19 broods)					
1	Wbb	0.272	0.272	6.35	0.022
2	Gsw	0.190	0.462	5.66	0.030
Brood size					
+ Bbdev (10 broods)					
1	Bbdev	0.583	0.583	11.21	0.010
2	Gsw	0.154	0.738	4.12	0.082
3	Wbb	0.149	0.887	7.89	0.031
− Bbdev (19 broods)					
1	Wbb	0.327	0.327	8.25	0.017

^a Proportion (%) of variance explained by the variables entered in the model.

^b Total proportion (%) of variance explained by the model.

bark-living beetle developed earlier (Table 2). Female three-toed woodpeckers also produced earlier broods in habitats with a higher number of great spotted woodpeckers, including adults and nestlings. Besides an effect of breeding time, the woodpecker brood size (Brood) was positively related to the timing of prey development (Bbdev) and the amount of wood-boring beetles (Wbb) (Table 2). Accounting for most of captures, the abundance of bark beetles, including the species living on spruce, was associated with the total number of individual beetles collected.

In line with these results, linear and logistic regressions revealed that variation in the brood size and fledging date in the three-toed woodpecker were mainly explained by a combination of nestling food profitability (Bbdev) and abundance effects (Wbb) (Tables 3 and 4). In general local prey phenology accounted for most of the observed variation.

Prediction 2: Temperature and breeding performance

A preliminary analysis done on different periods (Nov.–Dec., Jan.–Feb., Mar.–May) separately showed significant effects of temperature on reproductive variables for each period, so the months were pooled in the final analysis (Table 5). In eastern Finland (1996–1999), female woodpeckers in the same five habitat patches produced, on average, larger broods with fledglings leaving earlier in years with warmer springs (April–May; an increase in monthly

mean temperature from 2.3 to 4.35 °C) (Table 5). The same pattern holds if averaging the annual values for the whole population (Fig. 1) (Spearman rank correlation: $n = 4$, $p < 0.001$). Temperature conditions of the preceding winter (November–March) also influenced significantly the reproductive decisions of spring individuals, with earlier breeding following colder winters (Table 5). However, this was probably because, during the 4 years of the study, warmer springs tended to occur following colder winters ($r = -0.462$, $p = 0.040$).

Prediction 3: Spring temperature, autumn dispersal and winter population size

Unlike the original prediction, in Finland (1973–2004) neither the number of dispersing juveniles nor the subsequent woodpecker winter population density increased linearly with the

Table 4. Results of logistic regression (stepwise forward) of three-toed woodpecker brood size (large (4–5) vs. small (2–3)), with and without information on local prey phenology (Bbdev). See Table 1 for explanation of acronyms.

Variable	Model log LR	–2log LR	df	<i>p</i>
+ Bbdev (10 broods)				
Bbdev	–6.931	10.340	1	0.001
– Bbdev (19 broods)				
Wbb	–12.504	4.894	1	0.027

Table 5. ANCOVA table for the effect of winter (Nov.–Mar.) and spring (Apr.–May) average monthly mean temperature on subsequent three-toed woodpecker fledging date and brood size, with territory as a random factor. Variables were log-transformed for normality, if necessary.

Dependent variable	Source of variation	df	MS	<i>F</i>	<i>p</i>	<i>b</i> ^a	SE ^a
Fledging date	Winter <i>T</i>	1	0.305	26.948	< 0.001	0.440	0.085
	Spring <i>T</i>	1	0.112	9.916	0.008	–0.423	0.134
	Territory	4	0.023	1.960	0.160		
	Error	13	0.011				
Brood size	Winter <i>T</i>	1	0.044	1.148	0.304	–0.168	0.156
	Spring <i>T</i>	1	0.164	4.274	0.059	0.513	0.248
	Territory	4	0.062	1.608	0.231		
	Error	13	0.038				

^a Slope of the regression equation, followed by the standard error of the slope.

