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Late-hatched Great Tits *Parus major*: how do they contribute to the next year breeding population?

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Late-hatched Great Tits *Parus major* have often a lower local recruitment rate than those hatched early. However, estimates of recruitment usually neglect differential disappearance due to dispersal. We report on the proportions of late-hatched breeders in two Great Tit breeding populations (near St. Petersburg, NW Russia, and on the Courish Spit, Eastern Baltic). Using a novel method, late-hatched birds (hatching in July) were distinguished in the next breeding season by the incomplete moult of their tail feathers. Based on this method, we were able to estimate the percentage of late-hatched individuals in all first-year birds, including immigrants. The proportion of late hatched breeders was considerable in some years, and appeared related to the proportion of late fledglings in the previous year. In the Courish Spit population we found no significant difference in the global recruitment rate (accounting for both local birds and immigrants) of early- and late-hatched Great Tits. In the St. Petersburg population, the annual percentage of late-fledged breeders was significantly lower than the percentage of late-hatched fledglings in the previous year. However, in the St. Petersburg population we cannot definitely conclude that the global recruitment rate of late fledglings was lower than that of early fledglings because of peculiarities of the study site. We also can suggest that it may be a result of competition between early and late fledglings, winter residents and newcomers in spring (especially in males), as well as a result of different survival of early- and late-born individuals during the first year.

Key words: *Parus major*, recruitment rates, survival, extent of moult

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INTRODUCTION

Recruitment rates of birds hatched late in the breeding season are widely believed to be negligible. In the Great Tit *Parus major*, for example, young birds fledged early in the breeding season are more likely to recruit into the breeding population than young that fledged late (e.g. Verboven & Visser 1998). This was found to correlate with their higher fledging body mass (Tinbergen & Boerlijst 1990, Both *et al.* 1999, Monrós *et al.* 2002). However, fledging early is not the best

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option every year as was shown for a Spanish population of the species (Monrós *et al.* 2002).

The seasonal decline in fledgling recruitment may have several causes. First, it may be the different survival of early and late-hatched birds. It has been shown that late-hatched Great Tits survive less well after fledging (Kluyver 1951, Perrins 1965, Dhondt 1979, Linden *et al.* 1992). Survival of juveniles is positively correlated with fledging mass (Perrins 1965, Dhondt 1971, Tinbergen & Boerlijst 1990), which itself may decline with date. Similar results were obtained by radio-tracking of Great and Coal Tit *Parus ater* fledglings. In a Swiss population of tits about one-half of the chicks died shortly after leaving the nest, predation being the main cause of mortality. Moreover, the effect of fledgling condition on survival increased with season: the survival of birds fledged both late and in poor condition was below 20% (more than three times less than in birds fledged early in the season) (Naef-Daenzer *et al.* 2001).

A second cause of low recruitment rates of locally late-born individuals may be date-related dispersal (Dhondt & Huble 1968, van Balen & Hage 1989) and lower recapture probabilities of birds outside the study area. However, there was no evidence for hatch date dependent dispersal in the Wytham population (England) of the Great Tit (Verhulst *et al.* 1997). In general, the potentially high permanent emigration rates of young from late and second broods prohibits a detailed analysis of recruitment rates and hence an unbiased estimate of the importance of producing late and second broods to fitness of the birds. Most of the studies were based on birds ringed within limited breeding areas so that it is difficult to separate real mortality from disappearance resulted from dispersal. A lot of first-year immigrants participating in breeding were not included in such analyses. If late-born young are more likely to move away from their natal area, they are more likely to be in the group of first-year immigrants in the areas under control. The proportion of immigrants in breeding Great Tit populations is very high. For instance, a parasitological study (Markovets & Palinauskas 2003) has shown that about 36% of birds trapped while breeding on the Courish Spit came from a distance of at least 30 km from this study area.

In addition, the seasonal decline in fledgling recruitment may be a result of competition between early and late fledglings (Kluyver 1971, Verhulst *et al.* 1995). In experiments with Great Tits, in which density of early fledglings was reduced, the local survival of late fledglings increased (Tinbergen *et al.* 1985, Verhulst 1992). This competition may cause late-hatched young to leave the natal area in search for areas with lower competition.

