

Breeding performance, natal dispersal, and nest site fidelity of the three-toed woodpecker in the German Alps

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I studied the breeding biology of the three-toed woodpecker *Picoides tridactylus* in order to determine factors that influence annual and seasonal variations. Data from 37 pairs showed that 79% of nests produced at least one fledgling. The median laying date was not affected by elevation, and annual clutch and brood sizes did not differ significantly across the years. Seasonal trends supported the advantage of early breeding. More than 70% of clutches were laid within the span of 9 calendar days. Clutch and brood sizes declined with later laying dates and earlier breeders were more successful. Females paired with older males laid eggs earlier than those that were paired with younger males. Woodpeckers showed nest site fidelity across the years. Laying date relative to the rest of the local population, rather than the absolute laying date, should be regarded as an important determinant for breeding success in three-toed woodpeckers.

Introduction

Reproductive success in birds is associated with the timing of breeding and with other aspects of breeding performance including clutch and brood sizes, and hatching and fledging rates. The crucial decision of when to initiate egg laying and how many eggs to lay may be influenced by body condition, social position, climate, and hormonal interplay (Bairlein 1996).

The annual (i.e. between seasons) timing of breeding in birds that forage on tree-surface insects is well synchronized with the peak abundance of food for nestlings and fledglings (Lack 1950, Perrins 1991, Blondel *et al.* 1993). Since insects and other arthropods usually emerge from winter shelters when air temperature reaches a certain threshold (Lobinger 1994), timing of

breeding in temperate zones is often associated with spring air temperatures (Matthysen 1989, Wesolowski 1998, Pasinelli 2001). However, the observed relationship between the temperature and annual onset of breeding is likely to be indirect in nature, and may instead reflect the bird's ability to use temperature-related environmental features to initiate laying. For instance, insectivorous birds use bud-burst (Wiktander *et al.* 2001) or leafing (Schmidt 1984) as proximate cues to start egg laying. On the other hand, between-season trends seem to be inconsistent with patterns of other reproductive parameters (e.g. clutch size, breeding success, fledging success) of tree-surface foraging, insectivorous birds (Perrins & McCleery 1989, Sinclair 1989, Nilsson 1991, Smith 1993, Pasinelli 1999, Wiktander *et al.* 2001).

Seasonal (i.e. within a season) variation of individual laying dates around the population mean may have significant consequences for individual fitness. Early offspring fledge earlier and benefit from a longer post-fledging period before facing critical periods that are usually associated with increased mortality (e.g. natal dispersal, migration, over-wintering) (Nilsson 1989a, Svensson 1997). Competitive advantages of earlier-fledged birds in settling in empty territories may also be important (Wesołowski 1998). A decline in clutch size associated with later laying dates appears to be general in birds (Daan *et al.* 1988, Crick *et al.* 1993, Kristin *et al.* 2000). Some other reproductive parameters (e.g. hatching, fledging, breeding success) also decline with the progress of the season (Daan *et al.* 1988).

Thus, strong selective pressure for early breeding seems likely and numerous researchers have investigated proximate factors, which might accelerate or delay the timing of breeding in birds. Female traits such as nutritional state (Martin 1987) or age (Saether 1990), and male traits such as song (Wright & Cuthill 1992) or courtship feeding (Nisbet 1973) were all found to affect laying dates in birds. Characteristics of the pair bond such as duration (Fowler 1995) or affiliative behaviour (McGraw & Hill 2004) are also regarded as important determinants of breeding onset.

In the context of conservation biology, detailed information on breeding performance under varying conditions is needed to identify factors that influence reproductive success. Reproductive success often reflects habitat quality, which is often measured by some particular vegetative features (Hall *et al.* 1997). Vegetative features (e.g. forest structure) can be affected by management decisions, and thus assessing habitat quality is of paramount importance for wildlife management. However, most management decisions for endangered or rare species are still based on bird population density estimates, although these were often misleading with regard to habitat quality (Van Horne 1983). Even if factors that impact breeding behaviour and success cannot be controlled (e.g. age of the breeding birds, weather conditions during breeding), they must be considered when habitat quality is to be assessed for conservation actions. For instance, in order to estimate how many breeding pairs are needed for a self-sus-

taining population, demographic factors must be taken into account (e.g. Reed *et al.* 1993).