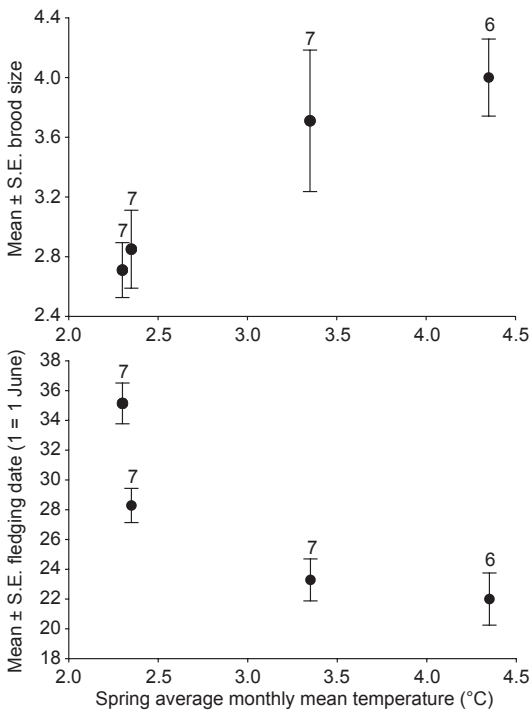


Fig. 1. Mean ($\pm$ SE) brood size and fledging date of three-toed woodpecker in relation to spring (April–May) monthly temperature (1996–1999), eastern Finland. Nest sample sizes are given above error bars.

preceding spring temperature, for a temperature range between 1.9–7.4 °C (Fig. 2). Instead, woodpecker numbers seemed to reach maxima following springs with temperatures between 3 and 6 °C, although a considerable inter-annual variation was apparent. Interestingly, especially

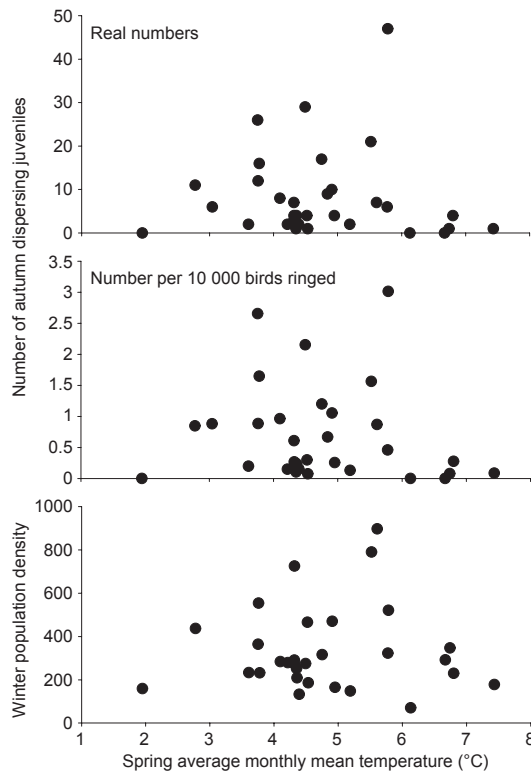


Fig. 2. Number of three-toed woodpeckers counted at Finnish ringing stations as dispersing juveniles (1973–2004) and during national winter bird inventories (1975–2004, summed censuses) as a function of the temperature of the preceding spring (April–May).

fewer young individuals were observed in years with unusually hot springs (i.e., with an average monthly mean temperature > 6 °C) (Table 6).

Table 6. One-way ANOVA on number of three-toed woodpeckers counted at Finnish ringing stations and during national winter bird inventories (all, early-, mid-, late-census) following usually warm (average monthly mean temperature $T < 6$ °C) and abnormally hot springs ($T > 6$ °C) (Apr.–May). n refers to the number of years with data. Variables were log-transformed +1 for normality.

