Reproductive investment and moult-breeding overlap in the collared flycatcher *Ficedula albicollis*: an experimental approach

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We manipulated brood sizes of 132 pairs of the collared flycatcher to investigate whether or not an investment in reproduction was traded against an investment and timing of the post-nuptial moult. Our manipulations did not affect the probability of moult-breeding overlap in males, and there was no effect on their moult scores at fledging time of the young. Males and young birds initiated moult earlier than females and old birds, respectively. Very few females started moulting during the period of nestling care. Reproductive success in terms of recruitment rate of fledglings was independent of parental moult stage during reproduction, which indicates that the manipulation did not induce a trade-off between moult and post-fledging care. Furthermore, the survival probability of adults was independent of brood size manipulations and their moult stage at fledging time. Thus, our brood size manipulations showed no evidence for a trade-off between reproductive and moult investments in the collared flycatcher.

1. Introduction

One of the central tenets in life-history theory is that investments in a current reproductive attempt have to be traded against investments in future reproductive attempts (e.g., Williams 1966, reviews in Lindén & Møller 1989, Roff 1992). Several different, and non-exclusive, causal mecha-nisms have been proposed to explain how current reproductive investment may impose costs in terms of reduced future investment potential. For example, high reproductive investments may suppress the immune system and lead to increased risk of contractinging infectious diseases (e.g., Gustafsson *et al.* 1994). Indeed, several experimental studies have provided evidence for such a

trade-off (Norris *et al*. 1994, Richner *et al*. 1995, Sheldon & Verhulst 1996, Allander 1997). Another possible reproductive cost arises when a current reproductive investment results in depletion of energy and time needed for maintenance and reconstruction of somatic tissues (Williams 1966, Tuomi *et al*. 1983, Perrin 1992). In birds, the annual investment in new feathers is a fundamental process to ensure survival (Holmgren & Hedenström 1995). This moult process is energetically costly, involving both feather production costs and increased thermoregulatory expenses (Payne 1972, Lindström *et al*. 1993, Klaassen 1995, Murphy & Taruscio 1997). An additional cost of wing moult is impaired flight performance (Pennycuick 1975, Swaddle & Witter 1997), which will increase the energetic costs of flight (Chai 1997), as well as predation risks (Slagsvold & Dale 1996).

Trade-offs between reproduction and moult in birds have been studied both by correlative methods and by experimental manipulations of reproductive investment, but the results from the different studies are equivocal (Table 1; *see* also Pie-

tiäinen *et al*. 1984, Langston & Rohwer 1996). One reason for this may be relatively small sample sizes, low frequencies of moult-breeding overlap, or a combination of these factors in some of the studies. Further experimental studies are, therefore , required to clarify the relationship between a reproductive investment and moult. The aim of the present study was twofold. First, we wanted to provide an experimental analysis of the hypothesis that individuals making a great reproductive investment will have to delay their moult (cf. Siikamäki *et al*. 1994). To do this, we manipulated the reproductive investment of pairs of collared flycatchers (*Ficedula albicollis*) by either increasing or decreasing the parental reproductive effort by means of brood size manipulations. We expected an increased probability of moult-breeding overlap among parents rearing reduced broods, and if there is a trade-off between reproductive investment and moult, a decreased probability of moult-breeding overlap among parents rearing enlarged broods. Second, we investigated possible fitness consequences of the brood

Table 1. Synopsis of moult-reproduction trade-off studies that have either included manipulations of reproductive investment or natural correlations between brood size and moult. "Manipulation" refers to timing and degree of brood size manipulation, "scored" to number of days before fledging that the adults were scored for moulting. % = percentage moulting females/males. The effect of manipulations or correlations (number of individuals sampled) is presented as: delayed/advanced = individuals with large broods initiate moult later/earlier than individuals with small broods; none = no relationship; numbers in brackets = total number of pairs scored for moulting (including controls); *N* = number of manipulated broods (excluding control groups); RC = whether or not the experimental manipulation imposed any reproductive costs (y = yes; n = no). Natural variation refers to correlative studies of reproductive investment and timing of moult.

| | | | | Effect of manipulation | | | | |
| | | | | --- | --- | | | |
Species	Manipulation	Scored	% moulting	Females	Males	*N*	RC	Ref.
Branta canadensis	Brood (+1)	*	100/100	delay (45)	none (35)	159	y	1
Ficedula hypoleuca	Clutch (±1, ±2)	1–2	27/60	delay (137)	none (49)	86	y	2
Ficedula hypoleuca	Clutch (±2)	2	15/24	none (38)	none (41)	44	y	3
Parus montanus	Brood (±2)	5–6	1.5/3.8	none (363)	none (337)	193	n	4
	Natural variation							
Cygnus columbianus	Clutch size	*	100/–	advance (10)	–			5
Branta leucopsis	Brood size	*	100/100	advance (648)	delay (597)			6
Phylloscopus trochilus	Brood size	**	**	delay (7)	–			7
Ficedula hypoleuca	Brood size	3	62/100	delay (26)	delay (33)			8
Ficedula hypoleuca	Brood size	2	41/67	none (101)	none (90)			9