In the three-toed woodpecker *Picoides tridactylus*, whose populations are declining in most of Europe (Tucker & Heath 1994, Mikusiński & Angelstam 1997), conservation actions are urgently needed to ensure survival of the species. However, there is almost no detailed information on which factors influence breeding behaviour and success, and which specific parameters (e.g. clutch size and brood size, fledging rate) may be responsible for the overall low population density of the three-toed woodpecker (Ruge 1974, Ruge *et al.* 2000, Fayt 2002). To bridge this gap, I examined annual and seasonal patterns of reproductive timing and performance of the species from 1993–2004 in Berchtesgaden National Park (southeastern Germany). I also investigated natal dispersal, and nest-site fidelity (including additional data from 2005). My study site included one of the remaining high-density populations of the three-toed woodpecker, thus providing a rare opportunity to investigate the breeding biology of this species in a stable, dense population.

Material and methods

Study area

The study was conducted in Berchtesgaden National Park, Germany (47°32'N, 12°56'E). Alpine forest dominated by spruce *Picea abies* and larch *Larix decidua* covers 8100 ha of the Park. The topography of my study area (i.e. about 4600 ha of this forest) includes steep slopes that face northwest to northeast (64%) and thus are shaded, and 19% that face the west. All are between 600 and 1700 m above sea level (Rall 1990). In contrast to the surrounding areas of extensively managed forest, the 30 m³ ha⁻¹ of dead wood scattered throughout the Park (Konnert 2000) provides excellent woodpecker habitat.

Study species

The three-toed woodpecker is a medium size (65–75 g), inconspicuous and elusive, non-migratory bird that inhabits taiga of the north and alpine

coniferous forests close to the timber line in some mountain ranges south of the boreal belt (Winkler & Christie 2002). In Berchtesgaden National Park, home-range sizes vary between 102 and 154 ha per pair (Pechacek 2004). During breeding, these woodpeckers feed mainly on spiders and wood-boring beetle larvae (Pechacek & Kristin 2004). Three-toed woodpeckers are single-brooded and within my study area excavate a new nesting cavity each year (Pechacek 2001). Their mating system is characterized by predominant social and genetic monogamy (Pechacek *et al.* 2005). As in all other woodpecker species, the nest is the roost cavity of the male and he is always the parent that is in the cavity with eggs or small nestlings at night (Jackson 1976). Estimated breeding density of the three-toed woodpecker in Berchtesgaden National Park ranges between 0.9–1.0 pairs per km² (Pechacek 1995), and 35–40 pair territories are found within the study area.

Trapping and tracking

I trapped 55 adults (28 males and 27 females of 37 pairs) during the breeding seasons of the study. Each bird was tagged with an individual combination of colour rings; to facilitate nest search in rough, mountain terrain, 38 woodpeckers were also fitted with a 1.5-g radio transmitter (Type BD 2G, Holohil Ltd., Canada). Radio-telemetry was the only practical means to monitor duration of parental care after fledging. I felt confident that the transmitters did not affect the behaviour of the birds, as I worked simultaneously with radio-tagged and untagged woodpeckers and did not observe any marked differences between the groups (*see* Pechacek 2004 for further details on trapping, radio-tagging, and tracking equipment).

Aging of adults was not possible. However, I assumed that unknown birds caught in the spring in formerly occupied territories were yearlings. I based this assumption on the fact that among all colour-ringed adults, I never observed an individual outside its former home range in the years following ringing. I never recorded any adult breeding dispersal, or any floaters and it was reasonable to assume that when one or both of the pair members disappeared from one season to the next, they had died (Pechacek *et al.* 2005).

Observations on breeding performance

Each year, I observed the woodpeckers from the first days in April until 15 September. When I found a nest being excavated, I recorded its Gauss-Krüger-grid coordinates along with elevation and visited the site three to five times per week to check on the excavation progress. I determined first-egg dates by climbing the tree and inspecting nests daily with a light and mirror during the time when egg-laying was expected (i.e. 8.4 ± 6.4 (mean \pm SD) days after finishing excavation; Pechacek *et al.* 2005). In cases when I missed the whole laying, I estimated the laying date by back-dating from the observed clutch size and hatching/fledging date (assuming one egg per day, which is the general pattern in woodpeckers; Winkler *et al.* 1995 and found also in my population). I determined the clutch size by inspecting a nest daily until no more eggs appeared. The hatching date and number of hatchlings were determined by inspecting nests daily during the time when hatching was expected. The number of fledglings was determined two or three days before the expected fledging date. I assumed an incubation time of 12 days, beginning the day following clutch completion (Ruge 1974, own unpubl. data) and a nestling period of 24 days (Pechacek 1995b). After fledging, I checked the nests for potential dead chicks.

