A sexual conflict in collared flycatchers, *Ficedula albicollis*: early male moult reduces female fitness

Christer Hemborg* and Juha Merilä

Department of Zoology, Uppsala University, Villavägen 9, S-752 36 Uppsala, Sweden

A sexual conflict over levels of parental care occurs in most animals with biparental care, and studies of sexual differences in levels of parental care have usually focused on its intra-annual fitness consequences. We investigated inter-annual fitness consequences of a sexual difference in timing of feather replacement (moult) in collared flycatchers (*Ficedula albicollis*). In this study, males overlapped reproduction and moult more often than females, they also initiated their moult at an earlier stage of breeding than females. Females mated to males with a moult-breeding overlap had significantly lowered survival chances than females mated with males initiating moult after breeding. Furthermore, females mated with moulting males risked a lowered future fecundity in terms of a delayed start to breeding in the following season. However, early moulting males achieved a similar reproductive success as males initiating moult after breeding. Likewise, male survival probability to the following breeding season did not differ between early and late moulting individuals, nor was there any evidence that males gained or lost in future mating advantages by moulting early. These results show not only that a sexual conflict over timing of moult may operate, but also that it can impose severe fitness consequences, in terms of future reduced fecundity and survival probability, upon the 'losing' sex.

Keywords: costs of reproduction; moult-breeding overlap; sexual conflict; trade-off

1. INTRODUCTION

Whenever biparental care occurs in a species, the sexes may have different optima of parental effort, and thus there is always a potential for a conflict over the respective levels of reproductive investments of the two sexes (Williams 1966; Trivers 1972; Clutton-Brock 1991). Sexual differences in levels of parental care have been studied in a large number of species, above all in birds, in which a great variation exists in the amount of care given by the parents (Ketterson & Nolan 1994). A number of experimental studies have been designed to investigate the relationship between the level of sex-specific parental care and reproductive success in birds (Wolf *et al.* 1988; Wright & Cuthill 1989; Bart & Törnes 1989; Clutton-Brock 1991). Numerous studies have investigated intra-annual fitness consequences on a sexual difference in levels of parental care, but only a few studies have investigated inter-annual fitness consequences of female compensation. These studies found no relationship between female reproductive investment and survival probability (Ketterson *et al.* 1992; Bensch 1996; but, see Slagsvold *et al.* 1994; Käär *et al.* 1998), or future fecundity (Bensch 1996).

A sexual conflict over levels of parental care may arise as a consequence of males and females allocating differently to reproduction and self-maintenance functions, respectively. For example, in birds where somatic investment in new feathers is traded against reproductive

investment (Siikamäki *et al.* 1994; Nilsson & Svensson 1996), a sexual conflict may arise if one sex initiates moult during breeding and reduces its reproductive investment accordingly (Creutz 1955; Ezaki 1988; Svensson & Nilsson 1997). In fact, despite numerous potential costs (e.g. Lindström *et al.* 1993; Swaddle & Witter 1997), moult has been found to overlap with nestling feeding in many bird species (review in Jenni & Winkler (1994)). Although moult-breeding overlap occurs in females, it is much more common and of longer duration among males (review in Jenni & Winkler (1994)).

One experimental study has demonstrated that induced feather loss in adult pied flycatchers (*Ficedula hypoleuca*) during nestling feeding had a negative effect on reproductive success (Hemborg & Lundberg 1998). That particular experiment also showed that males with a moult-breeding overlap had lower survival probability than control males which postponed their moult until after breeding. However, the fitness consequences of a sexual difference in moult-breeding overlap are little explored. Ezaki (1988) reported that nestling mortality increased if male great reed warblers (*Acrocephalus arundinaceus*) deserted their brood to start moulting. An extensive moult-breeding overlap in male blue tits (*Parus caeruleus*) has also been found to increase nestling mortality (Svensson & Nilsson 1997), and it has been suggested that the sexual difference in timing of moult can create a conflict between male investment in self-maintenance and female reproductive success. Alternatively, an early-moult among males may, in fact, be the result of the sexual conflict over

*Author for correspondence (christer.hemborg@zoologi.uu.se).

levels of parental care. Nevertheless, there is a potential intra-annual fitness cost to passerine females because of a widespread male tendency of starting moult before their nestlings have fledged.