	Spring $T < 6$ °C mean ($\pm$ S.D.) (n)	Spring $T > 6$ °C mean ($\pm$ S.D.) (n)	F	p
Natal dispersal				
True numbers	9.67 ($\pm$ 10.67) (27)	1.20 ($\pm$ 1.64) (5)	9.78	0.004
No. per 10 000 birds ringed (adjusted to ringing effort)	0.80 ($\pm$ 0.80) (27)	0.09 ($\pm$ 0.11) (5)	5.71	0.023
Winter density				
All censuses	359.28 ($\pm$ 204.80) (25)	223.40 ($\pm$ 106.79) (5)	3.12	0.088
Early census (1–14 Nov.)	126.80 ($\pm$ 60.62)	82.40 ($\pm$ 53.39)	5.66	0.024
Mid-census (25 Dec.–7 Jan.)	120.20 ($\pm$ 90.70)	68.40 ($\pm$ 29.97)	1.58	0.218
Late census (21 Feb.–6 Mar.)	112.28 ($\pm$ 65.68)	72.60 ($\pm$ 37.89)	1.74	0.198

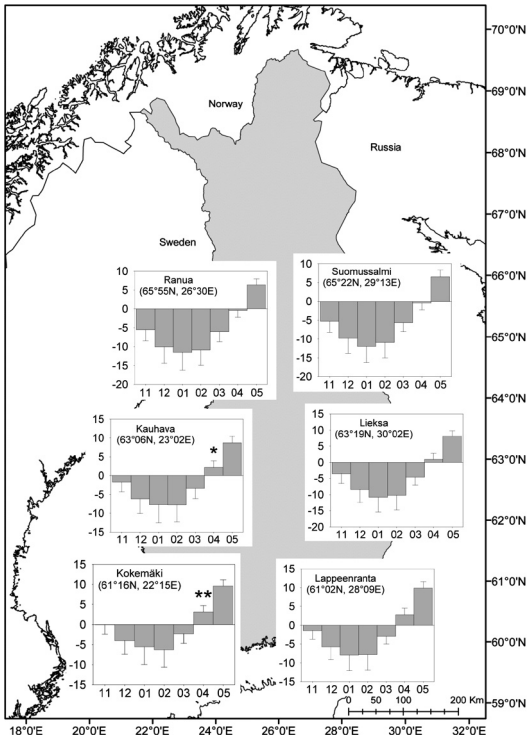


Fig. 3. Trends in monthly mean temperature (Nov.–May) over Finland for the period 1972/73–2003/04 ($n = 32$). Asterisks denote significant increase (* = $p < 0.05$, ** = $p < 0.01$).

Looking at long-term trends in monthly temperatures recorded at different weather stations (Nov.–May 1972/1973–2003/2004), only April became warmer over the years, although significant changes were limited to the western parts of the country ($61^{\circ}16'N$, $22^{\circ}15'E$: $r_s = 0.480$, $p = 0.005$; $63^{\circ}06'N$, $23^{\circ}02'E$: $r_s = 0.425$, $p = 0.015$) (Fig. 3). A similar trend although not (yet) significant was observed in southeast Finland ($61^{\circ}02'N$, $28^{\circ}09'E$: $r_s = 0.310$, $p = 0.084$). Meanwhile, the yearly number of dispersing juveniles and population size in the early winter declined markedly (natal dispersal: $r_s = -0.410$, $n = 32$, $p = 0.020$; winter density (01–14 Nov.): $r_s = -0.348$, $n = 30$, $p = 0.059$).

Discussion

In this study, I considered the effects of a variety of ecological factors on breeding time (fledging

date) and output (brood size) of the three-toed woodpecker. Among factors likely to influence reproductive decisions by woodpeckers were food abundance for nestlings (especially long-horn beetles), food phenology, and the abundance of potential competitors for food resources. Due to sample size limitations I omitted from the analyses the possible impact of parental age and pair-bond duration on reproductive performance (Sæther 1990, Wiklander 1998).