Starting in 1998, I used a noose to pull nestlings out of the nest hole for color ringing and aging when they became > 13 days old (Jackson 1982). Alternatively, I chiseled out a fist-sized opening above the cavity bottom at the backside of the nesting hole, and sealed the opening after ringing the young. I measured duration of parental care after fledging by monitoring when a parent was staying close to its fledglings (sometimes also providing food).

Observations on nest-site fidelity and natal dispersal

Each year, I monitored colour-ringed birds from December to February by carefully walking through all parts of their breeding territory, as well as in adjacent areas one to three times per

month. Woodpecker locations were marked on a 1:10 000 map, and coordinates, superimposed on the map, were recorded. From 1999 onwards, I searched opportunistically each time I was in the field for birds that were colour ringed as nestlings. Additionally, I also made three to five 8-hour forays per year into forests outside of my study area during breeding seasons. My goal was to cover a total radius of 15–20 km around each nest. Thus, the total area that was searched for possible detection of natal dispersal encompassed > 200 km². I often used playbacks of drumming and “vetvetvetvet” calls to increase the detection rate for woodpeckers (Andretzke *et al.* 2005). Nevertheless, a small number of birds may have remained undetected given the large search radius.

Data analyses

I usually collected breeding data in only one year for each pair (during the same year as they were discovered) to avoid pseudoreplication. However, some individuals within my sample were paired to different individuals during the observation period (due to divorce or widowhood). Differences in sample sizes were due to missing data. For instance, it was not always possible to revisit nests that were difficult to access as often as desired (with regard to alpine topography, bad weather and/or nest tree condition).

The laying date refers to the date of laying of the first egg in the clutch; clutch size is the number of eggs in the full clutch; brood size refers to the number of young that left the nest; fledging rate (i.e. fledging success) refers to the proportion of eggs resulting in fledged young; and breeding success refers to the percentage of nests from which \geq one young fledged (i.e. successful nests). Data presented here consider first clutches only (two secondary polyandrous clutches were excluded; Pechacek *et al.* 2006).

I used relative laying dates to rule out the effects of annual timing of breeding, and thus to justify combination of all years for my analysis of seasonal trends. To accomplish this, I standardized laying dates by setting the annual median to zero and considered individual laying dates as a deviation from this.

Based on the rule that air temperatures decrease at higher elevations, the relative effect of ambient temperature is reflected by elevation. Given the large elevation differences in my study forest (up to 1100 m within the Park boundary) and the fact that all nests were on slopes with shaded aspects, I used relative elevations at nests to obtain an alternative measure of ambient temperature for each nest. I used relative elevations as a substitute for temperature data. To account for differences in ambient temperatures among years, I set the annual median elevation of all nests to zero and regarded elevations at individual nests in a given year as a deviation from this.

I measured nest-site fidelity by calculating the distances from points where woodpeckers were observed to their nest sites in a given season (i.e. to the past nest if observations were made before 31 December, and to the future nest after this date) by Pythagorean theorem. Distances were measured to a calculated mean location of a bird during breeding in cases when I did not find the nest. I used the same calculation method to measure distances between individual nest sites in consecutive years, and between nests of the nearest neighbours within a season.

I measured a natal dispersal as a distance between the hatching site of a woodpecker and its first known nest site as an adult. In cases when I did not find the nest, or when several nests of a recovered bird were found in consecutive years, calculated mean location of the woodpecker at its discovery site, or the mean nest location was used to measure the distance to the birth site.

Tests are two-tailed and non-parametric except when data meet the requirements of normality. Results are given as means \pm SD, and are considered significant at $P < 0.05$.

