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Timing of Breeding and Reproductive Costs in Collared Flycatchers

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Many recent studies of birds have attempted to measure a cost of reproduction by correlating current investment with subsequent parental survival and reproductive performance (see Dijkstra et al. 1990, Roff 1992, Stearns 1992). Demonstrating a link between current and future reproduction provides an important test of within-generation life-history tradeoffs (Williams 1966, Gadgil and Bossert 1970, Charnov and Krebs 1974, Daan et al. 1990, Stearns 1992). Studies of birds have typically relied on experimental manipulations of brood size (e.g. Gustafsson and Sutherland 1988, Nur 1988) because brood size often is correlated with the amount of care provided by parents and with the number of offspring subsequently recruited into the population.

Timing of breeding is another factor that may be significantly correlated with parental survival (e.g. lower survival for late breeders; Harvey et al. 1988, Wiggins 1991, Verhulst et al. 1995) and offspring recruitment (e.g. decreased recruitment with later breeding; Price et al. 1988). Although recent experimental work has demonstrated a direct link between the timing of breeding per se and annual reproductive success (Verhulst and Tinbergen 1991, Brinkhof et al. 1993, Norris 1993), such studies have not assessed the long-term effects of breeding-date manipulations on subsequent parental survival or reproduction. If breeding date per se is negatively correlated with parental survival or future reproduction (e.g. owing to time constraints related to initiation of molt or migration), then experimental delays in breeding should result in reduced parental survival or reproduction in subsequent years. The limited available evidence is equivocal: Verhulst et al. (1995) found that female quality, but not breeding date, was responsible for the seasonal trend of decreasing female survival in Great Tits (*Parus major*), whereas among Blue Tits (*P. caeruleus*), delayed breeding led to poor adult survival and lower future reproductive success (Nilsson and Svensson 1996).

Experimental manipulations of breeding date are difficult to achieve without inducing concurrent effects on parental body condition. The two most common methods used to alter breeding date, clutch removal and temporary clutch replacement with dummy eggs, may result in considerable increases in en-

ergetic effort by males (in species where incubation feeding is common, such as *Ficedula* flycatchers) and females (via increased incubation costs; e.g. Moreno and Carlson 1989). Although previous studies have typically concluded that such experimental effects are minimal (e.g. Verhulst and Tinbergen 1991, Brinkhof et al. 1993, Nilsson and Svensson 1996), one of the primary concerns in our study was to delay the timing of hatching while minimizing the energetic consequences (potentially induced by prolonging the incubation period) for males and females.

In this study, we attempt to link the timing of breeding per se with the subsequent survival and reproductive success of adult Collared Flycatchers (*Ficedula albicollis*). Thus, in contrast to most previous studies of reproductive costs in birds, our approach was to manipulate the timing (by extending incubation), rather than the level (by changing brood size) of parental care. However, because offspring production is correlated with timing of breeding, we also consider how the interaction of timing and brood size may affect the future survival and reproduction of parents. If later breeding per se entails significant costs to the parents (e.g. via decreased time available for molt prior to migration, and/or increased overlap between molt and breeding), then a delay in breeding date may have significant effects on subsequent parental survival and/or reproduction (cf. Nilsson and Svensson 1996).

Study area and methods.—The study was carried out in 1992 and 1993 on the island of Gotland (57°10'N, 18°20'E) in the southern Baltic Sea (see Pärt and Gustafsson 1989 for description of study site). Flycatchers return to the island in early May, lay eggs from mid-May to mid-June, and leave the island in July and August. To determine clutch initiation dates, we checked nest boxes every two to three days from early May to early June. During the nestling phase, we measured and banded most adults and all nestlings.

In 1992, we delayed hatching by seven days in 108 randomly chosen experimental nests. Clutches were removed on the (presumed) morning of clutch completion, placed in a refrigerator at 7°C, and replaced by an equal number of artificial eggs. Nests were rechecked for a new egg on the day (or days) following clutch removal. If a new egg was present, it was added to the original clutch and replaced with a dummy egg. Clutches were replaced in their original nests seven days after clutch completion, thus extending

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TABLE 1. Reproductive traits (1992 only) and between-year survival of control and delayed pairs of Collared Flycatchers. Values are $\bar{x} \pm SD$, with n in parentheses. Laying dates of control pairs were within the range of laying dates for experimentally delayed pairs.