*) Adults scored for moult stage at different brood ages.
**) Only moulting females studied during the post-fledging period.
Refs: 1: Lessells 1986; 2: Siikamäki *et al*. 1994; 3: Sanz 1997; 4: Orell *et al*. 1996; 5: Earnst 1992; 6: Larsson 1996; 7: Bensch *et al*. 1985; 8: Slagsvold & Lifjeld 1989; 9: Hemborg 1999a.

size manipulations and moult-breeding overlap in terms of recruitment rate of fledglings and adult survival probability to the following breeding season. In other words, we investigated whether or not there were any inter-annual effects of our manipulations, and possibly of moult, on adult fitness (*see* Siikamäki *et al.* 1994, Nilsson & Svensson 1996).

2. Methods

This study was carried out during the breeding seasons of 1993 and 1994 in a nest box breeding population of collared flycatchers on the southern part of the island of Gotland (57°N, 18°E), Sweden. The collared flycatcher is a long-distance migrant which arrives to the study area in late April to early May. Females alone build nests and incubate eggs, while both parents participate in feeding the nestlings. The nestling period lasts for about 15 days, and the fledglings become independent approximately one week after leaving the nest. After breeding, and before the onset of autumn migration to Africa, all adult birds undergo a complete moult in which nearly all feathers are renewed (Cramp & Perrins 1993). More details about the study species and area are given by Pärt and Gustafsson (1989).

All the nest boxes were inspected regularly to determine the onset of egg laying, and to collect data on clutch size, hatching day, number of hatched and fledged young. When the nestlings were 13 days old, they were measured for the tarsus length (to nearest 0.1 mm), weighed with a Pesola spring balance (to nearest 0.1 g), and ringed with individually numbered aluminium rings. Parents were captured when their offspring were 13 or 14 days old and measured for tarsus, wing and tail length as described by Merilä and Gustafsson (1993), as well as scored for primary and tail feather moult using the British Trust for Ornithology scoring scheme (Ginn & Melville 1983). Following this scheme, remiges and rectrices were given a score from 0 for an old feather, and from 1 to 5 depending on the stage of development of new feathers. Because all adults were checked for moulting just before the young fledged, the moult score also provides an estimate of how long an individual has been simultaneously moulting and feeding the nestlings. Thus, the higher the moult score, the longer the overlap between moult and nestling care. In some instances, parents were captured when the nestlings were 15–16 days old, but these individuals constitute only 1.6% of males and 1.6% of females in 1993, and 1.6% of males and 0.7% of females in 1994, respectively. Results and conclusions were not different when these birds were excluded from the analyses.

All birds were sexed and aged as either young, i.e. born the previous year, or older (Svensson 1992). In the case of previously ringed birds, exact age could be determined.

When assessing adult and fledgling survival, birds which were recaptured as breeders in the study area in any of the subsequent years (1994–1996) following the experiments were considered as "survivors" or "recruits", whereas individuals not recaptured were regarded as "non-survivors". In this study area, there are good reasons to regard this a reliable estimate of true survival because dispersal distances of collared flycatchers are very short (*see* Pärt & Gustafsson 1989, Pärt 1990).

To investigate whether or not the onset of moult is affected by reproductive effort, brood size manipulations were performed by either reducing or increasing the original brood size with two young (for further details, *see* Merilä 1996, 1997). All swaps were performed when nestlings were two days old, and between two nests with the same hatching date and original clutch size. We also had a control group consisting of nests in which half of the young were reciprocally exchanged between nests without changing the original brood size, and a control group in which the nestlings were left unmanipulated. These two control groups did not differ in breeding time (unpaired *t*-test, $p = 0.30$), adult moult status (χ^2-test, $p > 0.15$ for both males and females), or moult score (Mann-Whitney *U*-test, $p > 0.10$ for both sexes). Therefore, these two groups were pooled and will be referred to as the control group. The number of control nests were 71 and 76, in 1993 and 1994, respectively. In 1993 and 1994, 68 and 64 pairs of broods, respectively, were manipulated. There were no differences in clutch size between study groups and years, but hatching date differed between years (Table 2). Mean brood size after manipulations was significantly larger for enlarged broods as compared to control or reduced broods (Table 2). All moult scoring was done without prior knowledge of the experimental status of examined birds, and there was no difference between the three study groups in date for analysis of moulting (ANOVA, 1993, $F_{2,137} = 1.12$, $p = 0.33$; 1994, $F_{2,137} = 0.07$, $p = 0.93$).