Results

Overall breeding performance

Over all years of the study, the laying dates of first clutches ranged from 9 May to 6 June (28 days) (Table 1) with the largest proportion of clutches (40.5%) initiated between 19 and 24 May (Fig. 1a). The median laying date of three-toed woodpeckers was 20 May ($n = 37$). The

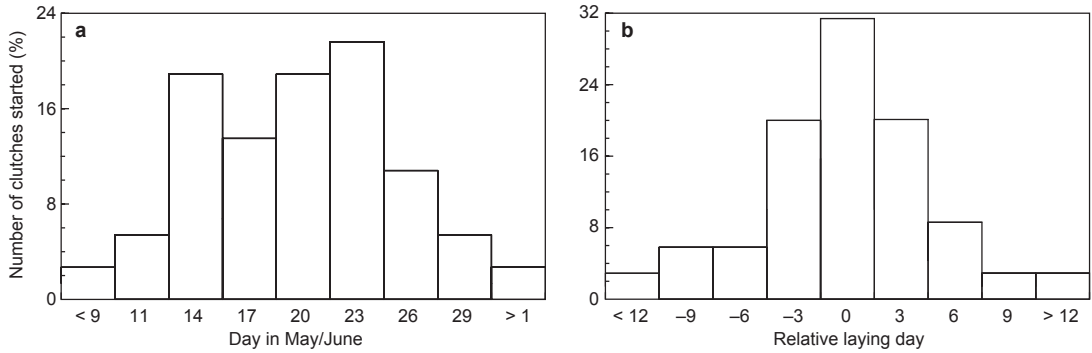


Fig. 1. — **a:** Three-toed woodpecker clutches ($n = 37$) in relation to median calendar date, Berchtesgaden National Park, 1994–2004. Values on the x -axis denote the middle day for each three-day period. Note that the latest clutch was laid on 6 June (2003). — **b:** Three-toed woodpecker clutches ($n = 35$) in relation to relative laying date (i.e. where the annual median is set to zero), Berchtesgaden National Park, 1997–2004. Values on the x -axis denote the middle day for each three-day period.

clutch size averaged 3.4 ± 0.8 eggs ($n = 23$), and the number of nests with clutch sizes 2, 3, 4, and 5 eggs was 3, 10, 8, and 2, respectively. The brood size and fledging rate averaged 1.6 ± 1.0 ($n = 37$) and 0.4 ± 0.3 ($n = 23$), respectively. In the case of successful nests, brood size was 2.0 ± 0.9 ($n = 30$). Breeding success was $79\% \pm 21\%$

($n = 38$). Parents ($n = 13$) were mostly observed to accompany their fledged young between 40 and 60 days after fledging (total span 82 days), with 9 September being the latest date recorded.

In eight of 38 breeding attempts (21.1%), no fledged young were produced. Eggs failed to hatch in two cases for an unknown reason

Table 1. Annual breeding parameters of the three-toed woodpecker clutches in Berchtesgaden National Park, 1993–2004. Note that no nests were found in 1995 and 1997, and that the range of egg-laying dates extended to 6 June in 2003. Differences in sample sizes were due to missing data.

Year	Laying date, May median, (n), range	Clutch size mean \pm SD, (n)	Brood size ¹ mean \pm SD, (n)	Fledging rate ² mean \pm SD, (n)	Breeding success ³ (%) \pm SD, (n)
1993	13, (1), –	–	3.0, (1)	–	100 (1)
1994	22, (1), –	3.0, (1)	2.0, (1)	0.67, (1)	100 (1)
1996	14.5, (4), 12–17	3.0, (1)	2.5 ± 0.6 , (4)	1, (1)	80 (5)
1998	22, (3), 20–23	3.7 ± 0.6 , (3)	1.0, (3)	0.28 ± 0.05 , (3)	100 (3)
1999	24, (5), 9–29	4.3 ± 1.2 , (3)	1.6 ± 0.6 , (5)	0.38 ± 0.04 , (3)	100 (5)
2000	20, (5), 12–14	3.3 ± 0.5 , (4)	0.8 ± 0.8 , (5)	0.21 ± 0.25 , (4)	60 (5)
2001	22, (2), 20–24	4.0, (1)	2.5 ± 0.7 , (2)	0.5, (1)	100 (2)
2002	21.5, (6), 13–26	3.0 ± 1 , (3)	1.8 ± 0.8 , (6)	0.44 ± 0.10 , (3)	100 (6)
2003	21, (8), 18–6	3.2 ± 1 , (6)	1.4 ± 1.7 , (8)	0.17 ± 0.3 , (6)	50 (8)
2004	12.5, (2), 10–15	3.0, (1)	1.5 ± 2.1 , (2)	1, (1)	50 (2)
All	20, (37), 9–6	3.4 ± 0.8 , (23)	1.6 ± 1.1 , (37)	0.36 ± 0.30 , (23)	79 ± 21 , (38)
Statistic	$\chi^2 = 12.7^4$	$\chi^2 = 5.6^4$	$\chi^2 = 10.7^4$	$F = 3.4^5$	–
d.f.	9	8	9	8	
P	0.174	0.697	0.298	0.023	

¹ Number of young that left nests (including totally failed nests).