The aim of the present study was to investigate whether the sexual difference in timing of moult in collared flycatchers (*Ficedula albicollis*) may impose inter-annual fitness costs upon females. It also aims to explore the potential costs and benefits of early moult accruing to males, in order to better understand the adaptive background to sexual differences in moult schedules.

2. METHODS

This study was conducted during the breeding seasons of 1993 and 1994 in a nest box breeding population of the collared flycatcher on the island of Gotland, Sweden. Collared flycatchers are small insectivorous passerine birds which spend the winter in tropical Africa. The female builds the nest and incubates the eggs, but both sexes participate in nestling care. We regularly inspected the nest boxes to determine date of egg laying, clutch size and hatching date of eggs. To manipulate adult workload during nestling feeding, we performed brood size manipulations. Two days after hatching we swapped nestlings such that some broods were reduced and others enlarged by two nestlings. A control group was achieved by swapping nestlings between nests, but without changing brood size. In total, we manipulated 132 pairs of collared flycatchers, while the number of control nests, including unmanipulated breeding attempts, was 147. These brood size manipulation experiments have earlier been shown to have no effects on timing of adult moult (Hemborg & Merilä 1999).

At day 13 after hatching (i.e. just before the young leave the nest), we captured all adults when they were feeding the nestlings. Adults and offspring were ringed, or identified from rings from previous years, and measured according to standard procedures (see Merilä & Gustafsson 1993; Merilä 1996, 1997). Adult wing moult was recorded, and we classified all individuals as either 'moulting' (thus having a moult-breeding overlap) or 'non-moulting' (thus postponing the moult until after reproduction). All individuals were also assigned a moult score according to a standard moult scoring system, where an old feather was 0, growing and missing feathers were 1 to 4, and a completely grown feather was 5 (see Ginn & Melville 1983). The moult score of an individual was calculated as the mean score of all flight feathers in each wing. The sexual difference in moult-breeding overlap is the difference in moult scores between the male and the female of a pair.

To examine whether moult-breeding overlap imposed fitness costs, we examined fledgling condition, and the number of fledglings and adults that survived to the following breeding season. The return rate of collared flycatchers in our study area is high (Gustafsson & Sutherland 1988; Pärt & Gustafsson 1989), and when assessing adult and fledgling survival we considered birds which were recaptured as breeders in the study area in any of the subsequent years (1994–1996) as 'survivors' or 'recruits', whereas non-recaptured individuals were regarded as 'non-survivors'. Furthermore, we compared future fecundity of surviving females in terms of date of egg-laying and clutch size. In male collared flycatchers, the white forehead patch is a sexually selected character and has an important role in male–male competition (Pärt & Qvarnström 1997; Sheldon *et al.* 1997b). We measured the change in male forehead patch area (standardized for original patch area) from one year to the next

to investigate whether a moult-breeding overlap might bring any fitness benefits (i.e. increased forehead patch area) or costs (i.e. reduced forehead patch area) to males (cf. Gustafsson *et al.* 1995). We also investigated whether timing of moult might affect the wing length (standardized for age) that a male achieved after the moult, or the timing of future breeding attempts.

The return rate of adults was analysed using a logistic regression model, where all interactions between the independent variables were initially included, and the best model was found by backward elimination of non-significant variables. The residuals from a regression of mean brood mass on mean brood tarsus length were used as an estimate of fledgling condition (Merilä 1996). Non-significant interaction terms have been deleted if not otherwise stated. All significance levels are two-tailed.

