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Population biology of European woodpecker species: a review

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Understanding temporal dynamics of populations is important for the management of endangered and/or harvested populations as well as for evolutionary biology. Population sizes usually fluctuate over time because of changes in reproduction, mortality/survival, immigration and emigration. I reviewed the state of knowledge with respect to these vital demographic parameters on nine European woodpecker species. Only 4.2% of over 2100 publications found on these species reported on one or more of the vital rates, indicating severe knowledge gaps with respect to these traits. For most species, I found some information on reproduction (nest and fledging success), but generally much less on adult survival and immigration. No study quantitatively reported on emigration. No information on vital rates was found for *Picus canus* and *Dendrocopos syriacus*. Results are discussed in relation to geographic distribution and trends of the studied populations as well as with respect to life-history aspects and factors influencing vital rates.

Introduction

Population biology aims at understanding how assemblages of individuals of a given species are influenced by abiotic and biotic conditions across space and time. A central quantity of population biology is population size, which is usually estimated by the number of individuals of an organism at a given time and place (Williams *et al*. 2002). The size of wild populations is hardly ever constant over time, and ecologists and evolutionary biologists often focus on possible causes of these temporal changes and how they are related to individual fitness. Simply put, the temporal dynamics of populations is the result of gains and losses in a given population, which can be expressed by the equation

$$N(t + 1) = N(t) + B(t) + I(t) - D(t) - E(t) \quad (1)$$

Following Williams *et al*. (2002), $N(t + 1)$ and $N(t)$ refer to the sizes of a population at the times $t + 1$ and t, respectively; the gains of a population in the time period t to $t + 1$ result from reproduction $B(t)$ and immigration $I(t)$, while the losses are due to mortality $D(t)$ and emigration $E(t)$. These four variables, $B(t)$, $I(t)$, $D(t)$ and $E(t)$, are referred to as the four vital rates of a population and are primarily responsible for changes in population size (Williams *et al*. 2002). Knowledge of these vital rates is not only important for understanding population processes from an evolutionary viewpoint, but is essential for predicting population changes, for example in relation to habitat management, harvesting or global warming. Furthermore, vital rates are at the core of population viability models (Beissinger & Westphal 1998) and are thus of primary importance in conservation biology.

Woodpeckers are often considered good indicators of forest condition (Mikusiński *et al.* 2001, Scherzinger 2003). Ten woodpecker species regularly breed in Europe, and there exists a considerable body of literature on their abundances, habitat use and foraging behavior (for reviews *see* Glutz von Blotzheim & Bauer 1980, Cramp 1985, Winkler & Christie 2002, Michalek & Miettinen 2003, Pasinelli 2003). Much less is known, however, on how populations of these species are regulated, and what role the four vital rates play with respect to woodpecker population dynamics. Here, I review the current state of knowledge in terms of the four vital rates by comparing the number of publications reporting on one or more of these vital rates relative to all publications on a given species. I also give a detailed overview on the actual values of these vital rates, which may be useful for theoretical or applied studies, and examine differences among species and selected life-history aspects. Finally, I discuss some of the factors found to affect the vital rates in European woodpeckers.

Material and methods

For this review, I focused on nine of the ten woodpecker species breeding in Europe, these being lesser spotted woodpecker *Dendrocopos minor*, middle spotted woodpecker *D. medius*, great spotted woodpecker *D. major*, Syrian woodpecker *D. syriacus*, white-backed woodpecker *D. leucotos*, three-toed woodpecker *Picoides tridactylus*, green woodpecker *Picus viridis*, grey-faced woodpecker *Picus canus* and black woodpecker *Dryocopus martius*. I omitted the wryneck *Jynx torquilla*, because it is the only migratory woodpecker species in Europe, which may put its vital rates under different selective pressures than those of the resident species. I searched the following online databases for literature on the vital rates of the nine woodpecker species: Web of Science (Institute for Scientific Information (ISI)), Wildlife & Ecology Studies Worldwide (National Information Services Corporation (NISC)) and Zoological Records Plus (Biological Abstracts, Inc. (BIOSIS)). The inclusion of three databases, and particularly of the latter two, assured a fairly comprehensive coverage also of more local journals, which often provided very valuable information. All studies found from the time period from 1935 to August 2005 were included. In a first step, the databases were separately searched for each species using as key words its Latin, English and German names. For the three spotted woodpeckers, the Syrian woodpecker and the white-backed woodpecker, the Latin genus names *Dendrocopos* and *Picoides* were both used in conjunction with the respective species name (for example, both *Dendrocopos medius* and *Picoides medius* for the middle spotted woodpecker). In the case of *Picus canus*, grey-faced woodpecker and grey-headed woodpecker were both used as English search terms. The records found were imported into Endnote 7.0 (Thomson ISI ResearchSoft 1988–2003). Multiple entries of the same record were manually removed as were publications referring to the non-Eurasian range of a species (i.e. Africa in the case of the green and grey-faced woodpecker, North America in the case of the three-toed woodpecker). I added handbook chapters (Glutz von Blotzheim & Bauer 1980, Cramp 1985, Michalek & Miettinen 2003, Pasinelli 2003), Master and Ph.D. theses, and books not found in the online database search, but known to me, to each species-specific Endnote library. The records in each library represented the total number of publications for the species in question. In a second step, each Endnote library was searched with the key words, one at a time, 'breeding success', 'survival', 'mortality', 'immigration', 'emigration' and 'population'. I also included 'recruitment' as a search term, because it is also an important parameter in population biology. The resulting records were checked for information on one or more of the four vital rates, including recruitment.