Trait	Control pairs	Delayed pairs	F or G ^a	P
Laying date	21.9 \pm 3.4 (104)	21.6 \pm 3.0 (98)	0.45	0.50
Clutch size	5.9 \pm 0.7 (104)	6.3 \pm 0.5 (98)	13.90	0.0003
Brood size at fledging	4.6 \pm 2.2 (104)	1.4 \pm 1.6 (98)	139.87	0.0001 ^b
Female mass loss ^c	1.22 \pm 0.65 (45)	1.42 \pm 0.62 (46)	2.15	0.15
Male body condition ^d	0.03 \pm 0.57 (99)	-0.01 \pm 0.70 (67)	0.15	0.70
Female overwinter survival	0.48 \pm 0.5 (99)	0.41 \pm 0.5 (97)	0.77	0.46
Male overwinter survival	0.51 \pm 0.5 (89)	0.57 \pm 0.5 (67)	0.58	0.55

^a Overwinter survival of females and males tested with G-test; all other tests are ANOVA.

^b Effect experimentally induced; see text.

^c Measured from day 7 of incubation to hatching.

^d Measured from day 7 of brood-rearing period.

the incubation period from approximately 13 to 20 days. In 44 of the experimental clutches, one egg was removed to mimic the seasonal decrease in clutch size (see Wiggins et al. 1994a).

We used a similar experimental protocol in a pilot study in 1991 and observed no negative effects of refrigeration on hatching success (unpubl. data). However, the viability of refrigerated eggs was significantly reduced in 1992; of 108 refrigerated clutches, 18 hatched no young, 42 hatched only one young, and in only 4 did all eggs hatch. The reasons for the poor viability are unclear, but exceptionally warm weather during the 1992 laying period may have led to relatively early embryonic development and, thus, subsequent embryonic death during refrigeration. Rather than remove these pairs (with reduced hatching success) from the analyses, we included them because they provide an interesting combination of birds with both delayed breeding and relatively low reproductive success.

For controls, we used unmanipulated pairs in the same woodlots and within the same range of laying dates as experimental pairs. As in previous studies

involving this population (e.g. Schluter and Gustafsson 1993; Wiggins et al. 1994a,b), we measured body condition of parents as the residual from the linear regression of body mass on tarsus length. To control for seasonal and daily variation in body mass, we measured parents between 0800 and 1200, while they were feeding seven-day-old young. Banded adults that we did not capture in the following year were assumed to have died (see Pärt and Gustafsson 1989). This is an important assumption because in some species, adult dispersal is known to increase with decreasing reproductive success. We feel this assumption is justified because the birds in our population are highly philopatric and breed in relatively restricted parts of our study area.

Our results are organized around determining the effects of the experimental hatching delay on: (1) overwinter survival and (2) future reproductive success of the parents. However, because brood size varied within control and delayed groups, we also include brood size as a key variable in our analyses.

Results.—Laying dates of experimental and control birds were similar in 1992, but experimental pairs laid larger clutches (Table 1). In addition, experimentally induced hatching failures led to significantly smaller brood sizes among delayed pairs. Critically, the experimental delay had no significant effect on mass loss among incubating control and experimental females, nor on male body condition during chick feeding (Table 1). In addition, there were no apparent differences in overwinter survival between control and experimental birds (Table 1; but see below).

We used logistic regression to assess the relative effects of the experimental delay, body condition (when feeding nestlings), and brood size on overwinter survival of parents (Table 2). In this procedure, the effect of each of the three sources on overwinter survival was measured while simultaneously controlling for variation in the other two variables. Among females, the only significant effect (when controlling for the other two variables) was a decline in overwinter survival as a result of the experimental

TABLE 2. Results of multiple logistic regression testing for independent effects of experimental delay in hatching, parental body condition, and brood size at fledging on overwinter survival of adult Collared Flycatchers.