2.1. Statistical procedures

Logistic regression models, using backward elimination variable selection, were used to investigate variables that may affect moult-breeding overlap and adult survival. In these models, fledging date is set to hatching date +15 days. Given the prediction that the manipulations affected adult work load, we expected the proportion of moulting individuals to be highest when the brood size was reduced and lowest for individuals with enlarged broods. This prediction was tested with ordered heterogeneity test (Rice & Gaines 1994a, 1994b, 1994c). The same prediction was used to test if our manipulations affected the number of fledglings that were recruited to the population in the following breeding seasons. If not otherwise stated, all ordered heterogeneity tests were based on statistics from Kruskal-Wallis tests. Statistical analyses were performed with SPSS® 6.1 for Macintosh.

3. Results

3.1. Frequency of moulting individuals

Of the 506 breeding individuals scored for moult, 36.8% of the males ($n = 246$) but only 3.1% of the females ($n = 260$) were moulting with their offspring still in the nest (Table 3). More individuals were simultaneously breeding and moulting in 1994 as compared with 1993. This may relate to the fact that the hatching date of the young was on average seven days later in 1994 than in 1993 (Table 2). The percentage of moulting males was similar among controls and experimental categories, and there was no indication that birds attending enlarged broods started moulting later than those attending control or reduced broods (Table 3). No female with an increased brood showed a moult-breeding overlap, but this overlap was infrequent also among controls and females attending decreased broods. To allow a formal test of the possible effect of breeding time on moult initiation, we performed a logistic regression of moult status on manipulation, adult age, study year, sex and fledging date. Moult status was independent of manipulation, but was significantly dependent on adult age, sex and breeding date (Table 4 and Fig. 1). A further test of the brood size manipulations did not support the prediction that the proportion of moulting individuals should be highest for birds attending reduced broods and lowest for pairs attending nests with enlarged

broods (ordered heterogeneity test, males: $r_sP_c = 0.537$, $k = 3$, $p > 0.10$; females $r_sP_c = 0.381$, $k = 3$, $p > 0.10$). Independently of brood size manipulation, the percentage of moulting males increased as the season progressed (Table 4 and Fig. 2A). Moult-breeding overlap among females was independent of fledging date of their young (Fig. 2B).

3.2. Extent of moult-breeding overlap

Analyses of the moult scores (Table 3) largely confirmed the results of the foregoing analyses. Male and female moult scores were independent of experimental treatment (Fig. 3A and B). A directional test of the predicted relationship between experimental manipulation and moult scores was neither significant for young nor for old males (ordered heterogeneity test, young, $r_sP_c = 0.140$, $k = 3$, $p > 0.30$; old, $r_sP_c = 0.00$, $k = 3$, $p > 0.50$), but young males had higher moult scores than the old ones (Fig. 3A; Mann-Whitney U-test, $z = 4.14$, $p = 0.001$). There were few females with a moult-breeding overlap and no age difference in moult scores was found (Mann-Whitney U-test, $z = 0.75$, $p = 0.45$), and the moult scores were independent of the manipulations (Fig. 3B). Furthermore, female moult scores in the three study groups did not support the predicted relationship between manipulation and moult score (ordered heterogeneity test, young, $r_sP_c = 0.225$, $k = 3$, $p > 0.40$; old, $r_sP_c = 0.470$, $k = 3$, $p > 0.10$). We also com-

Table 2. Descriptive statistics on collared flycatcher nests included in experiments in 1993 and 1994. Sample sizes in 1993 (Reduced = 34, Control = 72, Enlarged = 34) and in 1994 (Reduced = 32, Control = 76, Enlarged = 32). Means ± SE are presented.

	Reduced	Control	Enlarged	Two-way ANOVA		
				F_{exp}	F_{year}	$F_{exp \times year}$
Clutch size						
1993	6.4 ± 0.10	6.2 ± 0.08	6.4 ± 0.10			
1994	6.1 ± 0.10	6.2 ± 0.11	6.1 ± 0.09	0.09^{ns}	2.39^{ns}	1.46^{ns}
Hatching date + Day 1 = 1 May						
1993	33 ± 0.6^a	34 ± 0.5^a	33 ± 0.6^a			
1994	40 ± 0.8^b	40 ± 0.4^b	40 ± 0.8^b	0.43^{ns}	162.1^*	0.72^{ns}
Brood size						
1993	4.0 ± 0.15^a	5.1 ± 0.20^b	7.4 ± 0.17^c			
1994	3.9 ± 0.17^a	4.9 ± 0.21^b	7.6 ± 0.26^c	99.2^*	0.52^{ns}	0.43^{ns}