3. RESULTS

A temporal moult-breeding overlap was found in both sexes, but males started moulting during nestling feeding more often than females (36.8% versus 3.1%, respectively; $\chi^2=87.5$, d.f.=1, $p<0.0001$). At 13 days after hatching, males had, on average, a much higher moult score than females (moult score $\pm$ s.e.: males ($n=247$), 1.3 ± 0.1 ; females ($n=261$), 0.03 ± 0.01 ; Mann–Whitney test: $z=9.77$, $p<0.001$). A comparison of the moult scores of birds with moult-breeding overlap showed that males, on average, were in a more advanced moult stage as compared to females (moult score $\pm$ s.e.: males ($n=91$), 3.5 ± 0.3 ; females ($n=8$), 0.94 ± 0.2 ; Mann–Whitney test: $z=3.37$, $p<0.001$). The sexual difference in moult scores was independent of the brood size manipulation experiments (moult score difference $\pm$ s.e.: reduced broods ($n=57$), 1.2 ± 0.3 ; control broods ($n=120$), 1.2 ± 0.2 ; enlarged broods ($n=59$), 1.3 ± 0.3 ; Kruskal–Wallis test: $H_2=1.34$, $p=0.51$) but it increased as the season progressed (Spearman rank correlation: $r_s=0.322$, $p<0.001$, $n=236$). Moulting males were, on average, breeding two days later than non-moulting males (Mann–Whitney test: $z=5.19$, $p<0.001$), while no significant difference was observed in breeding date for moulting and non-moulting females (Mann–Whitney test: $z=1.26$, $p=0.21$).

When controlling for breeding time, male moult status during breeding did not affect fledgling condition (residual condition $\pm$ s.e.: non-moulting males ($n=153$), 0.03 ± 0.08 ; moulting males ($n=90$), 0.001 ± 0.10 ; ANCOVA: $F_{1,235}=0.96$, $p=0.33$), but there was a significant effect of brood size manipulations (residual condition $\pm$ s.e.: reduced broods ($n=64$), 0.383 ± 0.10 ; control broods ($n=139$), -0.026 ± 0.08 ; enlarged broods ($n=65$), -0.341 ± 0.14 ; ANCOVA: $F_{2,235}=6.90$, $p=0.001$). There was no difference between moulting and non-moulting males, in the number of young recruited to the breeding population (ANCOVA: $F_{1,242}=0.40$, $p=0.84$) or among experimental groups (ANCOVA: $F_{2,239}=0.85$, $p=0.43$). The change in male forehead patch size to the following year did not differ between moulting and non-moulting males or among the experimental groups (two-way ANOVA: male moult status, $F_{1,77}=1.17$, $p=0.28$; brood size manipulations, $F_{2,77}=1.21$, $p=0.30$). Similarly, male wing length and breeding time in the following breeding season were independent of male moult status

Table 1. Logistic-regression of factors determining survival probability (returning versus non-returning) of female collared flycatchers

variable	-2logLR	<i>p</i>
variables in the model		
moult status of mate	7.61	0.01
year	3.39	0.07
variables not in the model		
moult status of female	0.02	0.88
manipulation	1.01	0.60
hatching date	0.25	0.62

and brood size manipulations (two-way ANOVA: all *F*-values <1.45, all *p*-values >0.20). Male survival was independent of his own moult status, the moult status of his partner, experimental treatment, study year and breeding time (logistic regression: all *p*-values >0.15).

Female survival was independent of her own moult status just before the fledging of the young, timing of breeding, brood size manipulations and study year, while females mated to moulting males had a significantly lower return rate as compared to females mated to a non-moulting male (table 1 and figure 1). Furthermore, if female reproductive investment increased as a result of male moult-breeding overlap, it is to be expected that this might also affect female future fecundity. Among surviving females, those mated with males previously showing moult-breeding overlap started breeding significantly later than females that were aided by a non-moulting male (table 2). However, male moult status at 13 days after hatching had no significant effect on surviving females' clutch size (table 2). Brood size manipulations neither affected future breeding time or clutch size (table 2).