In line with the first prediction, three-toed woodpeckers in eastern Finland started breeding earlier and reared larger broods in habitat patches where the bark-beetle community developed earlier and/or faster and where wood-boring beetles were more abundant. Among estimates of food supply, only the index of prey development was related to the fledging date, showing the importance of prey phenology on reproductive decisions by woodpeckers. Accordingly, I found that as expected the mean fledging time was earlier and the brood size was larger in years with warmer springs (April–May), if laying date was related to prey phenology, which is temperature-dependent (Chararas 1962, Annala 1969, Salonen 1973). Similarly, although they did not relate their results to the development time of insect prey, Hogstad and Stenberg (1997) found white-backed woodpeckers *Picoides leucotos* — another predator of large wood-boring beetle larvae — to breed earlier, lay larger clutches and produce heavier fledglings in years and places with warmer winters and early springs. They also observed that pairs breeding in warmer places with shorter winters brought more wood-boring larvae for their young as compared with pairs from colder places, despite similar feeding rates in both areas. Frank (2002) noticed that white-backed woodpeckers preferred to breed in steep, south-exposed habitats, i.e. in habitats with the largest dead wood supply and the earliest prey development.

None of the food variables I measured were correlated with the breeding density and success of the great spotted woodpecker. Accordingly, Rolstad *et al.* (1995) found that breeding great spotted woodpeckers spent about equal time foraging in arboreal (canopies) as on the ground. Three-toed woodpeckers, by contrast, are exclusive arboreal feeders, searching for

prey from trunks and thick branches (Villard 1994). Furthermore, great spotted woodpeckers feed in winter mostly on seeds of coniferous trees (Dobrowolski *et al.* 1994), while three-toed woodpeckers forage on spruce bark-beetles (Fayt 1999), emphasising differences in niches and factors underlying their population dynamics. That the two species would not compete for the same food resources, although both species rely on animal food to provision offspring (Torok 1990, Pechacek & Krištín 1996), is further supported by the observation of earlier three-toed woodpecker reproduction in those patches with higher number of great spotted woodpeckers.

Developing beetles undergo seasonal changes in their caloric content and thereby their profitability, putting the reproductive decisions of predatory three-toed woodpeckers under strong natural selection in order to match nestling demand to a prey supply that varies annually. Among potential environmental cues that would help in accurately predicting future feeding conditions, the abundance and size of spruce bark beetles in spring could be one option. For example, earlier studies showed how three-toed woodpeckers ignore bark-beetle larvae younger than 3.5 to 4 months which presumably are too small to be profitable (Koplin & Baldwin 1970). In spring and early summer however, when fully-grown larvae become pupae (Fayt 2003), the use of bark-beetle timing of development as a cue to assess the benefits of reproduction would imply that females could discriminate among the different developmental stages. One way to distinguish the stages may be their nutritive content but this seems doubtful because the sizes are similar. Alternatively, by developing earlier, the larger-sized wood-boring longhorn beetle larvae are expected to become bigger and more profitable for a woodpecker than the smaller bark beetles. As supported by this study, I argue that females use the profitability (size) and abundance of longhorn beetle larvae at the time of egg-laying to adjust laying date and clutch size to the best time for rearing young.

Based on my results from eastern Finland, where I found that the productivity of the woodpecker population increased when the spring monthly mean temperature increased from 2.3 to 4.35 °C, I expected the number of juveniles dis-

persing annually over Finland to increase with the temperature of the preceding spring. Instead, a 32-year data set that encompassed years with spring temperatures between 1 and 8 °C revealed that natal dispersal rate reached a maximum following springs with a temperature between 3–6 °C, although large inter-annual variation was apparent. In particular, the number of dispersing young individuals was especially low in those few years with exceptionally warm spring (average monthly temperature > 6–8 °C). A similar pattern was found for the early winter density (assumed to be much influenced by the number of juveniles dispersing over the landscape). Among the most likely explanations, warmer springs could trigger larger food supply, causing most juveniles to settle closer to their birth place. As a result, fewer wandering woodpeckers would be noticed outside their breeding range in warmer years, with dispersal distances negatively correlated with local and regional prey abundances (Drent 1984, Hannon *et al.* 1987, Sonnerud *et al.* 1988). Large-scale eruptions of juvenile birds have typically been reported in late summer and autumn during years of high breeding density with subsequent food shortage (Perrins 1966, Eriksson 1971). However, this would hardly explain the higher autumn woodpecker counts in those years with intermediate spring temperatures.