Because 'rates' in the narrow sense were hardly ever given, I focused on nest success (defined as the percentage of nests that produced at least one fledgling relative to all nests) and fledging success (number of young per successful nest shortly before or after leaving the breeding cavity) with respect to reproduction. In some studies, fledging success was only reported from the early nestling stage, while in others, fledging success had to be manually calculated based on the data given; all such cases are indicated in Table 1. Survival refers to the percentage of adults surviving from one year to the next and was used instead of mortality, because most publications referred to survival rather than mortality. Immigration was defined as the percentage of unbanded individuals appearing in a study site relative to all banded and unbanded individuals, while emigration referred to birds banded in one study area or plot and seen somewhere else in subsequent breeding seasons. Local recruitment was defined as the number of banded fledglings that survived and subsequently bred in the study area. In very few cases (< 0.5% of all publications), it was unclear how the vital rates reported had been defined, and these publications were excluded from all analyses.

Medians and ranges are given for nest success, means and standard deviation for fledging success. To examine differences among species (green, grey-faced and Syrian woodpeckers excluded in all the following analyses), one-way ANOVAs were calculated on the basis of the values in Table 1 with species as a factor and nest success (arcsine-square root transformed) and fledging success (untransformed) as the dependent variables, respectively. To examine relations between reproductive traits and survival, mean values per species were calculated. Nest success and survival rates were arcsine-square root transformed before averaging. Wing length (mm) was used as a measure of body size. For each species, I calculated the average wing length based on all the data for adult birds of the respective species given in Cramp (1985).

Results

General findings

In total, I found 2173 publications on the nine European woodpecker species. The number of publications per species varied from 62 on the Syrian woodpecker to 554 on the great spotted woodpecker. Only 4.2% of all publications reported on one or more of the vital rates, while the majority was concerned with distribution, abundance estimation, habitat use, foraging behavior, social behavior, and forest management. No study on any species addressed emigration, which I therefore will not further point out in the following.

What is known about the vital rates of European woodpeckers?

Lesser spotted woodpecker

A total of 191 studies were found, but only very few of them reported on some of the vital rates (Fig. 1). Median nest success was 78.0% (range 74.2%–83.0%, $n = 4$ studies). Fledging success (from successful nests) was on average 4.2 (± 0.5, $n = 4$) young. Adult survival ranged from 59 to 64% (median 60%, $n = 3$), and local recruitment was 6% in the one study reporting on it (Table 1). Immigration was estimated to be 34% (± 17%), based again on one study only.

Studies reporting on vital rates were conducted in three countries, with two populations investigated in southern Sweden and southern Germany, respectively. The third study conducted in Great Britain was based on nest record cards collected by the British Trust for Ornithology (BTO), covering the time period from 1939 to 1989 (Glue & Boswell 1994). The German population experienced a slight decline during the study period (K. Höntsch pers. comm.), while the others appeared to have been stable (Glue & Boswell 1994, Olsson 1998, Wiktander 1998).

Middle spotted woodpecker

Of the nearly 200 studies reviewed, only five reported on nest success and four on fledging success, the respective figures being 74.3% (42.1%–89.7%) and 4.1 (± 1.4). Adult survival was estimated at 66.6% and 71.8% in two studies; the latter was derived from the annual adult mortality, which was estimated from the proportion of yearlings among breeders. Local recruitment and immigration rates were estimated to