4. DISCUSSION

Studies of the reproductive consequences of a low or missing level of male parental care have usually focused on nestling growth and survival to independence (reviews in Wolf *et al.* 1988; Bart & Tornes 1989; Clutton-Brock 1991), while the reproductive costs that the female may have to pay because of decreased male care have largely been ignored. The sexual conflict over level of parental care may be influenced by several factors, such as paternity probability, and in birds, also by a sexual difference in timing of moult (Creutz 1955; Ezaki 1988; Svensson & Nilsson 1997). On Gotland, male collared flycatchers regularly moulted during nestling feeding and initiated their moult earlier in the breeding cycle as compared to the few females that began moulting before the young had fledged. Timing of male moult neither affected fledgling condition nor the number of young that were recruited to the breeding population in the next year. Thus, male moult status during nestling feeding seemed not to affect offspring quality. By contrast, females mated to early moulting males had significantly lower survival probability than females aided by a non-moulting male. Although surviving females that were mated with early moulters did not suffer from reduced future fecundity in terms of a lowered clutch size, they bred later the

Figure 1. Survival rate of female collared flycatchers mated with non-moulting males (open bars) versus moulting males (closed bars). Numbers above bars are sample sizes.

following year than females mated to non-moulting males. As in many other passerine birds, early breeding in collared flycatchers is advantageous (Wiggins *et al.* 1994), and hence, females mated to moulting males seemed to suffer a reduced future fecundity. Our results contrast with those obtained for the blue tit, where an early male moult increased nestling mortality (Svensson & Nilsson 1997), but female survival was independent of male moult status (E. Svensson, personal communication). Thus, in the collared flycatcher the female pays a significant costs of an early male moult, whereas in blue tits the costs are laid on the offspring. This difference between the two species can have several explanations, but it may relate to the large difference in clutch size. The relatively small clutch size of the collared flycatcher, as compared to the blue tit, may indicate a higher reproductive value of each offspring. Thus, to our knowledge, this study is the first to suggest that a sexual difference in an allocation of time and energy between reproduction and self-maintenance may impose lifetime fitness costs on the 'losing' sex.

The mechanisms causing fitness costs in terms of reduced survival probability and reduced future fecundity on females mated to males with moult-breeding overlap are not known. However, it may be related to the fact that there is a negative relationship between moult-breeding overlap and amount of parental investment, as has been found in the closely related pied flycatcher (Siikamäki 1998; Hemborg 1998) and in other species (Morton & Morton 1990; Amat 1995; Nilsson & Svensson 1997; see also Swaddle & Witter 1997). Thus, it is possible that male collared flycatchers reduced their level of parental care when they initiated moulting, and that the females suffered from reproductive costs if they increased their reproductive investment in response to male moult-breeding overlap (cf. Qvarnström 1997; Sheldon *et al.* 1997a). A previous study of collared flycatchers has shown that female survival probability may decrease when their reproductive investment is experimentally increased

Table 2. *Future breeding performance of female collared flycatchers in relation to brood size manipulations (exp) and the moult status of their mate*

	non-moulting mate mean $\pm$ s.e. (<i>n</i>)	moulting mate mean $\pm$ s.e. (<i>n</i>)	two-way ANOVA	
			<i>F</i> _{exp}	<i>F</i> _{moult status}
laying date ^a	-0.14 $\pm$ 0.1 (59)	0.32 $\pm$ 0.2 (32)	0.86 ^{n.s.}	4.86*
clutch size	6.2 $\pm$ 0.2 (59)	6.0 $\pm$ 0.2 (32)	0.13 ^{n.s.}	0.34 ^{n.s.}

^a Laying date was standardized within years.^{n.s.} Not significant.**p* < 0.05.