Note: Means marked with different symbols are significantly different (Tukey's post-hoc tests: $p < 0.05$). ns = non-significant, * = $p < 0.001$.

pared the onset of moult in relation to the current breeding cycle of birds with overlapping reproduction and moult, thus having excluded non-moulting individuals. The manipulation did not affect the duration of a male moult-breeding overlap (Kruskal-Wallis test, young, $H_2 = 1.51$, $p = 0.47$; old, $H_2 = 0.69$, $p = 0.71$), but young males started moulting earlier in the breeding cycle than old males (Mann-Whitney *U*-test, $z = 2.50$, $p = 0.012$). Two females attending reduced broods and six control females showed a moult-breeding overlap, but none of the females attending enlarged broods had this overlap. There was no detectable difference in the duration of the moult-breeding overlap among these three groups (Kruskal-Wallis test, ages pooled, $H_2 = 0.03$, $p = 0.86$). Neither in males nor in females did the variation in the duration of the overlap follow our prediction (ordered heterogeneity test, young males, $r_sP_c = 0.00$, $k = 3$, $p > 0.50$; old males, $r_sP_c = 0.145$, $k = 3$, $p > 0.30$; females (ages pooled), $r_sP_c = 0.140$, $k = 3$, $p > 0.30$).

3.3. Reproductive success and adult survival

The number of recruits was independent of our manipulations (Kruskal-Wallis test; $H_2 = 1.21$, $p = 0.55$; ordered heterogeneity test, $r_sP_c = 0.226$, $k = 3$, $p > 0.20$), and there was no difference between non-moulting and moulting adults in number of recruits (Mann-Whitney *U*-test, males, $z = 0.87$, $p = 0.38$; females, $z = 1.30$, p = 0.11). Recruitment rate (recruits per fledgling) was 17% for the reduced brood group, 15% for controls, and 11%

for enlarged broods (Kruskal-Wallis test, $H_2 = 2.38$, $p = 0.30$). This relationship was also non-significant when testing the expected order of means of brood size manipulations and the recruitment rate (ordered heterogeneity test, $r_sP_c = 0.696$, $k = 3$, $p > 0.05$). Finally, the moult status of parents at fledging did not affect the recruitment rate of their offspring (Mann-Whitney *U*-test, males, $z = 0.07$, $p = 0.94$; females, $z = 0.98$, $p = 0.33$).

The survival rate of adults from 1993 to the following breeding seasons was 38% for males and 39% for females, and from 1994, 42% and 52%, respectively. The survival rate of adults was analysed with logistic regression, where manipulation, sex, an adult moult score, breeding time (date of fledging young), and a study year were predictor variables. None of these variables had a significant effect on survival of an adult, nor were any of the interactions significant (Logistic regression, all *p*-values > 0.09).

4. Discussion

In this experimental analysis of reproductive investment and moult, we found that the moult-breeding overlap was most common among male, as compared to female, and young, as compared to old collared flycatchers. Our manipulations of reproductive investment had no significant effect on the moult process of males during nestling feeding. Neither moult scores nor the duration of the moult-breeding overlap were dependent on our brood size manipulations. Our findings, therefore,

Table 3. Proportion of moulting collared flycatchers and mean moult score of males and females in different experimental groups in the two study years. *n* = number of individuals scored for moult.