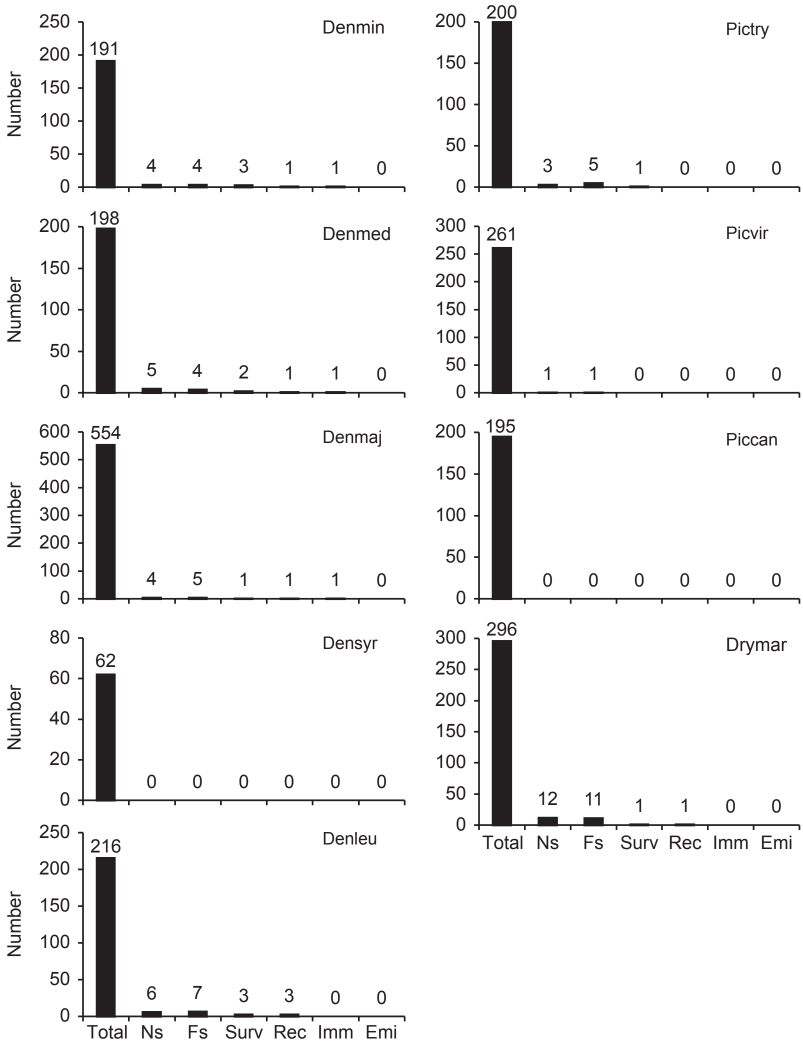

Fig. 1. Number of studies found per woodpecker species. Total = all studies; other categories refer to number of studies reporting on nest success (Ns), fledging success (Fs), adult survival (Surv), local recruitment (Rec), immigration (Imm) and emigration (Emi).

be 0% and 55.5%, respectively, in one study only.

The studies were conducted in five countries. Of the studied populations, the one in southern Sweden was declining (and ultimately went extinct) during the study period (Pettersson 1985), which may explain the low nest and fledging success found there (Table 1). In the Austrian study (Michalek *et al.* 2001), the species declined in two of the three study plots, while the population studied in western Germany appeared to be increasing (Wirthmüller 2002). The populations studied in northern Switzerland (Pasinelli 2001) and southwestern Russia (Kossenko 2003, Kossenko & Kaygorodova 2003) did not show any trend.

Great spotted woodpecker

Despite being the species with the highest number of publications found, a surprisingly small fraction of these report on demographic parameters (Fig. 1). Nest success averaged 79.5% (57%–85%, $n = 4$), while mean fledging success was 3.4 (± 0.8, $n = 5$). Adult survival (57.4%), local recruitment (5.5%) and immigration (43.0%) were estimated in one study population only.

The studies were conducted in six countries. Over the course of the studies, population numbers declined in Austria (Michalek *et al.* 2001), were stable in France (Bavoux 1985) and probably also in Great Britain (two studies: Tracy 1938, Glue & Boswell 1994), the Canary Islands

Table 1. Demographic parameters of European woodpecker species. Ns = nest success, Fs = fledging success, Surv = adult survival, Rec = local recruitment, Immi = immigration, *n* = number of nests. Emigration omitted because of missing studies. Superscript letters refer to remarks, superscript numbers to sources (presented in alphabetical order within each species).

Woodpecker	Ns (%)	*n*	Fs	*n*	Surv (%)	Rec (%)	Immi (%)	Location of study sites	Remarks	Source
Lesser spotted	83.0	>60	4.2[A]	32[A]				Great Britain	[A]nestlings counted ≥ 13 days after hatching	Glue & Boswell (1994)
	74.2	31	3.6	21	60.0[B]			S Germany	[B]averaged over sexes, own calc.	Rossmanith (2005)
	76.0	34	4.5	31	59.0[1]		34.3[C,1]	S Sweden	[C]own calc.	Wiktander *et al.* (1994), [1]Wiktander (1998)
	80.0	76	4.6	67	64.0[2]	6.0		S Sweden		Wiktander *et al.* (2001b), [2]Wiktander *et al.* (2001a)
Middle spotted	89.7	68	5.4	63	71.8			SW Russia		Kossenko & Kaygorodova (2003)
	89.5	38	5.1[D]	16[D]	66.6[3]	0.0[4]	55.5[4]	E Austria	[D]nestlings counted between days 5 to 16 after hatching	Michalek *et al.* (2001), [3]Michalek & Winkler (2001), [4]Michalek *et al.* (1999)
	74.3	35	3.2	26				NE Switzerland		Pasinelli (2001)
	42.1	19	2.7	8				S Sweden		Pettersson (1985)
	72.7	11						W Germany		Wirthmüller (2002)
Great spotted			2.7	98?				France		Bavoux (1985)
	85.0	>100	3.6[E]	144[E]				Great Britain	[E]nestlings counted ≥ 13 days after hatching	Glue & Boswell (1994)
	81.0	32	3.4[F]	37				Central Poland	[F]average (weighted by sample size) of two years, own calc.	Mazgajski (2002)
			4.8[G,5]	53[G,5]	57.4[6]	5.5[7]	43.0[7]	E Austria	[G]nestlings counted between days 5 to 16 after hatching	[5]Michalek *et al.* (2001), [6]Michalek & Winkler (2001), [7]Michalek *et al.* (1999)
			3.9[H,5]	7[H,5]				E Austria	[H]nestlings counted between days 17 to 23 after hatching	[5]Michalek *et al.* (2001)
			1.8	6				Spain (Canary Islands)		Nogales *et al.* (1993)
	78.0	14						S Sweden		Pettersson (1984)
	57.0	35						Great Britain		Tracy (1938)
White-backed			2.5[I,8]	15[I,8]	77.0[9]	12.5[10]		Central Sweden	[I]own calc.	[8]Aulén (1988), [9]Aulén & Carlson (1990), [10]Carlson & Aulén (1992)
	77.8	9	3.1	7				SE Norway		Bringeland & Fjaere (1981)
	84.0	30						SW France		Grange *et al.* (2002)