(Cichon *et al.* 1998). By contrast, some other studies have found that male pied flycatchers may respond more to brood size manipulations than females, for example in terms of increased feeding rates (Moreno *et al.* 1995), or reduced survival probability (Siikamäki *et al.* 1997).

There are several potential benefits of starting moult early. One benefit may be that the moult can be initiated during a period of high food abundance, which usually coincides with the nestling feeding (Perrins 1991; see also Ginn & Melville 1983), and/or that more time will be available for completing the moult before the start of autumn migration. Furthermore, in a previous study of collared flycatchers on Gotland, a trade-off was observed between male reproductive investment and their forehead patch area in the following year (Gustafsson *et al.* 1995). The forehead patch is an intra- and intersexually selected male character (Pärt & Qvarnström 1997; Sheldon *et al.* 1997b). Thus, one possible benefit for early moulting males could derive from their opportunity to allocate more resources to their somatic maintenance, with the consequence that they might return in the following breeding season with larger forehead patches, or with longer wings. The latter may be advantageous for a rapid spring migration to the breeding area. In the present study, we were unable to identify any benefits accruing to early moulting males, although such are likely to occur in view of the widespread occurrence of male moult-breeding overlap (Jenni & Winkler 1994). This interpretation is also supported by the lack of negative fitness effects of moult-breeding overlap on males in this study.

In conclusion, the sexual difference in timing of moult may have important inter-annual consequences in terms of reduced female survival probability and future fecundity. A sexual difference in allocation of time and energy between reproduction and somatic maintenance may be an important factor underlying the sexual conflict over parental care in birds, and most likely also in other animals with biparental care.

We thank all field assistants for excellent help during the field work. We also thank Staffan Ulfstrand, Ben Sheldon, Mariusz Cichon, Arne Lundberg, Erik Svensson, Pirkko Siikamäki and one anonymous referee for improving the manuscript. This study was funded by grants from Stiftelsen Zoologisk Forskning (to C.H. and J.M.) and from the Swedish Natural Science Research Council (to J.M.).

REFERENCES

- Amat, J. A. 1995 Parent-offspring feeding relationship of coots (*Fulica atra*) in a varying environment. *Behaviour* **132**, 519–527.