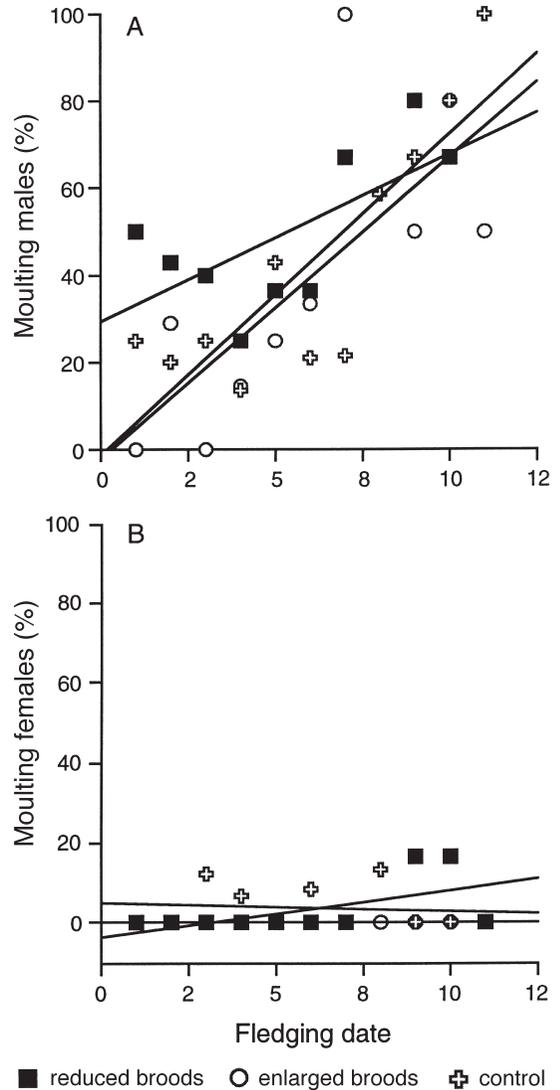|	% moulting			Mean (± SE) moult score		
	Reduced % (*n*)	Control % (*n*)	Enlarged % (*n*)	Reduced	Control	Enlarged
Females						
1993	0.0 (31)	4.7 (64)	0.0 (32)	0.0	0.03 ± 0.02	0.0
1994	6.3 (32)	4.3 (70)	0.0 (31)	0.06 ± 0.05	0.05 ± 0.03	0.0
Combined	3.2 (63)	4.5 (134)	0.0 (63)	0.03 ± 0.02	0.04 ± 0.02	0.0
Males						
1993	35.7 (28)	31.7 (63)	22.6 (31)	0.4 ± 0.2	1.1 ± 0.3	0.9 ± 0.4
1994	53.3 (30)	38.1 (63)	45.2 (31)	1.9 ± 0.5	1.5 ± 0.4	1.6 ± 0.5
Combined	44.5 (58)	34.9 (126)	33.9 (62)	1.2 ± 0.3	1.3 ± 0.2	1.3 ± 0.3
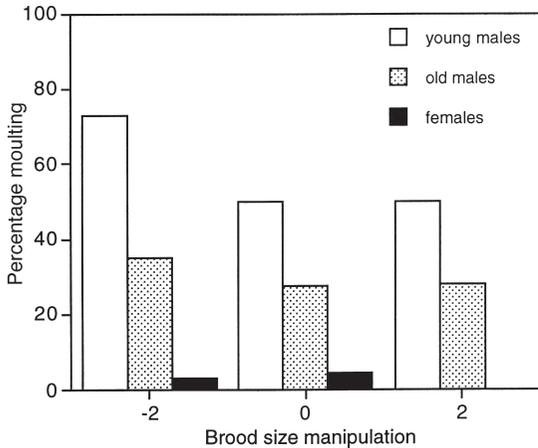
Fig. 1. Percentage of male and female collared flycatchers with a moult-breeding overlap in relation to brood size manipulation.

suggest that an experimental increase in the reproductive investment does not cause a delay in the onset of moult in male collared flycatchers. The manipulations of reproductive effort had no effect on the timing of female moult. However, the results for female collared flycatchers are difficult to interpret because very few females actually showed the moult-breeding overlap. We found conspicuous sex and age differences in the moult-breeding overlap in the collared flycatcher. The ultimate reasons for a sexual difference in timing of moult is not clear, but its has been shown to have important inter-annual fitness consequences for female passerine birds. Females mated with males showing the moult-breeding overlap seem to have higher reproductive effort and lower survival probability than females mated to males

reduced broods ◯ **enlarged broods** ✚ **control**

Fig. 2. Percentage of (A) male and (B) female collared flycatchers with moult breeding overlap in relation to brood size manipulation and breeding time (day 1 = 8 June).

postponing their moult until after breeding (Hemborg & Merilä 1998, Hemborg 1999b).

Other studies involving brood size experiments did not revealed a clear picture of a physiological trade-off between reproduction and moult (Table 1). For passerine birds, only one clutch size manipulation experiment, using pied flycatchers, produced evidence for such a trade-off (Siikamäki *et al.* 1994). However, that particular study differs from ours, because it also included enlarged incubation costs (Siikamäki 1995), and therefore,

Table 4. Results of logistic-regression (backward elimination) of moult status (non-moulting vs. moulting) in collared flycatchers.

Variable	Estimate	−2log LR	df	*p*
Manipulation	−2.08	5.04	2	0.081
Age	0.53	13.5	1	0.002
Sex	2.60	119.6	1	0.0001
Fledging date	0.15	30.4	1	0.0001
Manipulation × Sex	1.90	5.35	2	0.069

Note: Factor (year) and interactions not presented were non-significant with *p*-values > 0.15.

may have imposed stronger effects on a female reproductive investment than the manipulation with two days old nestlings. Furthermore, the study by Siikamäki *et al.* (1994) also allowed a longer time for the adults to adjust their moult to their reproductive investments as compared with our manipulations of brood size.