	91.4	70	2.4	38	86.0[J,11]	11.1[J,11]	W Norway	[J]averaged over sexes, own calc.	Hogstad & Stenberg (1997), [11]Stenberg & Carlson (1998)
	95.2	42	2.9[K]	40[I]	80.0	1.7	SE Finland	[K]own calc., only successful nests, 1988–1991	Virkkala *et al.* (1993)
			2.6[L]	20[L]			SE Finland	[L]1970-1987	Virkkala *et al.* (1993)
	57.7	26	3.4	7			E Poland		Wesołowski (1995)
Three-toed			1.6	9			S Germany	assumed mean of range given 1.4–1.8	Andris & Kaiser (1995)
	79.0	38	2.0	30	66.2[M,12]		SE Germany	[M]averaged over sexes, own calc.	Pechacek (in review), [12]Pechacek *et al.* (2005)
	75.0	16	2.3	16			SE Switzerland		Ruge (1974)
	75.0	8	1.7	6			S Germany		Ruge *et al.* (2000)
			1.2	6			S Germany		U. and V. Dorka cit. in Hölzinger *et al.* (2001)
Green	85.3	>100	3.9[N]	53[N]			Great Britain	[N]nestlings counted ≥ 13 days after hatching	Glue & Boswell (1994)
Black	80.2	86	2.7	69			Danish/German island of Jütland	[O]own calc. over both sexes	Christensen (1995)
	79.7	118	2.8	94		11.0[O]	Dito		Christensen (2002)
	92.0	25	3.1	23			NE France		Cuisin (1981)
					70.1[P]		Island of Bornholm, Denmark	[P]weighted average over sexes, own calc	Hansen (1999)
	80.2	96	3.6	77			E Denmark		Johansen (1989)
	96.0	70					W Germany		Kühlke (1985)
	96.0	134	3.3	128			S Germany		Lang & Rost (1990)
	91.0	177	3.0	140			Central Germany		Lange (1996)
	75.0[Q]	43	2.7	38			E Germany	[Q]average of two years, own calc.	Möckel (1979)
	60.9	69	3.7	39			Central Sweden		Nilsson *et al.* (1991)
			4.0	9			Finland		Pynnönen (1939)
	55.0	165					SE Norway		Rolstad *et al.* (2000)
	86.0	70	2.8	60			Central Germany		Rudat *et al.* (1981)
	74.0	62	3.8[R]	46			Central Sweden	[R]weighted mean of farmland and forest estimates, own calc.	Tjernberg *et al.* (1993)

(Nogales *et al.* 1993), Poland (Mazgajski 2002), and southern Sweden (Pettersson 1984).

Syrian woodpecker

The Syrian woodpecker can be considered the least known species among the European woodpecker species. Not only did I find just 62 publications, but also none of these reported on any of the vital rates relevant for this review.

White-backed woodpecker

Median nest success of six out of 216 studies found on this species was 87.7% (57.7%–100.0%). Average fledging success amounted to 2.8 (± 0.3, $n = 7$) young. Three studies reported on adult survival, which ranged from 77%–86%. Local recruitment varied between 1.7% and 12.5% ($n = 3$). No study reporting immigration rates was found.

Two studies were conducted in Norway, the other four in Finland, Sweden, Poland and France (Table 1). Populations declined over the study period in Finland (Virkkala *et al.* 1993) and Sweden (Aulén 1988, Aulén & Carlson 1990), but were stable in Poland (Wesołowski 1995), Norway (Bringeland & Fjaere 1981, Stenberg 1998) and presumably also in France (Grange *et al.* 2002).

Three-toed woodpecker

A total of 200 publications were found, of which three and five reported on nest and fledging success, respectively. Median nest success was 75% (75.0%–79.0%) and thus in the range of the estimates for the other woodpecker species reviewed. In contrast, fledging success was 1.8 (± 0.5) young per successful nest, well below the values of the other species. Estimates of survival were found in one study, which reported annual adult survival of males to be 71.8% (95% confidence intervals 62.3%–81.9%, $n = 28$) and of females 60.5% (46.3%–75.6%, $n = 27$). No data on local recruitment or immigration were found for this species.

All the three studied populations were located in central Europe, representing thus only a very small portion of the species' range in Eurasia (Winkler & Christie 2002). One of the two German studies focused on an area where the three-toed woodpecker has been expanding during the last two decades of the past century (Ruge *et al.* 2000), while the other study in Germany as well as the one in Switzerland were done in stable populations (Ruge 1974, Pechacek 2006).