Source	df	Coefficient	χ^2	P
Females				
Experimental delay	1	-0.994	5.15	0.02
Body condition	1	0.302	3.30	0.07
Brood size	1	0.077	0.75	0.39
Model	3	—	7.73	0.05
Males				
Experimental delay	1	0.572	1.63	0.20
Body condition	1	-0.601	4.96	0.03
Brood size	1	-0.119	1.51	0.22
Model	3	—	6.91	0.07

TABLE 3. Differences from 1992 to 1993 in laying date and clutch size between control and experimentally delayed Collared Flycatchers. Sexes were analyzed separately because pairs rarely remain together for two seasons.

Treatment	<i>n</i>	Difference in laying date			Difference in clutch size		
		$\bar{x} \pm \text{SE}$	<i>t</i> ^a	<i>P</i>	$\bar{x} \pm \text{SE}$	<i>t</i> ^a	<i>P</i>
Females							
Delayed	39	-6.4 ± 0.9	0.5	0.63	0.0 ± 0.1	2.2	0.03
Control	50	-5.7 ± 1.1			0.4 ± 0.1		
Males							
Delayed	30	-6.7 ± 0.8	0.6	0.52	-0.1 ± 0.2	1.3	0.19
Control	46	-5.7 ± 1.0			0.2 ± 0.1		

^a Comparison between treatments within sexes.

delay (i.e. timing per se). Among males, however, only body condition showed a significant (positive) relationship with overwinter survival.

There were no significant between-year differences in the laying date of control and delayed parents that returned to breed in 1993 (Table 3). However, control females laid significantly larger clutches, relative to 1992, than did delayed females (Table 3). This result was largely due to significantly smaller clutch sizes in 1993 among delayed females that raised "normal-sized" broods in 1992 (Fig. 1). Although the between-year difference in clutch size was not significant for control and delayed males (Table 3), there was a similar pattern of smaller clutches in 1993 among delayed males raising "normal-sized" broods in 1992 (Fig. 1). Thus, the experimental delay in hatching date had a significant negative effect on future clutch size among both females and males raising large broods.

Discussion.—Studies of unmanipulated bird populations have shown relatively high overwinter survival among early breeding females (Wiggins 1991, Smith 1993, Verhulst et al. 1995) and males (Harvey et al. 1988). However, such correlations may simply be the result of age or quality differences among early and late-breeding birds. Therefore, only experimental manipulations of breeding time can tease apart these timing/quality correlations. In several recent studies, breeding time has been experimentally altered to assess its effects on annual reproductive success, but the effects on the parent birds in subsequent years have rarely been assessed (Verhulst and Tinbergen 1991, Brinkhof et al. 1993, Norris 1993).

As mentioned earlier, attempts to experimentally manipulate breeding time are confounded by the possibility of concurrent effects on energy expenditure by the parents. If clutches are removed, then males must renew courtship feeding activities and females must accumulate sufficient reserves for another bout of egg production. If temporary clutch removals are used (as in this study), the incubation period is extended, with potential effects on both males

(who provide females with food throughout the incubation period) and females (if incubation behavior entails energetic costs). We found no evidence that extending the incubation period had a significant effect on female mass loss, or on male body condition (Table 1). Thus, although we assume that the delay in hatching date had some effect on parental energy budgets, such effects appear to have been minimal.

Verhulst et al. (1995) found that overwinter survival of experimentally delayed female Great Tits was similar to that of controls and concluded that the negative correlation between breeding date and female overwinter survival was due to quality differences among females. More recently, Nilsson and Svensson (1996) showed that delaying the hatching date caused both decreased survival and lower subsequent reproductive success among Blue Tit parents. Our results suggest that overwinter survival of female Collared Flycatchers was directly related to hatching date, independent of brood size or female body condition. In contrast, overwinter survival of males was dependent only on male body condition during brood rearing.