It is possible that a high reproductive investment affects the moult process after the young have fledged. Little is known about whether or not timing of moult can affect adult survival, although Newton (1966) found some evidence for a decreased survival among late moulting Bullfinches (*Pyrrhula pyrrhula*). On the other hand, testosterone treated male dark-eyed juncos (*Junco hyemalis*) with delayed moult showed the same survival rate as control birds (Nolan *et al.* 1992). Moreover, adult survival probability in the pied flycatcher seems to be independent of their moult status at fledging time of the young (Siikamäki *et al.* 1997, Hemborg 1999b). In our study, neither the experimental treatment nor an individual's moult stage at fledging time of the young had a significant effect on adult survival probability to the following breeding season. We also measured recruitment rate of fledglings, which should be a good indicator of the amount of post-fledging care devoted to the young. However, brood size manipulations and adult moult status seemed to have no effect on recruitment rate. This suggests that the parents with enlarged broods managed to increase their reproductive effort to produce fledglings of a good quality. Thus, the quality of post-fledging care was neither affect by brood size manipulation nor adult moult stage during nestling feeding.

Even though in this study we did not find any trade-off between reproduction and moult, we cannot exclude the possibility that such a trade-off does exists. Several other experiments have indeed demonstrated both physiological and ecological trade-offs between these two activities. For example, direct support for a negative relationship between moult and reproductive performance was found in experiments with delayed breeding time of pied flycatchers (Siikamäki 1998, Hemborg 1998), and induced moult-breeding overlap (Hemborg & Lundberg 1998). These studies showed that individuals which started moulting during nestling feeding had reduced fledging suc-
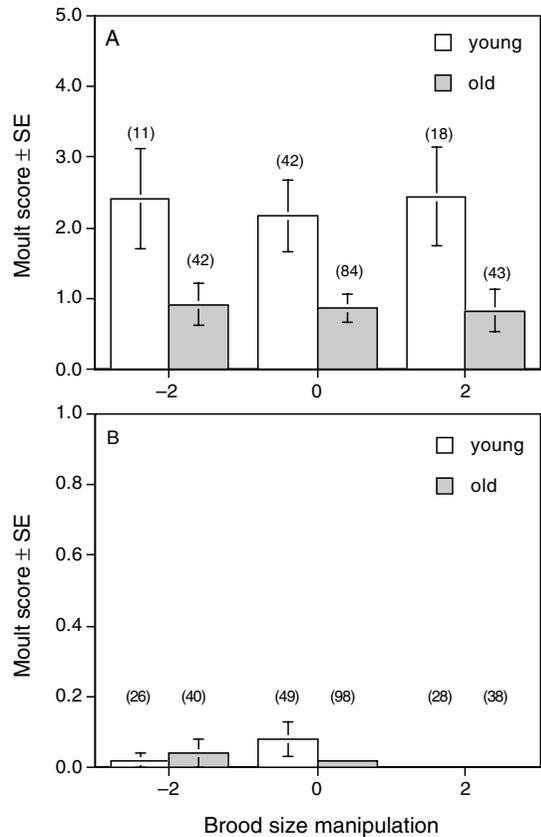
Fig. 3. Mean ± SE moult scores of (A) male and (B) female collared flycatchers. The moult scores were independent of manipulations for both males (Kruskal-Wallis test; young, $H = 0.66$, df = 2, $p = 0.72$; old, $H = 0.53$, df = 2, $p = 0.77$), and females (Kruskal-Wallis test; young, $H = 1.80$, df = 2, $p = 0.41$; old, $H = 1.25$, df = 2, $p = 0.53$). Number above bars are sample sizes.

cess or fledglings with relatively low body weight. Nilsson and Svensson (1996) provided indirect evidence for a negative relationship between reproductive and somatic investments in the blue tit (*Parus caeruleus*). They increased reproductive effort by delaying breeding attempts, which resulted in increased thermoregulatory costs and reduced adult survival during the subsequent winter. They suggested that a high reproductive investment may have negative effects on the moult and therefore result in the production of a plumage with reduced insulation capacity. Thus, reproductive investments resulting in negative effects on the moult may be one mechanism generating reproductive costs in birds (Nilsson & Svensson 1996).

The few experimental studies that have analysed the trade-off between reproduction and moult have not revealed any clear picture of this relationship (Lessells 1986, Siikamäki *et al.* 1994, Sanz 1997, this study). A delayed or constrained moult caused by a high reproductive investment may be a mechanism causing reproductive costs (Siikamäki *et al.* 1994, Nilsson & Svensson 1996), but this relationship clearly needs further experimental studies.