² Proportion of eggs resulting in fledged young (including totally failed nests).

³ Percentage of nests from which \geq one young fledged.

⁴ Kruskal-Wallis test.

⁵ One-way ANOVA, using arcsin transformations for proportions.

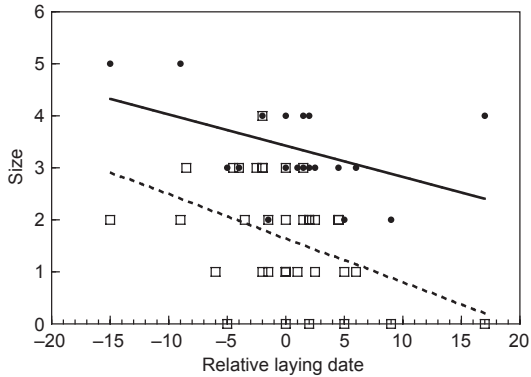


Fig. 2. Relationship between clutch size (filled circles and thick line) ($n = 23$ pairs), brood size (empty squares and dashed line) ($n = 37$ pairs) and relative laying date (i.e. where the annual median is set to zero) in three-toed woodpeckers in Berchtesgaden National Park, 1994–2004.

and in one case because the female became polyandrous and her male did not cope with this situation (Pechacek *et al.* 2006). The cause of fledging failure was mostly a mysterious depredation with nestlings decapitated, but not eaten by an unknown predator (three times), a loss of the male whereupon the female failed to rear the brood alone (once), and small nestlings being left alone at night (once) although the male was still alive (Pechacek 2005). All failures occurred prior to the middle of the nestling period.

The partial losses ($n = 14$) occurred at an early breeding stage (one to three days). They were due to unhatched eggs (nine times), the death of small young that were evicted from the nest (four times) (in one observed case by the female; own unpubl. data), or a combination of the two (once) (in this exceptional case, death of the young was due to depredation described above, when one of the three chicks in a nest survived the predator attack, while another two did not; one was decapitated and one left dead without any visible injury).

Annual breeding performance

The span of laying dates within years was far shorter than that of all years of the study, and all pairs laid in a period of 2–20 days (Table 1). Although the annual median laying date of

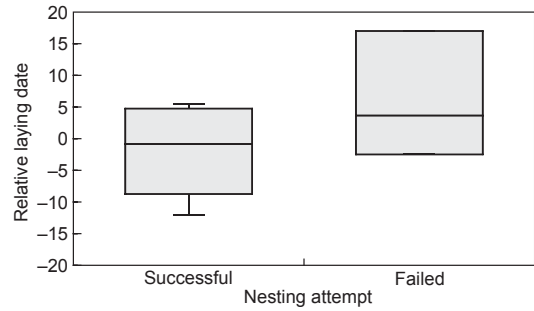


Fig. 3. Relative laying date (i.e. where the annual median is set to 0) of three-toed woodpeckers ($n = 35$ pairs) in relation to breeding success in Berchtesgaden National Park, 1994–2004. Whiskers show 5th and 95th percentiles, boxes 10th and 90th percentile and the horizontal line the mean.

the earliest and latest year differed by 11.5 days (considering years with > 1 found clutch only), timing of egg-laying (Julian date) did not significantly vary among years (Table 1), and was far from being associated with the relative elevation (Spearman's rank correlation: $r = 0.067$, $P = 0.704$). Annual mean clutch size varied between 3.0 and 4.3 eggs, but the between-year differences were not significant (Table 1). The annual mean clutch size also did not show any relation to annual median laying date (Spearman's rank correlation: $r = -0.340$, $P = 0.113$). The mean brood size did not significantly differ among years (Table 1). In contrast, fledging rate varied significantly among years, differing between 28% and 100%, whereas annual breeding success only varied from 50% to 100% (Table 1).