Here we report the data on the percentage of late-hatched birds in two Great Tit breeding populations of Europe. Our study was performed using an original method that allows us to say with a good precision in what period of the previous breeding season a first-year breeding bird has hatched, irrespective of whether it was ringed as a nestling or not. Using this method, we avoided the problem of differential dispersal and estimated the percentage of late-born individuals in the group of first-year immigrants, which was never done before.

MATERIAL AND METHODS

The data were collected in the countryside about 60 km from St. Petersburg (60°30'N, 31°30' E; 85 nestboxes in 3 km^2 area) in 2000–2005. On the Courish Spit (55°05'N, 20°44'E, 450 nestboxes) the data were collected in 1999–2002 in an area which is a 10 km long and 0.3–0.8 km wide part of woodland situated along the spit. The hatching date for each nest was either recorded by direct observation, or was back-calculated from the wing-length of nestlings. The number of young fledged was also recorded for each nest. Late broods usually contained fewer young than early broods. We calculated the percentage of late-fledged birds as a proportion of fledglings in a season that hatched after 30 June (further called proportion of late-hatched fledglings). For the Courish Spit we used the data on 136 nests in 1999, on 90 nests in 2000 and on 96 nests in 2001. When calculating the proportion of early and late fledglings for the St. Petersburg region we used the data on

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36 nests in 2000, on 41 nests in 2001, on 35 nests in 2002 and 2003, and on 37 nests in 2004. For 1999 we used the data of O.P. Smirnov (pers. comm.) on 32 nests from the nestbox area situated 70 km apart from our study area.

During breeding Great Tits were trapped at nests with various types of automatic or remotely controlled traps. In the St. Petersburg study area, much effort was spent to trap all breeders. The remotely controlled trap enabled us to perform selective trapping while the other bird fed the nestlings. Only few birds escaped identification, most of them males. In this population we captured 97% of females and 89% of males nesting in the nestboxes (170 pairs under control during 2000–2005). In 7 pairs, males were not recorded at all during two periods of 2–3 hours of observation near the nest (the number of chicks was very low in such nests); three males did not feed chicks themselves but gave food to females near the nestboxes. At the Courish Spit only females of the first broods (220 nests) were controlled rather well. Here we trapped 94% of females but only 32% of males.

Our analysis depends critically on the difference in the extent of post-juvenile moult between juveniles hatched before June 16 and hatched in July. According to our earlier experimental and field study of post-juvenile moult, Great Tits with incomplete moult of rectrices can be with a high reliability identified as born late in the breeding season (at least at our study sites). This statement is based on the following results. (1) The data from caged birds (Rymkevich & Bojarinova 1996) have shown that the extent of moult in the Great Tit is photoperiodically controlled. Birds with late hatching date (from late repeat and second broods) decrease the extent of moult in tail feathers because of the photoperiodic conditions of their moult. (2) In the field, we analysed the effect of hatching dates, nestling conditions, time of moult and body mass during moult (Bojarinova *et al.* 1999), and found that nothing except the hatching dates influenced the extent of moult. (3) The data of retraps of nestlings in NW Russia (latitude 60–61°N) have shown that all tits (n = 15) hatched in July (second broods), retrapped in the field, had reduced tail moult, whereas 97% (n = 111) of tits hatched from 16 May to 16 June (first broods) replaced the tail feathers completely (Bojarinova *et al.* 2002a). The individuals with a reduced moult of the tail feathers among birds from first broods were only females (Table 1). Among birds from repeat clutches (hatching 19 June – 29 June), 3 out of 14 individuals reduced the extent of tail moult. Similar results were obtained in Finland at the same latitude (Bojarinova *et al.* 1999): only one tit out of 25 birds from first broods decreased the extent of tail moult and none of the birds from second broods (n = 10) moulted the tail completely. (4) The data on retraps of nestlings from the Courish Spit (latitude 55°N) have shown that there 97% (n = 73) of tits hatched from 14 May to 16 June (first broods) moulted their tail completely. Again, as in the St. Petersburg population, the individuals with reduced tail moult among birds from first broods were only females (Table 1). The difference with the latitude 60°N was the following: some birds

Table 1. Percentage of birds with incomplete moult of rectrices in birds with different hatching dates.