References

Allander, K. 1997: Reproductive investment and parasite susceptibility in the great tit (*Parus major*). — *Funct. Ecol.* 11: 358–364.

Bensch, S., Gezelius, L., Grahn, M., Hasselquist, D., Lindström, Å. & Ottosson, U. 1985: Influence of brood size on moult in female willow warblers. — *Ornis Scand.* 16: 151–152.

Chai, P. 1997: Hummingbird hovering energetics during moult of primary flight feathers. — *J. Exp. Biol.* 200: 1527–1536.

Cramp, S. & Perrins, C. M. 1993: *The birds of Western Palearctic. Vol. VII. Flycatchers to shrikes.* — Oxford University Press, Oxford.

Earnst, S. L. 1992: The timing of wing molt in tundra swans: energetic and non-energetic constraints. — *Condor* 94: 847–856.

Ginn, H. B. & Melville, D. S. 1983: *Moult in birds. Guide No. 19.* — British Trust for Ornithology. Tring, UK.

Gustafsson, L., Nordling, D., Andersson, M. S., Sheldon, B. C. & Qvarnström, A. 1994: Infectious diseases, reproductive effort and the cost of reproduction in birds. — *Phil. Trans. R. Soc. Lond.* B 346: 323–331.

Hemborg, C. 1998: Sexual differences in the control of postnuptial moult in the pied flycatcher. — *Anim. Behav.* 56: 1221–1227.

Hemborg, C. 1999a: Annual variation in the timing of breeding and moulting in male and female pied flycatchers *Ficedula hypoleuca*. — *Ibis* 141: 226–232.

Hemborg, C. 1999b: Sexual difference in timing of moult and female reproductive costs in pied flycatchers. — *J. Anim. Ecol.* 68: 429–436.

Hemborg, C. & Lundberg, A. 1998: Costs of overlapping reproduction and moult in passerine birds: an experiment with the pied flycatcher. — *Behav. Ecol. Sociobiol.* 43: 19–23.

Hemborg, C. & Merilä, J. 1998: A sexual conflict in collared flycatchers *Ficedula albicollis*: early male moult reduces female fitness. — *Proc. R. Soc. Lond.* B 265: 2003–2007.

Holmgren, N. & Hedenström, A. 1995: The scheduling of molt in migratory birds. — *Evol. Ecol.* 9: 354–368.

Klaassen, M. 1995: Moult and basal metabolic costs in males of two subspecies of stonechats: the European *Saxicola torquata rubicula* and the East African *S. t. axillaris*. — *Oecologia* 104: 424–432.

Langston, N. E. & Rohwer, S. 1996: Molt-breeding trade-offs in albatrosses: life history implications for big birds. — *Oikos* 76: 498–510.

Lessells, C. M. 1986: Brood size in Canada geese: a manipulation experiment. — *J. Anim Ecol.* 55: 669–689.

Lindén, M. & Møller, A. P. 1989: Costs of reproduction and covariates of life history traits in birds. — *Trends Ecol. Evol.* 4: 367–371.

Lindström, Å., Visser, G. H. & Daan, S. 1993: The energetic cost of feather synthesis is proportional to basal metabolic rate. — *Physiol. Zool.* 66: 490–510.

Merilä, J. 1996: Genetic variation in offspring condition: an experiment. — *Funct. Ecol.* 10: 465–474.

Merilä, J. 1997: Expression of genetic variation in body size of the collared flycatcher under different environmental conditions. — *Evolution* 51: 526–536.

Merilä, J. & Gustafsson, L. 1993: Inheritance of size and shape in a natural population of collared flycatchers, *Ficedula albicollis*. — *J. Evol. Biol.* 6: 375–395.

Murphy, M. E. & Taruscio, T. G. 1997: Sparrow increase their rates of tissue and whole-body protein synthesis during the annual molt. — *Comp. Biochem. Physiol.* 111A: 385–396.

Newton, I. 1966: The moult of the Bullfinch *Pyrrhula pyrrhula*. — *Ibis* 108: 41–67.

Nilsson, J.-Å. & Svensson, E. 1996: The cost of reproduction: a new link between current reproductive effort and future reproductive success. — *Proc. R. Soc. Lond.* B 263: 711–714.

Nolan, V. Jr., Ketterson, E. D., Ziegenfus, C., Cullen, D. P. & Chandler, C. R. 1992: Testosterone and avian life histories: effect of experimentally elevated testosterone on prebasic molt and survival in male dark-eyed juncos. — *Condor* 94: 364–370.