Seasonal breeding performance

Most clutches (71.4%) were started within 9 days around 0, when I used relative laying dates to account for differences between years (Fig. 1b). The relative laying dates were not associated with the relative elevation (Spearman's rank correlation; $r = -0.084$, $P = 0.633$). Both clutch and brood sizes (Fig. 2) showed a significant declining trend in relation to the relative laying date (Spearman's rank correlation: $r = -0.462$, $P = 0.030$ and $r = -0.349$, $P = 0.034$, respectively). I did not find any relationship between the rela-

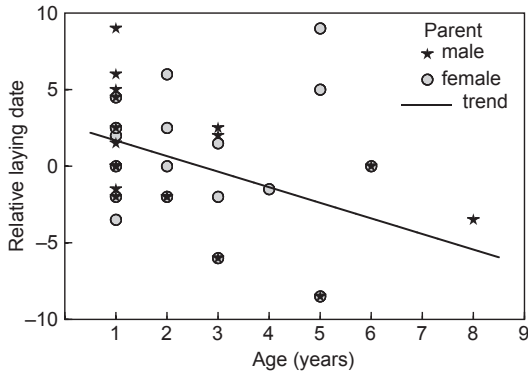


Fig. 4. Relationship between relative laying date (i.e. where the annual median is set to zero) and age of parent three-toed woodpeckers ($n = 19$ pairs) in Berchtesgaden National Park, 1994–2004.

tive laying date and fledging rate (Spearman's rank correlation: $r = -0.116$, $P = 0.597$).

Failed and successful breeding attempts differed significantly in the relative laying date (one-way ANOVA: $F_{1,33} = 4.273$, $P = 0.047$). Successful breeding attempts ($n = 28$) were initiated, on average, 4.5 days earlier than those that failed ($n = 7$) (Fig. 3). I also investigated age effect on start of egg-laying by analysing relative laying dates in pairs of known age. Whereas the age of the female did not appear to affect the date of egg-laying (Spearman's rank correlation: $r = -0.025$, $P = 0.940$), females mated with older males began egg-laying significantly earlier in the season (Spearman's rank correlation: $r = -0.523$, $P = 0.021$) (Fig. 4).

Natal dispersal

From 1998 to 2004, 56 young in 19 broods were ringed. Of these, eight young from seven nests were later observed between 110 and 11 700 m from their hatching place (median = 6350 m). Interestingly, one pair produced three recoveries in two years. I did not find differences in the relative laying date among nests producing recoveries and those that did not (i.e. young from these nests may have died after fledging, or dispersed beyond my 15–20-km search radius) (one-way ANOVA: $F_{1,17} = 0.009$, $P = 0.925$; note, however, that I had laying data only for five nests which produced recoveries).

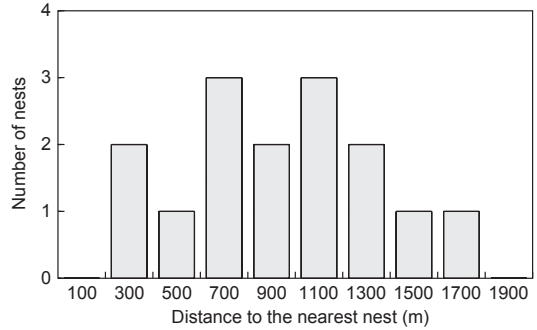


Fig. 5. Distance to the nearest conspecific nest in three-toed woodpeckers ($n = 15$ nests), Berchtesgaden National Park, 1994–2004. Values on the x-axis denote the middle distance for each 200-m distance category.

Nest-site fidelity

Most nests of neighbours (53.3%) were separated by 600–1200 m (Fig. 5). Woodpeckers that bred in consecutive years ($n = 24$) had a mean distance of 430 ± 330 m (range 80–1130 m) between successive nests (based on nests found in both years: 27%, nests found in one year and mean locations of the birds in another year: 61%, and mean locations of the birds in both years: 12%). For two additional woodpeckers whose mates were not ringed, the distance between the successive nest sites in consecutive years was also within this range (510 and 700 m, respectively).

Of these 26 woodpeckers, 16 later (after \geq two years) remated (due to death or divorce) and bred with new mates. The identity of nine new mates remained unknown due to lack of color ringing. For these 16 birds, I compared differences in distances between nest sites of original pairs with both (1) distances between nest sites of newly-formed pairs breeding with a new mate that was known, and (2) distances between nests of newly-formed pairs with a new mate of unknown identity. My results were not significant; i.e. between years when woodpeckers kept their previous mate and (1) years when they bred with a new mate of known identity (Wilcoxon test: $Z = -1.6$, $P = 0.091$), and (2) when they bred with a new mate of unknown identity (Wilcoxon test: $Z = -0.3$, $P = 0.735$).