Green woodpecker

Although a fairly large number of publications was found for this species (261), only one reported on nest and fledging success, these being 85.3% and 3.9. No information was found on other demographic parameters relevant for this review.

The study reporting on reproductive parameters was based on BTO nest record cards, covering the time period from 1939 to 1989 (Glue & Boswell 1994). During this period, parts of the Green woodpecker population in Great Britain appeared to have been stable (SE and SW England), while the species re-colonized other parts during the 20th century (N England and Scotland).

Grey-faced woodpecker

I did not find any study reporting on demographic parameters relevant for this review among the total of 195 publications. Three studies may contain valuable information, but I could not access them, because they were published in North Korean (Choe & Pak 1990), South Korean (Won & Koo 1986) or Chinese journals (Du 1987).

Black woodpecker

The black woodpecker can be considered the best-studied woodpecker species in Europe, at least in terms of reproduction. Median nest success was 80.2% (55.0%–96.0%, $n = 12$); it is remarkable that sample sizes were above 40 nests in all but one of these 12 studies (Table 1). The average number of fledglings per successful nest calculated over 11 studies was 3.3 (± 0.5). On the other hand, just one study out of a total of 296 reported on adult survival and another one on local recruitment, but none on immigration. Survival rates of adult males and females were 77% and 65%, respectively. Local recruitment was 11.3% in males and 10.7% in females.

The species was studied in six countries (Table 1), from which Germany and Denmark stand out by yielding estimates from five and three different populations, respectively. At least four populations in Denmark, Germany and Sweden were stable over the course of the studies (Johansen 1989, Lang & Rost 1990, Tjernberg *et al*. 1993, Christensen 1995), and probably two others in Germany and Norway as well (Lang & Rost 1990, Rolstad *et al*. 2000), while one study population on the Island of Bornholm, Denmark, was declining (after an initially strong increase, *see* Hansen 1999), and no conclusive information was found for the remaining five (Pynnönen 1939, Möckel 1979, Cuisin 1981, Rudat *et al*. 1981, Kühlke 1985).

Differences across species and life-history aspects

Nest success did not differ among species (Table 2), indicating that in this reproductive trait variation within and between species was similar. On the other hand, species identity explained 56% of the variation in fledging success; here, variation within species was significantly smaller than between species (Table 2). Post-hoc Tukey-Kramer tests (with adjustment of p values for multiple comparisons, Proc GLM, SAS Institute Inc. 2002–2003) indicated that fledging success of the three-toed woodpecker was significantly lower than in every other species considered. In addition, fledging success was significantly lower in the white-backed woodpecker compared to the lesser spotted woodpecker. All other comparisons were nonsignificant.

There were no significant relations between nest success and adult survival (Spearman rank correlation: $r_s = 0.60$, $p > 0.21$, $n = 6$) or between fledging success and adult survival ($r_s = -0.43$, $p > 0.39$, $n = 6$, Fig. 2). Further, neither nest success nor fledging success or adult survival were related to body size (nest and fledging success: $r_s = 0.49$, $p > 0.32$, $n = 6$; adult survival: $r_s = 0.57$, $p > 0.22$, $n = 6$).

Discussion

State of knowledge

The current state of knowledge in terms of reproduction, adult survival, local recruitment, immigration and emigration varies considerably among the nine European woodpecker species reviewed. Besides this variation among species, levels of knowledge substantially differ between the vital rates themselves. If studies reported on one of these parameters, they most often provided data on nest success and fledging success. More specifically, there is fairly good information on the reproductive performance of the black woodpecker, which has been covered in a dozen studies. There is modest information on the reproductive performance of the lesser spotted woodpecker, the middle spotted woodpecker, the great spotted woodpecker, the white-backed woodpecker and the three-toed woodpecker, with three to seven studies, depending on the species, reporting on nest success and/or fledging success.

Table 2. Variation in reproductive traits among species. Results of one-way ANOVAs, with species as factor and nest success ($n = 33$) and fledging success ($n = 36$) as dependent variables. Nest success was arcsine-square root transformed before analysis. df = degrees of freedom, SS = sums of squares, MS = mean squares.

Dep. variable	Source	df	SS	MS	F	$P <$
Nest success	Intercept	1	32.46	32.46	1213.87	0.001
	Species	5	0.05	0.01	0.36	0.870
Fled. success	Intercept	1	338.08	338.08	672.43	0.001
	Species	5	18.86	3.77	7.50	0.001