Norris, K., Anwar, M. & Read, A. F. 1994: Reproductive effort influences the prevalence of haematozoan parasites in great tits. — *J. Anim. Ecol.* 63: 601–610.

Orell, M., Rytkönen, S., Koivula, K., Ronkainen, M. & Rahiala, M. 1996: Brood size manipulations within the natural range did not reveal intragenerational cost of reproduction in the willow tit *Parus montanus*. — *Ibis* 138: 630–637.

Payne, R. B. 1972: Mechanisms and control of molt. — In: Farner, D. S. & King, J. R. (eds.), *Avian biology*, vol. 2: 103–155. Academic Press, New York.

Pennycuick, C. J. 1975: Mechanics of flight. — In: Farner, D. S. & King, J. R. (eds.), *Avian biology*, vol. 5: 1–

75. Academic Press, New York.

Perrin, N. 1992: Optimal resource allocation and the marginal value of organs. — *Am. Nat.* 139: 1344–1369.

Pietiäinen, H., Saurola, P. & Kolunen, H. 1984: The reproductive constraint on moult in the ural owl *Strix uralensis*. — *Ann. Zool. Fennici* 21: 277–281.

Pärt, T. 1990: Natal dispersal in the collared flycatcher: possible causes and reproductive consequences. — *Ornis Scand.* 21: 83–88.

Pärt, T. & Gustafsson, L. 1989: Breeding dispersal in the collared flycatcher (*Ficedula albicollis*): possible causes and reproductive consequences. — *J. Anim. Ecol.* 58: 305–320.

Rice, W. R. & Gaines, S. D. 1994a: Extending nondirectional heterogeneity tests to evaluate simply ordered alternative hypotheses. — *Proc. Nat. Acad. Sci.* USA 91: 225–226.

Rice, W. R. & Gaines, S. D. 1994b: "Heads I win, tails you lose": testing directional alternative hypotheses in ecological and evolutionary research. — *Trends Ecol. Evol.* 9: 235–237.

Rice, W. R. & Gaines, S. D. 1994c: The ordered-heterogeneity family of tests. — Biometrics 50: 746–752.

Richner, H., Christie, P. & Oppliger, A. 1995: Parental investment affects prevalence of malaria. — *Proc. Nat. Acad. Sci.* USA 92: 1192–1194.

Roff, D. A. 1992: The evolution of life histories. — Chapman and Hall, New York.

Sanz, J. J. 1997: Clutch size manipulation in the pied flycatcher: effects on nestling growth, parental care and moult. — *J. Avian Biol.* 28: 157–162.

Sheldon, B. C & Verhulst, S. 1996: Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. — *Trends Ecol. Evol.* 11: 317–321.

Siikamäki, P. 1995: Are large clutches costly to incubate — the case of the pied flycatcher. — *J. Avian Biol.* 26: 76–80.

Siikamäki, P. 1998: Limitations of reproductive success by food availability and breeding time in pied flycatchers. — *Ecology* 79: 1789–1796.

Siikamäki, P., Hovi, M. & Rätti, O. 1994: A trade-off between current reproduction and moult in the pied flycatcher — an experiment. — *Funct. Ecol.* 8: 587–593.

Siikamäki, P., Hovi, M. & Rätti, O. 1997: Low male return rate due to clutch enlargements in the pied flycatcher (*Ficedula hypoleuca*). — *Écoscience* 4: 24–28.

Slagsvold, T. & Lifjeld, J. T. 1989: Hatching asynchrony in birds: the hypothesis of sexual conflict over parental investment. — *Am. Nat.* 134: 239–253.

Slagsvold, T. & Dale, S. 1996: Disappearance of female pied flycatchers in relation to breeding stage and experimentally induced moult. — *Ecology* 77: 461–471.

Svensson, E. & Nilsson, J.-Å. 1997: The trade-off between molt and parental care: a sexual conflict in the blue tit? — *Behav. Ecol.* 8: 92–98.

Svensson, L. 1992: Identification guide to European passerines. — Svensson, Stockholm.

Swaddle, J. P. & Witter, M. S. 1997: The effects of molt on the flight performance, body mass, and behavior of European starlings (*Sturnus vulgaris*): an experimental approach. — *Can. J. Zool.* 75: 1135–1146.

Tuomi, J., Hakala, T. & Haukioja, E. 1983: Alternative concept of reproductive effort, costs of reproduction and selection in life-history evolution. — *Am. Zool.* 23: 25–34.

Westneat, D. F. & Sherman, P. W. 1993: Parentage and the evolution of parental behavior. — *Behav. Ecol.* 4: 66–77.

Williams, G. C. 1966: Adaptation and natural selection. — Princeton University Press, New Jersey.