During winter months (December to February), woodpeckers ($n = 21$) were observed on average 710 ± 550 m (range 160–2780 m) from

their nesting site of the previous/next year, with no significant differences between sexes (Mann-Whitney test: $Z = -0.036$, $P = 0.972$).

Discussion

The three-toed woodpecker seemed to possess some peculiar behavioural traits which in numerous ways differ from the breeding behaviour of other European woodpeckers. First, it was the last bird species (including migrants) to commence breeding in my study area (pers. observation). The onset of egg-laying was on 20 May (median), similar to reports by Ruge (1974) (27 May, mean) from Switzerland. Another late breeder, the grey-headed woodpecker *Picus canus*, was reported to start egg-laying in central Europe mostly between the beginning and middle of May (Hudec 1983, Andretzke *et al.* 2005). Second, annual reproductive output was low because only 36% of eggs resulted in fledged young and only 1.6 young successfully left nests. Ruge (1974) and Ruge *et al.* (2000) found 1.7 fledglings per nest. In white-backed woodpeckers *Dendrocopos leucotos* (the next species with low reproductive success), Hogstad and Stenberg (1997) reported on average 2.4 fledglings. Third, parents were observed to care for their fledged young more than two months after fledging. This period was similar to that reported by Bürkli *et al.* (1975) from Switzerland, but was more than two times longer than that reported for sympatric woodpecker species (Cramp 1985, Winkler *et al.* 1995).

Some other aspects of the breeding biology of the three-toed woodpecker closely correlate with patterns known for other woodpecker species (Winkler *et al.* 1995, Winkler & Christie 2002). For instance, clutches were described to be small for woodpeckers that forage on wood-boring beetles (Koenig 1986, Hogstad & Stenberg 1997). Clutch size in my study area averaged only 3.4 eggs, a result identical to that of Ruge (1974). High overall breeding success of the three-toed woodpecker (79%) was typical for woodpeckers and may be attributed to the habit of excavating new breeding cavities each year (Pechacek 2001, Jackson & Jackson 2004), which in turn may reduce parasite infestation (Short 1979) and/or nest predation (Martin & Li 1992).

Synchronization of timing of breeding

Egg-laying among pairs during the study ranged from 9 May to 6 June. Although the annual median laying date differed by some 12 days between the earliest and latest years, differences among years were not significant. Within years, laying period ranged up to 20 days, but >70% of the clutches were laid within a span of 9 calendar days. In the light of well documented importance of early breeding among birds (Perkins 1996), the question of what constrains three-toed woodpeckers from earlier initiation of egg-laying is interesting. Perhaps the lateness of its breeding season may be related to unpredictably harsh conditions in the mountainous habitats which may negatively impact food availability (Pechacek & Kristin 2004) and nest cavity temperature (Wiebe 2001).

There was a lack of correlation for both clutch size and brood size of the three-toed woodpecker among study years, which was similar to findings for some other European woodpecker species (Hogstad & Stenberg 1997, Wiklander *et al.* 2001). Clutch size, however, was remarkably constant among seasons. Egg-laying was not related to elevation; this result counters the findings by Ruge (1974). Thus, given that relative elevation correlates with decreasing air temperature, ambient temperature may not have influenced timing of breeding both among and within seasons.

Given the prevailing food of adult and young three-toed woodpeckers in the German Alps during nesting (i.e. spiders and cerambycid larvae; Pechacek & Kristin 2004), ambient temperature around the time of egg-laying should not be a significant factor affecting the annual and seasonal onset of breeding. Spiders are available prey present early in the breeding season, although low temperatures may negatively influence their activity, and make them more difficult to capture efficiently (Avery & Krebs 1984). Cerambycid larvae are available in dead wood year-round, and despite some decline of this food source in late spring due to the emergence of adult beetles and pupation, two to four generations of younger larvae are always available, making the decline less marked (Jacobs & Renner 1988). However, larvae size may

matter, and the growth process of larvae should be mostly controlled by the ambient temperature (Fayt 2006). In areas where the diet of the three-toed woodpecker consists of scolytids that require higher temperatures for their development, the onset of breeding should be more temperature-dependent such as documented in boreal forests (Fayt 2002).