Alternatively, low numbers of dispersers following abnormally elevated spring temperatures may also result from the failure of breeding individuals to adjust their initiation date to the development time of their prey (longhorn beetle larvae) so that breeding time and nestling food profitability is mismatched. Presumably, under particularly cold spring conditions (< 3 °C), longhorn-beetle larvae may not reach a profitable size at time of egg-laying constraining females to lay later and smaller clutches to match nestling demand with food availability. On the other hand, in particularly warm springs (> 6 °C), too early and rapid prey development may prevent breeding woodpeckers from matching their initiation dates to local food supply such that they start breeding when prey availability (abundance, spatial distribution) or profitability (energetic content) of food is deteriorating. Adult woodpeckers may experience higher mortality

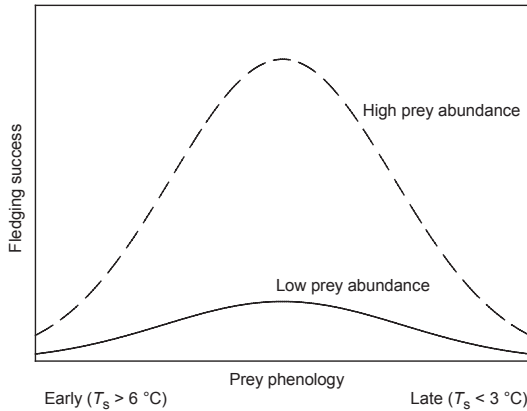


Fig. 4. Predicted annual variation in three-toed woodpecker fledging success, explained by a combination of nestling food profitability and abundance effects in relation to the heritable breeding time of the population. T_s is the spring (Apr.–May) average monthly mean temperature over Finland.

due to unsustainable metabolic effort when provisioning the offspring, as demonstrated for blue tits *Parus caeruleus* (Thomas *et al.* 2001). Brood reduction after hatch could be more prevalent than in the cold-weather case because parents may be fooled into laying an overly-large clutch size (K. Wiebe pers. comm.). The amount of food available for nestlings would depend not only on the timing of prey development but also on absolute prey abundance, both factors which may account for between-year variation in reproductive output and dispersal rate of three-toed woodpeckers (Fig. 4).

While parents would be able to lay the size of clutch appropriate for years with cold or usual spring temperature conditions, they may face increasing difficulties optimizing clutch size above some temperature threshold, with deadly implications for offspring survival. Thus, the idea of a mismatch between predator and prey caused by advanced spring development would depend on a food supply that not only peaks during the summer, but also crashes very rapidly. In contrast to conifer bark-beetles whose larvae develop in moist phloem and bark, part of long-horn beetles, whether shallow (e.g. *Tetropium* sp.) or deep (e.g. *Monochamus* sp.) borers, spend parts of their larval and pupal stages inside wood (xylem) after the first period spent in the phloem (Bílý & Mehl 1989). Such wood-boring activity

and pupation of larvae does not normally begin until late August of the beetle's first season (Rose 1957, Bílý & Mehl 1989), but warm springs—summers are expected to advance larval development, pupation, and adult emergence. When they reach the wood by gallery excavation from the phloem, larvae may suddenly become unavailable for the three-toed woodpecker, which uses bark scaling as its predominant foraging technique (Villard 1994). In Alaska, Murphy and Lehnhausen (1998) showed that three-toed woodpeckers fed mostly on bark beetles and fed only on wood-boring beetle larvae that were still in the phloem, i.e. in their first instar. It remains now to be seen how steep this food peak can be for three-toed woodpecker nestlings.

From November to May, only April has become significantly warmer in Finland over the last 32 years (Fig. 3), in parallel to a significant long-term decline in the number of dispersing juveniles and population size in the early winter. Although historical habitat loss clearly has had a profound negative impact on the density of three-toed woodpeckers in Finland during the last century (Järvinen & Väisänen 1979, Väisänen *et al.* 1986), I suggest that current changes in global surface temperature may be contributing to the woodpecker population decline, by promoting phenological disjunction between the predator and its prey. In particular, on-going increases in spring temperatures that so far have been limited to the warmest parts of the country may lead to uneven changes in selection pressures on laying dates over the geographic range of the woodpecker.

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