Hatching dates	St. Petersburg region		Courish Spit	
	Males % (n)	Females % (n)	Males % (n)	Females % (n)
16 May – 16 June (first broods)	0 (61)	6 (50)	0 (28)	4 (45)
19 – 29 June (repeat broods)	20 (10)	25 (4)	20 (5)	20 (5)
3 – 25 July (second broods)	100 (6)	100 (9)	67 (15)	100 (6)

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hatched in July (5 out of 21, all of them were males) also moulted their tail feathers completely. So, only some part of tits hatched in July can be identified as such by this marker at this study site. Two of 10 birds hatched in the second half of June (Table 1) reduced the extent of tail moult.

In our analysis we used the proportion of birds that originated from late (hatched in July, mostly second broods) or early (hatched in May – 16 June) broods in the breeding population of first-year birds in a certain year. The proportions have been calculated from the number of birds with reduced moult of tail feathers trapped during breeding (further called proportion of late-hatched breeders). According to our observations (Table 1), any female with complete tail moult (TM) definitely originated from an early brood, while females with reduced TM should be distributed between first and second broods using corresponding proportions previously found for such females. In other words, for example, for the St. Petersburg population 6% of females with reduced TM trapped during the breeding season originated from early (first) broods and 94% from late (second) broods. According to our data any nesting male with reduced TM is from a late (second) brood, but on the Courish Spit about 33% of males escape such identification because they moulted their tail completely. To simplify the calculations we do not take into account the birds from repeat (after failure of the first broods) broods, since their number in most years was negligible.

A similar difference in the extent of moult in first-year birds exists in more northern populations as well (data from the coast of the White Sea 64°30'N, J.G. Bojarinova, unpubl. data). Therefore the moult marker is valid also for possible immigrants from more northern populations.

To compare the data on the proportion of late-hatched birds with the data obtained with the ringing method, we calculated the proportion of late-hatched birds (hatched in July) among all the breeders ringed in the previous year as nestlings (further called proportion of local late-hatched breeders). The local recruitment rate was estimated as a probability that a fledgling is found nesting in the study area in one of the years following the year of fledging. Furthermore we compared the proportion of late-hatched breeders (determined by the moult method) and the proportion of local late-hatched breeders (determined by the ringing method) with the proportion of late-hatched fledglings (later than June 30) from the previous breeding season.

Statistical tests were done according to Zar (1999). Since we compared the percentages that were below 30% and the number in classes were often less than 5, we could not use χ^2-test. The proportions of late-hatched breeders determined by the moult and ringing methods were tested against the hypothesis that they remained the same as the proportion of late-hatched fledglings in the previous year. This was done by applying the two-tailed binomial test to data pooled for all the years. We used pooled data because of insufficient data on local recruitment rates (in some years neither early, nor late fledglings were recruited). The difference between the proportions of late-hatched breeders determined by the moult method and by the ringing method was also tested with the two-tailed binomial test. When comparing the difference between populations and the difference in recruitment rates we applied two-tailed Fisher's exact tests. We also performed a comparison year by year between the proportion of late-hatched breeders and the proportion of late-hatched fledglings in the previous year using t-test for paired comparisons. In this case the difference between the proportions was analysed after arcsine transformation of the data.

RESULTS

Late-hatched Great Tit breeders were present in all years in both breeding populations studied. In the countryside near St. Petersburg the percentage varied among years from 7–24% (average 16%), and on the Courish Spit between 10–22% (average 15%). No difference between the two populations in proportion of late-hatched breeders (Table 2, the data of all years pooled) was recorded (Fisher's exact test, $n_1 = 195$, $n_2 = 174$, $P = 0.88$.

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Table 2. Percentage of late-hatched birds among first-year Great Tits in the breeding population in two study areas. Number of trapped birds between brackets.

	St. Petersburg region							Courish Spit			
	2000	2001	2002	2003	2004	2005	All years	2000	2001	2002	All years
Sexes combined	24 (34)	7 (33)	10 (24)	11 (37)	17 (25)	24 (42)	16 (195)	22 (60)	12 (75)	10 (39)	15 (174)
Females	33 (22)	13 (17)	2 (13)	16 (19)	14 (16)	26 (23)	19 (110)	20 (48)	14 (61)	12 (32)	16 (141)
Males	8 (12)	0 (16)	18 (11)	6 (18)	22 (9)	21 (19)	12 (85)	33 (12)	0 (14)	0 (7)	12 (33)

Late-hatched breeding females were found in both populations in all the years. Their proportions varied between 2–33% in the St. Petersburg region and between 12–20% on the Courish Spit. Late-hatched breeding males in some years were absent. The percentage of late-hatched females was higher than that of males (Table 2, the data of all years pooled), but the difference was not significant (t-test for paired comparisons, $t = 0.86$, $df = 5$, $P > 0.05$ for the St. Petersburg population and $t = 1.10$, $df = 2$, $P > 0.05$).