Synchronization of timing of breeding is expected when food is abundant during a limited period (Lack 1950, Perrins 1991, Blondel *et al.* 1993). This is important in woodpecker species that rely on surface-living prey, which is abundant following the seasonal increase of air temperature during a limited time in spring. For instance, 95% of clutches of the lesser spotted woodpecker *Dendrocopos minor* were started within a 15 day-period (Wiktander *et al.* 2001), and 80% of clutches of the middle spotted woodpecker *Dendrocopos medius* were initiated within 11 days. On the other hand, laying dates of the white-backed woodpecker, which preys upon similar wood-living beetle larvae as the three-toed woodpecker, are in fact only correlated with air temperatures during months before egg-laying, but nevertheless highly synchronized among pairs (i.e. around 50% of pairs starts laying within 6 days of one another; Hogstad & Stenberg 1997).

Seasonal trends

Apart from patterns found with regard to synchronization of timing of breeding, seasonal trends clearly supported the advantage of early breeding. Successful breeding attempts started about 5 days earlier than those that failed. Both clutch size and brood size showed a decline in relation to the relative onset of egg-laying, similar to trends shown for other woodpecker species (Hogstad & Stenberg 1997, Wiktander *et al.* 2001). In three-toed woodpeckers, declining brood size was correlated with the relative fledging date, which actually also reflects the same pattern (Fayt 2002). Thus, the relative laying date was an important determinant for the clutch size of the three-toed woodpecker.

Older, more experienced woodpecker pairs (i.e. pair bonds of longer duration) may be expected to have better breeding performance

(i.e. earlier onset of egg-laying, and more fledglings) than newly-established pairs (Wiktander 1998). Owing to my study design (i.e. collecting breeding data in only one year for each pair), I did not have data to test for this hypothesis. However, females paired with older three-toed woodpecker males started egg-laying earlier than those that were paired with younger males, whereas the age of females did not affect the timing of egg-laying. Thus, the earlier initiation of breeding may be attributed to mating with more experienced males. This is another indication that the quality of males may be the key to understanding patterns of reproduction in woodpeckers.

Three-toed woodpecker males allocate significantly more time to territory defence, cavity excavation and feeding young than the females (Pechacek *et al.* 2005). As a rule, only males incubate and brood at night (Ruge 1971, Pechacek 2001). In cases of poor male breeding performance, females are suspected to compensate by becoming polyandrous (Pechacek *et al.* 2006). Since egg-laying can only begin after the nest is finished, males are the sex that may constrain timing of breeding. Old and experienced males may attempt earlier copulations (i.e., after finishing cavity excavation; Pechacek *et al.* 2005). Therefore, females paired with older males may benefit from earlier fertilization by being able to begin egg-laying earlier in comparison with females paired with younger males.

The seasonal decline in clutch size of single-brooded birds may be the result of physiological constraints on parental condition (Price *et al.* 1988). Alternatively, Daan *et al.* (1988) hypothesized that the seasonal decline in clutch size could be a strategic adjustment to laying date in response to declining reproductive value of late born young. Wiktander *et al.* (2001) confirmed this hypothesis for the lesser spotted woodpecker by showing lower survival of late fledglings. Hogstad and Stenberg (1997) showed for the white-backed woodpecker, a tendency for a heavy young (i.e. those born early) to survive better than lighter ones. Unfortunately, I did not find higher survival of early-born young in my study, but my sample size of recovered woodpeckers may have been too low to detect any differences.

Early territory occupancy may be important for successful establishment of young birds in species with life-long site fidelity, rigid territorial system and strict sedentary winter life (Nilson & Smith 1988, Nilsson 1989b). Because these characteristics are more or less found also in woodpeckers (Hogstad & Stenberg 1997, Michalek *et al.* 1999, Pasinelli 1999), Wiklander *et al.* (2001) argue that the number of fledglings recruited to the next breeding season may mainly depend on the laying date relative to the rest of the population, rather than on the absolute date of clutch initiation. Hence, the relative egg-laying date may be an important factor determining the future success of a woodpecker chick.

This line of reasoning may also be followed for three-toed woodpeckers. Fledglings dispersed in their first fall/winter, and once settled, showed remarkable nest-site fidelity. They bred only between 80 and 1130 m apart in consecutive years and stayed close to their former territories even if they later divorced, or remated. Despite a typical natal dispersion distance of less than 12 km from the hatching place (although larger distances could not be excluded), a low genetic similarity between mates suggested that pair members were unrelated (Pechacek *et al.* 2005). Woodpeckers also did not leave their breeding territories during winter. Thus, the relative laying date may be regarded as an important quality trait for a successful establishment of young three-toed woodpeckers.

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