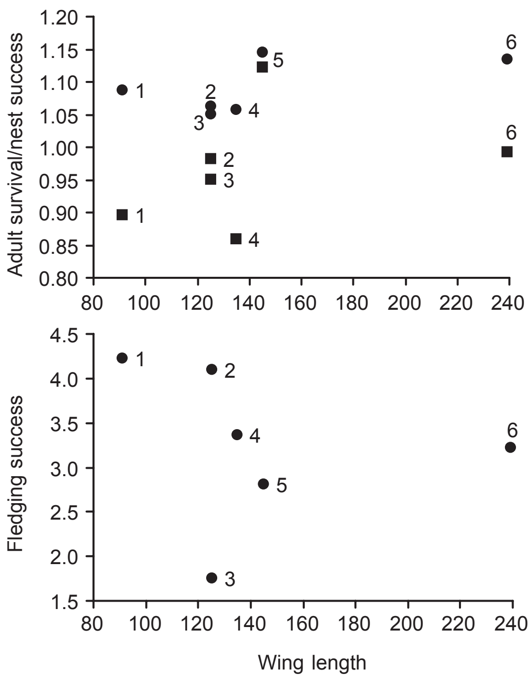

Fig. 2. Reproductive traits and adult survival in relation to body size. Top panel: means of arcsine-transformed values per species are given for adult survival (squares) and nest success (circles), respectively; bottom panel: means of fledging success per species. Body size estimated through wing length (mm) after Cramp (1985). Numbers refer to woodpecker species: 1 = lesser spotted woodpecker, 2 = middle spotted woodpecker, 3 = three-toed woodpecker, 4 = great spotted woodpecker, 5 = white-backed woodpecker, 6 = black woodpecker.

Very little is known on the reproductive performance of the green woodpecker (one study only), while we are completely ignorant in the cases of both the grey-faced and the Syrian woodpeckers. This finding is surprising with respect to the two *Picus* woodpeckers, because both are widely distributed, although scarcely anywhere very abundant (Cramp 1985, BirdLife International 2004). The rather secretive behavior of the grey-faced woodpecker (Spitznagel 1993) may explain the lack of data in this species, while this explanation is unlikely to hold for the green woodpecker. The Syrian woodpecker occupies the smallest range among the woodpecker species reviewed here (Cramp 1985), which, possibly together with its currently safe status (BirdLife International 2004), may be responsible for the lack of studies. On the other hand, examination of the ecological and behavioral mechanisms allowing coexistence of the closely related Syrian and great spotted woodpeckers as well as the causes and fitness consequences of hybrid matings would be very exciting.

Large knowledge gaps exist for all species with respect to survival, recruitment, immigration and emigration. Not a single study was found to quantify emigration, which may be attributed to the difficulties (1) of setting up and monitoring one color-banded population, let alone several such populations, and (2) of distinguishing between emigration and mortality. Estimates of immigration were given in a total of three studies, one each on the lesser spotted woodpecker, the middle spotted woodpecker and the great spotted woodpecker. Adult survival and local recruitment were best studied in the white-backed woodpecker and the lesser spotted woodpecker. Both species have experienced declines in Fennoscandia during at least the last three decades of the past century (Aulén 1988, 1993, Virkkala *et al*. 1993, Olsson 1998, Stenberg 1998, Wiktander 1998, BirdLife International 2004), which had prompted several detailed studies on the ecology of both species. As in the case of reproduction, no information on survival, recruitment or immigration was found for the green, the grey-faced and the Syrian woodpeckers. In the black woodpecker, just two studies reported on adult survival (Hansen 1999) and local recruitment (Christensen 2002), respectively, which is surprising, given that some of the studies reporting on reproductive parameters involved individually marked birds (e.g. Rudat *et al*. 1981, Nilsson *et al*. 1991, Tjernberg *et al*. 1993, Lange 1996, Rolstad *et al*. 2000). It is hoped that this review will stimulate publication of data concerning survival and immigration of the black woodpecker, and of data on the vital rates of other woodpecker species as well, if such data are available at all.

Why is there such a paucity of data on the vital rates of European woodpeckers? The answer is that woodpeckers are difficult to study for several reasons. First and probably foremost, woodpeckers do not use nest boxes for breeding, which makes them less suited for experimental research in evolutionary biology. Second, the efforts needed to gather enough data on reproduction to allow statistical analyses are substantial, because densities of most woodpecker species are considerably lower than those of other resident forest-inhabiting species of similar size, resulting in increased time required to locate breeding cavities. For example, average densities of the lesser spotted woodpecker are at least one order of magnitude lower than densities of the similar-sized nuthatch *Sitta europea* (Glutz von Blotzheim & Bauer 1993, Winkler & Christie 2002). In addition, if breeding cavities are found, not all of them can be accessed because many woodpecker species excavate breeding cavities in rotten or dead stems or limbs (Winkler & Christie 2002). Climbing trees for nest checks and banding nestlings is a further labor-intensive task. Third, capturing adults for banding is difficult and time-consuming, severely constraining the study of survival and dispersal. Fourth, woodpeckers are relatively long-lived (Winkler & Christie 2002), which necessitates long-term field studies for estimating life-time fitness of individuals and demographic traits of populations. Although the importance of long-term field studies for ecological, behavioral and evolutionary research is unquestioned, today's functioning and structure of academia in general, and of universities and research institutions in particular, do not encourage carrying out such studies.