At both sites the percentage of late-hatched fledglings in the previous year was positively correlated with the percentage of late-hatched breeders among first year breeders in the next breeding season (Fig. 1). This relationship was significant in both populations (Fig. 1). In the St. Petersburg region this correlation was significant for females ($r = 0.90$, $n = 6$, $P = 0.015$), but not for males ($r = 0.29$, $n = 6$, $P = 0.58$). On the Courish Spit the percentage of late hatched breeding males reached its maximum in the year (2000) following the year with a high number of successful second broods.

In the St. Petersburg population, the local recruitment rate of early-hatched tits (hatched before June 16) was three times higher (0.0225) than the local recruitment rate of late-hatched individuals (0.0067) (data of 2001–2005 pooled, Fisher's exact test, $n_1 = 1068$, $n_2 = 297$, $P = 0.10$, NS). In the St. Petersburg region the expected percentage of late-hatched birds among breeders according to the number of early and late-hatched birds in the previous years was 21.8% (Table 3) if

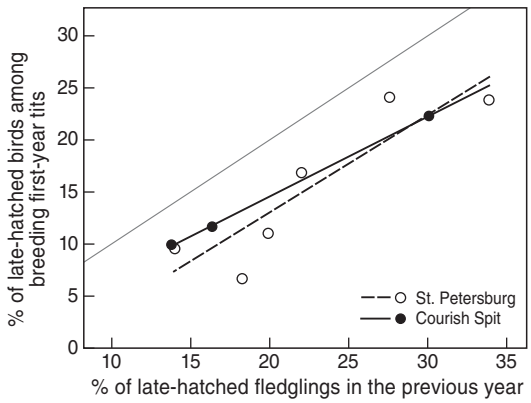

Figure 1. Percentage of late-hatched breeders in one year in relation to the percentage of late-hatched fledglings in the previous year (both sexes pooled). St. Petersburg population – open circles, dashed line: y = –5.75+0.93x ($F_{1,4} = 16.46$, $P = 0.015$); Courish Spit population – solid circles, solid line: y = –0.80+0.77x ($F_{1,1} = 535156.7$, $P < 0.001$). Dotted line represents y = x.

we assume that recruitment rates of first and second brood nestlings would have been equal. This value differed both from the proportion of late-hatched breeders determined by the extent of moult (16%) and from the proportion of local late-hatched breeders determined by ringing (7.7%). However, these differences were marginally non-significant (binomial test, $n_1 = 1365$, $n_2 = 195$, $P = 0.06$ and $n_1 = 1365$, $n_2 = 26$, $P = 0.08$ correspondingly). The proportion of late-hatched breeders each year was lower than the proportion of

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late-hatched fledglings in the previous year (Fig. 1, compare data with the x = y line). This difference ranged between 3.5 and 11.5% in different years. This conclusion is confirmed by paired *t*-test (t = 4.63, $df = 5$, $P < 0.01$).

In the Courish Spit population the local recruitment rate of early-hatched individuals was 0.0116, and 0.0074 in late-hatched tits (Fisher's exact test, $n_1 = 1726$, $n_2 = 408$, $P = 0.60$, NS). The proportion of late-hatched fledglings in this population (19.1%, all years pooled) (Table 3) did neither differ significantly from the proportion of local late-hatched breeders (13%) (binomial test, $n_1 = 2132$, $n_2 = 23$, $P = 0.46$), nor from the proportion of late-hatched breeders (15%) (binomial test, $n_1 = 2132$, $n_2 = 174$, $P = 0.18$). Here also the proportion of late-hatched breeders each year was lower than the proportion of late-hatched fledglings in the previous year (Fig. 1, compare data with the x = y line). This difference ranged between 4.1 and 7.8% in different years, but was not significant (*t*-test for paired comparisons, $t = 2.18$, $df = 2$, $P > 0.05$).