Collared Flycatchers are single-brooded, and pairs rarely remain together for more than one breeding season (0 to 6% pair stability between years; Pärt and Gustafsson 1989). Consequently, we looked for future reproductive costs separately among females and males. If delays in breeding are associated with delays in the onset of molt or migration (or some other factor acting on the parents), then in the following year we might expect a delay in the onset of breeding and/or a reduction in clutch size. For both females and males, hatching delay had no apparent effect on laying date in the following year. For females, however, hatching delay had a significant negative effect on clutch size in the following year. This effect was independent of any experimental effect on female body condition, suggesting that early breeding confers survival and future reproductive benefits for a variety of reasons. Early breeding may allow parents to avoid overlaps in offspring care and molting (e.g. Orell and Ojanen 1980, Ojanen and Orell 1982, Mor-

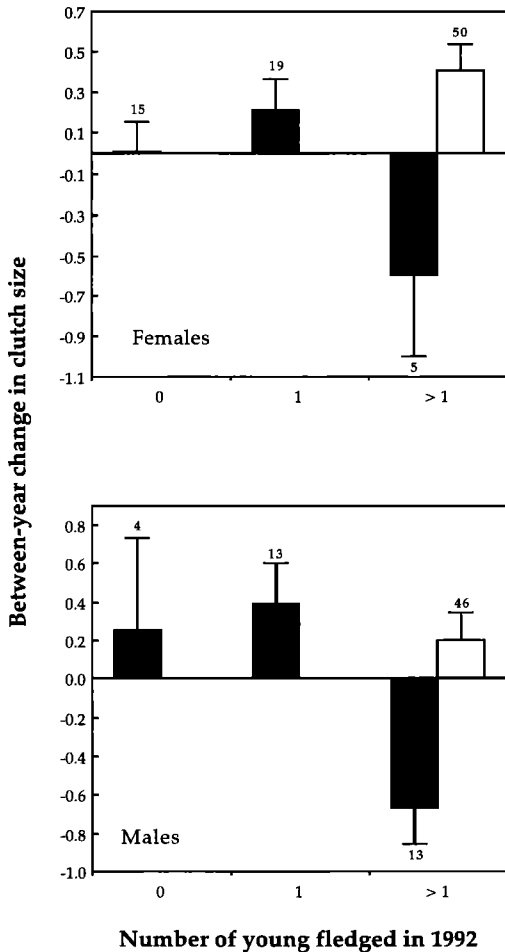


FIG. 1. Between-year change in clutch size relative to 1992 brood size among experimental (solid bars) and control (open bars) Collared Flycatcher parents. Between-year difference in clutch size was significant for experimental females ($F = 3.28$, $P < 0.05$) and experimental males ($F = 6.61$, $P < 0.01$). Mean brood size of experimental birds raising >1 young was 2.8 ± 1.3 for females and 3.6 ± 1.5 for males. Controls are plotted only for reference purposes.

ton and Morton 1990, Siikamäki et al. 1994, Nilsson and Svensson 1996), put on more body fat prior to migration, decrease the prevalence of parasites or infectious diseases (e.g. Gustafsson et al. 1994, Norris et al. 1994), or initiate migration earlier under relatively benign weather conditions. In addition, Nilsson and Svensson (1996) showed that experimentally induced later breeding resulted in an increase in energy expenditure during the following winter, apparently due to the effects of late breeding on the quality of newly molted feathers.

Brinkhof (1995) found that although experimentally advanced female European Coots (*Fulica atra*) showed relatively poor overwinter survival, the survival rate of delayed females was similar to that of controls. Nilsson and Svensson (1996) have provided clear evidence of the importance of the timing of breeding, and its apparent effects on the quality of molt, for future survival and reproduction in Blue Tits. In Collared Flycatchers, males molt significantly earlier than females (and thus have more time between the termination of breeding and the onset of migration), which may help explain why subsequent effects (e.g. overwinter survival, clutch size) of the delay were seen more clearly among females. Whatever the mechanism, our results suggest that, in addition to the level of parental care, the timing of reproduction per se also plays an important role in determining the future survival and reproductive success of parents.

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