Geographic distribution of studies

Given the overall paucity of studies reporting on the vital rates of the nine woodpecker species reviewed, it is not surprising to find that the coverage of the geographical ranges is far from complete for most species. In most cases, there are data from a handful of populations that were the subject of intense, and sometimes long-term, studies. Although these studies usually reported detailed and very relevant information on some of the vital rates, there is a lack of replication in space. For example, data on the highly specialized three-toed woodpecker were obtained from three populations studied in central Europe (S, SE Germany and SE Switzerland), although the Palearctic range of the species (Nearctic studies were excluded in this review) is very large (Cramp 1985, Winkler & Christie 2002). A similar clustering of studies was evident for the white-backed woodpecker, which has mainly been studied in Fennoscandia so far (Norway: Bringeland & Fjaere 1981, Stenberg 1998, Sweden: Aulén 1988, Aulén & Carlson 1990, Finland: Virkkala *et al.* 1993), while relatively little is known from the southern (but *see* Grange *et al.* 2002) or eastern parts (but *see* Wesołowski 1995) of its range. The same pattern was found for the black woodpecker, and although this species has received considerable attention, most studies were done in central and northern Europe (*see* Table 1), again with little information from the southern and eastern parts of the species' range. The lesser spotted woodpecker has been intensively studied in just two populations, one in southern Sweden (Olsson 1998, Wiktander 1998), the other in southern Germany (Höntsch 2005, Rossmanith 2005). Finally, data on the vital rates of both the middle spotted woodpecker and the great spotted woodpecker were reported from quite different parts of their ranges, despite the number of studies being far from high in each species.

Population status

Demographic parameters may vary in relation to population size and/or population trend (e.g. Thomson *et al.* 1997, Newton 1998, Courchamp *et al.* 1999, Stephens & Sutherland 1999), which to some extent was also evident in this review. Pettersson (1985) found very low nesting and fledging success in a population of the middle spotted woodpecker in the final stage before extinction. Such low success rates are unlikely to be representative for viable populations of the species (Table 1). Similary, Virkkala *et al.* (1993) reported low recruitment rates (1.7%) in the white-backed woodpecker during a period of population contraction, while current recruitment rates, after a period of population recovery, are within the range of those from other studies considered to be stable (approx. 10%, R. Virkkala pers. comm.).

Population trends were given in 22 studies, while no trend could be deduced from 15 others. If these 15 studies are assumed to have been stable over the study period (which seems reasonable, because both increasing and declining population trends are more likely to be reported than stable ones), 28 populations did not show any trend, seven were declining and two increasing. This suggests that most estimates of vital rates were not confounded by demographic processes that may act in declining or expanding populations.

Differences across species and life-history aspects

Nest success in woodpeckers typically varies between 70% and 100% (Winkler *et al*. 1995), so the absence of species-specific differences in nest success found here is not surprising. This result suggests that variation in nest success within the species examined is as large as between these species (cf. Table 2). On the other hand, fledging success differed among species, with three-toed woodpeckers fledging significantly fewer young than each of the other five species considered. This may reflect differences in the productivity of the species' main habitats. Three-toed woodpeckers typically inhabit coniferous forests (boreal or mountainous), which overall supposedly are less productive than mixed or deciduous forests preferred by the other species (Glutz von Blotzheim & Bauer 1980, Cramp 1985, Winkler & Christie 2002). If so, this would be in line with the food limitation hypothesis, stating that changes in food availability can lead to changes in clutch size (e.g. Martin 1987, Saether 1994a, 1994b), and hence annual fecundity.

Whatever their causes, the differences between species in fledging success may have implications for conservation. If a population viability analysis has to be done for a woodpecker species in an unstudied population, estimates of fledging success from other populations of the same species should be used rather than a 'generalized' woodpecker fledging success based on across-species estimates. The latter approach may be valid for nest success, given the lack of species-specific differences found.

One of the predictions of classical life-history theory is that annual fecundity is negatively related to adult survival rate (*see* references in Bennett & Owens 2002). Support for this prediction in birds has been presented and summarized by Bennett and Owens (2002). In the closely related group of species examined here, no significant relations between adult survival and nest success or fledging success were found. Sample size may have been too low to detect a significant correlation, but the sign of the correlation coefficient for adult survival *versus* fledging success was nevertheless in the expected direction. Bennett and Owens (2002) proposed that analyses across families and orders most likely reveal patterns of co-variation among key life-history traits. I compared members of the same subfamily (*Picinae*), which may explain why I did not find support for the expected relations. Finally, variation in nest site safety (open- *versus* cavity-nesting) has been suggested as an important ecological factor shaping life-history traits (Martin 1995, Bennett & Owens 2002). However, the woodpecker species studied are all primary cavity nesters, so variation in nest site safety may be insufficient to exert the selective pressure required for diversification of the life-history traits considered here.

Factors influencing vital rates

With respect to abiotic and biotic factors potentially influencing vital rates of European woodpecker species, I found the most often studied factors to be weather conditions, cavity age, habitat quality, and individual age. Despite nesting in cavities, which are assumed to provide shelter from inclement weather, there is fairly good evidence for some woodpecker species that weather conditions during the breeding season are important with respect to reproductive performance. For example, annual nest success was positively associated with mean daily temperature during the incubation period in the lesser spotted woodpecker (Wiktander *et al*. 2001b) and with mean temperature during the nestling period in the middle spotted woodpecker (Pasinelli 2001). Furthermore, the number of fledglings in the latter species was negatively related to the mean amount of rainfall during the nestling period (Pasinelli 2001); a similar negative relation between breeding success and rainfall in May was reported for the white-backed woodpecker, which in turn benefited from increased temperatures in May (Hogstad & Stenberg 1997). These weather influences likely reflect insufficient provisioning of nestlings by their parents rather than direct effects of adverse weather conditions, although this hypothesis has not experimentally been tested in any European woodpecker species.