- Bart, J. & Tornes, A. 1989 Importance of monogamous male birds in determining reproductive success. Evidence for house wrens and a review of male-removal studies. *Behav. Ecol. Sociobiol.* **24**, 109–116.
- Bensch, S. 1996 Female mating status and reproductive success in the great reed warbler: is there a potential cost of polygyny that requires compensation? *J. Anim. Ecol.* **65**, 283–296.
- Cichon, M., Olejniczak, P. & Gustafsson, L. 1998 The effect of body condition on the cost of reproduction in female collared flycatchers *Ficedula albicollis*. *Ibis* **140**, 128–130.
- Clutton-Brock, T. H. 1991 *The evolution of parental care*. Princeton University Press.
- Creutz, G. 1955 Der Trauerschnäpper *Ficedula hypoleuca* (Pallas). Eine Populationsstudie. *J. Ornithol.* **96**, 241–326.
- Ezaki, Y. 1988 Mate desertion by male great reed warblers *Acrocephalus arundinaceus* at the end of the breeding season. *Ibis* **130**, 427–437.
- Ginn, H. B. & Melville, D. S. 1983 *Moult in birds*. Tring, UK: BTO Guide 19.
- Gustafsson, L. & Sutherland, W. J. 1988 The costs of reproduction in the collared flycatcher *Ficedula albicollis*. *Nature* **335**, 813–815.
- Gustafsson, L., Qvarnström, A. & Sheldon, B. C. 1995 Trade-offs between life history traits and a secondary sexual character in male collared flycatchers. *Nature* **375**, 311–313.
- Hemborg, C. 1998 Sexual differences in the control of postnuptial moult in the pied flycatcher. *Anim. Behav.* (In the press.)
- 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. 1999 Reproductive investment and moult-breeding overlap in the collared flycatcher *Ficedula albicollis*: an experimental approach. (Submitted.)
- Jenni, L. & Winkler, R. 1994 *Moult and ageing of European passerines*. London: Academic Press.
- Käär, P., Jokela, J., Merilä, J., Helle, T. & Kojola, I. 1998 Sexual conflict and remarriage in preindustrial human populations: causes and fitness consequences. *Evol. Human. Behav.* **19**, 139–159.
- Ketterson, E. D. & Nolan, V. Jr 1994 Male parental behavior in birds. *A. Rev. Ecol. Syst.* **25**, 601–628.
- Ketterson, E. D., Nolan, V. Jr, Wolf, L. & Ziegenfuss, C. 1992 Testosterone and avian life histories: effects of experimentally elevated testosterone on behavior and correlates of fitness in the dark-eyed junco (*Junco hyemalis*). *Am. Nat.* **140**, 980–999.
- 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**, 375–398.
- Moreno, J., Cowie, R. J., Sanz, J. J. & Williams, R. S. R. 1995 Differential response by males and females to brood manipulations in the pied flycatcher: energy expenditure and nestling diet. *J. Anim. Ecol.* **58**, 305–320.
- Morton, G. A. & Morton, M. L. 1990 Dynamics of postnuptial molt in free-living mountain white-crowned sparrows. *Condor* **92**, 813–828.
- 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.
- Pärt, T. & Gustafsson, L. 1989 Breeding dispersal in the collared flycatcher (*Ficedula albicollis*): possible causes and reproductive consequences. *J. Anim. Ecol.* **58**, 305–320.
- Pärt, T. & Qvarnström, A. 1997 Badge size in collared flycatchers predict outcome of male competition over territories. *Anim. Behav.* **54**, 893–899.
- Perrins, C. M. 1991 Tits and their food supply. *Ibis* **133**, 49–54.
- Qvarnström, A. 1997 Experimentally increased badge size increases male competition and reduces male parental care in the collared flycatcher. *Proc. R. Soc. Lond. B* **264**, 1225–1231.
- Sheldon, B. C., Räsänen, K. & Dias, P. C. 1997a Certainty of paternity and parental effort in the collared flycatcher. *Behav. Ecol.* **8**, 421–428.
- Sheldon, B. C., Merilä, J., Qvarnström, A., Gustafsson, L. & Ellegren, H. 1997b Paternal genetic contribution to offspring condition predicted by size of male secondary sexual character. *Proc. R. Soc. Lond. B* **264**, 297–302.
- Siikamäki, P. 1998 Limitation 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., Amundsen, T. & Dale, S. 1994 Selection by sexual conflict for evenly spaced offspring in blue tits. *Nature* **370**, 136–138.
- 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.
- Swaddle, J. P. & Witter, M. S. 1997 The effect of molt on flight performance, body mass, and behavior of European starlings (*Sturnus vulgaris*): an experimental approach. *Can. J. Zool.* **75**, 1135–1146.
- Trivers, R. L. 1972 Parental investment and sexual selection. In *Sexual selection and the descent of man, 1871–1971* (ed. B. Campbell), pp. 136–179. Chicago, IL: Aldine.
- Wiggins, D. A., Pärt, T. & Gustafsson, L. 1994 Seasonal decline in collared flycatcher *Ficedula albicollis* reproductive success: an experimental approach. *Oikos* **70**, 359–364.
- Williams, G. C. 1966 Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.* **100**, 687–690.
- Wolf, L., Ketterson, E. D. & Nolan, V. Jr 1988 Paternal influence on growth and survival of dark-eyed junco young: do parental males benefit? *Anim. Behav.* **36**, 1601–1618.
- Wright, J. & Cuthill, I. 1989 Manipulation of sex difference in parental care. *Behav. Ecol. Sociobiol.* **25**, 171–181.