The difference between the proportions of late-hatched breeders determined by moult method and by ringing method (Table 3) did not differ significantly (binomial test: for the St. Petersburg population $n_1 = 195$, $n_2 = 26$, $P = 0.26$; for the Courish Spit population $n_1 = 174$, $n_2 = 23$, $P = 0.80$).

DISCUSSION

In both study areas the local recruitment rate of Great Tits into the breeding population based on the ringing results was very low compared for example with the same values in other populations in Central Europe (Verboven & Visser 1998, Verhulst *et al.*1997, Monrós *et al.* 2002). Such low values make it very difficult to evaluate the difference in recruitment rate of birds with different hatching dates.

Using our data on moult extent we have shown that at both study sites, the proportion of late-hatched birds was positively correlated with the percentage of late fledglings in the previous year. Late-born birds were present in all the years, and in some years their percentage was considerable (up to 24%).

In both populations (data pooled for all years) the percentage of late-hatched fledglings in the previous year was higher than the percentage of late-hatched breeders determined by the moult method which was higher than the percentage of local late-hatched breeders determined by ringing method (Table 3). All these values did not differ significantly. The percentage of late-fledged birds recruited into the breeding population each year was consistently lower than the proportion of late-hatched fledglings in the previous year. In St. Petersburg population this difference was statistically significant. Using the moult method we avoided the problem of differential dispersal by accounting for both local birds and immigrants. However, there may be still another explanation of

Table 3. Percentage of late-hatched Great Tits among fledglings and in the next year's breeding population, data of all years pooled. Sample size between brackets.

Population	Percentage of late-hatched fledglings in the previous year	Percentage of late-hatched breeders (determined by the moult method)	Percentage of local late-hatched breeders (determined by the ringing method)
St. Petersburg	21.8 (1365)	15.6 (195)	7.7 (26)
Courish Spit	19.1 (2134)	14.9 (174)	13.0 (23)

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the lower than expected number of late-hatched breeders besides the differential survival or dispersal. We made an assumption that the proportion of late fledglings in a given year within our study area is an unbiased estimate of the proportion of late fledglings also in the surrounding areas, from which most recruits originate. One of the suggestions why the percentage of late-fledged breeders was lower than the percentage of late-fledged birds in the previous year, is that at least in the St. Petersburg region, more second broods are produced in the study area compared to the surroundings. This may be due to the available free nestboxes (Smirnov & Tyurin 1981). In other areas tits are short of places for breeding, especially for second clutches. They often try to nest in the same nest-hole after the first brood, and often desert the second clutch because of the increasing number of fleas. We suggest that this is why the proportion of late fledglings within our study area is higher than the proportion of late fledglings in the surrounding areas, from which most recruits originate. Therefore we cannot definitely conclude that the global recruitment rate (accounting for both locals and immigrants) of late fledglings for this studied population is lower than that of early fledglings.

In comparison with other nestbox areas in the northern Europe, tits in our study area in St. Petersburg region produce similar or higher number of second broods. The incidence of second clutches, given as a proportion of pairs successfully fledging first broods are 20% (0–60%) in Southern Finland, 54% (19–70%) near Moscow, 10% (0–38%) in Northern Finland at 65oN (Cramp & Perrins 1993) and 51% (40–70%) in our study area. Therefore we can not explain the relatively high fraction of first year breeding birds with incomplete tail moult by the suggestion that these birds originated from more northern areas with a large proportion of Great Tits that produce second broods.