A relation between cavity age and nest or fledging success could be expected for at least two reasons. First, predators may remember the location of cavities from year to year and regularly revisit them (Sonerud 1985), so that the construction of a new cavity may reduce predation risk. Second, parasite load may be reduced in new as compared with that in old cavities (Short 1979). Both hypotheses predict an advantage of breeding in new cavities, but the evidence is ambiguous. On the one hand, Nilsson *et al.* (1991) found nest success of the black woodpecker to be significantly higher in new than in old cavities, but no such difference existed with respect to fledging success (considering successful nests only). These findings support the predator avoidance hypothesis, but not the parasite load hypothesis. On the other hand, no relations between cavity age and nest success were reported by Rolstad *et al.* (2000) in the black woodpecker and by Mazgajski (2002) in the great spotted woodpecker. Further, no association between cavity age and fledging success of black woodpeckers was found by Lang and Rost (1990) comparing successful nests and by Lange (1996) focusing on all nest attempts. Thus, so far there is no evidence from European woodpeckers to support the parasite load hypothesis and only weak evidence in favor of the predator avoidance hypothesis.

Territory quality may be another important determinant of reproductive success (e.g. Stacey & Ligon 1987, Catchpole & Phillips 1992, Aho *et al.* 1999), but the evidence in European woodpeckers is again controversial. In the black woodpecker, fledging rate (number of fledged young as percentage of clutch size) was higher in clear-cuts and young forests (containing remnant trees) as compared with that in middle-aged and old forest stands (Rolstad *et al.* 2000). As a tendency, the number of fledglings in the lesser spotted woodpecker positively correlated with foraging preference for lime (*Tilia* sp.), this preference being viewed as indicative of the total food availability in a territory (Olsson *et al.* 2001). In the middle spotted woodpecker, no relations between the number of fledglings and either the density of large oaks or the density of potential cavity trees were found (Pasinelli 2001), although these habitat variables had been shown to affect home range size of the species (Pasinelli 2000) and were therefore expected to reflect habitat quality.

In many bird species, young individuals generally reproduce less well than older ones (e.g. Saether 1990, Komdeur 1996), even if increased reproductive success with increased age may be explained by an improved access to high-quality territories with increasing age rather than by increased competence (experience or foraging skills, etc.) (Pärt 2001a, 2001b). In addition, the duration of the pair bond may also have significant effects on reproduction, in that pairs having bred together for several years usually are more successful than new pairs breeding together for the first time (e.g. Schiegg *et al.* 2002). Few studies have so far addressed such questions in European woodpeckers, not least because of the immense efforts required to obtain adequate sample sizes. In the lesser spotted woodpecker, Wiktander *et al.* (2001a) found evidence for improved reproductive success of old males (≥ 2-years old) as compared with that of 1-year-old males, while no such pattern was found in females. In addition, pairs having bred together for two or more years were significantly more successful in raising young than new pairs, even if new pairs consisted of individuals with breeding experience (i.e. having previously bred with another partner). In the middle spotted woodpecker, pairs with 1-year-old birds were not less successful than pairs with only 2-year or older individuals, but sample sizes were small in both categories (Pasinelli 2001).

Apart from reproductive performance, factors affecting adult survival have received some attention in European woodpecker species. For resident bird species in general, an influence of winter weather on survival perspectives has often been found, with severe winters reducing individual survival (e.g. Thomson *et al.* 1997, Newton 1998). In the white-backed woodpecker, mean annual survival of females was indeed positively related to temperatures in February and March, but also negatively related to the amount of precipitation during the same period; interestingly, no such patterns were found in males (Stenberg 1998). In contrast, no significant relations between winter temperatures and adult survival were found in the lesser spotted woodpecker, whereas male survival, but not female survival, was positively related to mean temperature during the nestling period (Wiktander 1998).

Conclusions

Considering that woodpeckers are important indicator species for forest condition, and that these species will likely be used in future assessments of forest habitats and management actions, there exist striking knowledge gaps regarding vital rates for all nine species reviewed here. The situation is particularly severe for the green woodpecker, the grey-faced woodpecker and the Syrian woodpecker. The latter two species along with the black woodpecker, middle spotted woodpecker, white-backed woodpecker, three-toed woodpecker and two subspecies of the great spotted woodpecker belong to Annex I of the Birds directive of the European Union listing threatened species that require special conservation measures to be taken for their habitats. Of these species, we have little idea which habitats can be considered sources or sinks, i.e. having population growth rates above or below 1 (Pulliam 1988). This makes it very difficult and speculative to delimit areas, which should effectively help to maintain viable populations of these species, particularly because focusing on density as the sole estimate of habitat quality can be misleading (Van Horne 1983, Kellner *et al*. 1992). There is thus an urgent need to study population dynamics of essentially all European woodpecker species in a systematic way, which includes replication in space (different biogeographic regions, different habitats) and in time (long-term studies on color-marked individuals). It is clear that such efforts can only work out if funding agencies are willing to provide substantial support and if researchers are able to conduct long-term studies on species that are comparatively difficult to study.

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