In both populations the percentage of late-born males was not correlated with the percentage of late-fledged birds in the previous year, suggesting that some other factors also influence their recruitment. It was shown that late-fledged males survived better than late-fledged females (Verboven & Visser 1998, Bojarinova *et al.* 2002b). Therefore the presence of late-born females among first-year breeders in all years and absence of late-born males in some years suggests that such males likely have problems with settling in preferred breeding areas as, e.g. the countryside in the St. Petersburg region. This may be due to fluctuations of sex and age composition of Great Tit populations in different habitats during the year. In northern Europe, most Great Tits for several winter months leave their home ranges in the forests and move to rural and urban habitats with artificial feeding (Smirnov & Noskov 1975, Lehikoinen 1986, Zimin 1988, Orell 1989, Bardin 1990, Semyonov-Tyan-Shansky & Guylyazov 1991). As shown earlier using the same method of identification of late-born individuals (Bojarinova *et al.* 2002b), such tits during winter mainly concentrate in urban habitats that provide ample food resources. In the countryside during the wintertime such males were absent at all in one year and were very rare in another (Bojarinova *et al.* 2002b). Thus adult and early born first-year males wintering in the countryside have more chances to settle in the breeding population as winter residents (Matthysen 1990, Sandell & Smith 1991) than late-born males returning to breeding places during spring movements. This is another possible explanation for the fact that the percentage of late-fledged birds recruited in the next year breeding population was lower than the percentage of birds fledged in July in the previous year. Moreover, in the Courish Spit population some males escaped identification because here only 67% of late-hatched males can be identified by the extent of moult (Table 1) and that is why their percentage probably is underestimated.

To summarize, we avoided the problem of differential dispersal by accounting for both local birds and immigrants, and found that 1) in the Courish Spit population there was no significant difference in the global recruitment rate of early- and late-hatched Great Tits; 2) in the St. Petersburg population we cannot definitely conclude that the global recruitment rate of late fledglings is

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lower than that of early fledglings because of the peculiarities of the study site. We also can suggest that this difference may be a result of competition between early and late fledglings (Kluyver 1971, Verhulst *et al.* 1995), winter residents and newcomers in spring (especially in males, see above), and, to some extent, of different survival of early- and late-born individuals during the first year.

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SAMENVATTING

De overleving van nestjong tot volwassen vogel is in de biologie een belangrijk gegeven, want het geeft aan hoeveel nakomelingen zelf ook weer gaan reproduceren. Dat is biologische 'fitness' en de kern van micro-evolutionair onderzoek. Nu is het niet makkelijk om dit te meten, want een deel van de vogels die overleeft, komt niet terug in het studiegebied en wordt daardoor makkelijk over het hoofd gezien. Terugmeldingen van vooral kleine zangvogels zijn immers schaars als je geringde vogels niet systematisch opzoekt. Fitnessberekeningen zijn daardoor bijna altijd gebaseerd op lokale overleving. Dit kan een probleem opleveren wanneer een bepaalde groep jongen een grotere kans heeft om het studiegebied te verlaten. Zo weten we van Koolmezen *Parus major* bijvoorbeeld dat jongen die in slechtere conditie uitvliegen, over een grotere afstand verhuizen van geboorteplaats naar broedplaats en daardoor dus makkelijker gemist kunnen worden dan vogels die in goede conditie uitvliegen. Metingen aan lokale overleving van jonge Koolmezen uit tweede broedsels laten zien dat ook zij heel slecht overleven, maar dit kan weer veroorzaakt worden doordat die jongen veel vaker het onderzoeksgebied verlaten en zich elders vestigen. Deze studie onderzoekt op een nieuwe manier wat de overleving is van jonge Koolmezen uit tweede broedsels. In twee gebieden in Rusland hebben de onderzoekers gekeken naar de rui van de staartveren van jongen uit eerste en tweede broedsels. Ze vonden dat jongen uit tweede broedsels geen volledige staartrui hebben in hun eerste jaar, en daardoor zijn zij in hun eerste broedseizoen nog steeds te onderscheiden van jongen uit eerste broedsels. Het aandeel jongen uit tweede broedsels onder broedvogels die buiten het studiegebied waren geboren, was in sommige jaren aanzienlijk (tot 24%). In een van de studiegebieden was het aandeel jongen uit tweede broedsels in de broedpopulatie gelijk aan het aandeel uitgevlogen jongen in het voorgaande jaar, wat suggereert dat de werkelijke overlevingskans van jongen uit tweede broedsels niet lager was dan van jongen uit eerste broedsels. In het andere gebied was het aandeel wel lager, wat er op wijst dat de werkelijke overleving van jongen uit tweede broedsels lager was dan jongen uit het eerste broedsel. In het algemeen lijkt het er op dat de overleving van jongen uit tweede broedsels hoger is dan verondersteld, omdat zij meer geneigd zijn om hun geboorteplaats te verlaten. Dit kan komen doordat zij de competitie met lokaal geboren jongen uit eerste broedsels verliezen. (CB)

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