

SEXUAL DIMORPHISM AND BREEDING SUCCESS IN TREE SWALLOWS AND COLLARED FLYCATCHERS¹

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The common pattern of small differences in body size between the sexes of many bird species has been related to a number of ecological factors, including functional differences in niche utilization (Selander 1966, Wallace 1974, Hogstad 1978), sexual differences in nest defense requirements (e.g., Wiklund and Stih 1983, Safina 1984), and to differential migration strategies (Ketterson and Nolan 1983). While a number of these studies assume that a small degree of sexual dimorphism in body size leads to differential flight performance (see Andersson and Norberg 1981), the possible consequences of such differences have rarely been investigated empirically.

Gosler (1987a, 1987b) suggested that sexual differences in the bill length of Great Tits (*Parus major*) may enhance the ability of pair members to acquire food, through decreased intrapair competition. This same argument has been made for the evolution of reversed sexual size dimorphism in raptors (Newton 1979), typically in reference to differences in wing size/shape and flight performance. This argument rests on the premise that pair members that differ in body size/shape are able to exploit a wider range of prey items. Gosler's (1987a, 1987b) studies of Great Tits provided such evidence and also drew a direct link between the degree of within-pair sexual dimorphism and breeding success. However, more recent work by Matthysen et al. (1991) found no such link among Blue (*P. caeruleus*) and Great Tits in Belgium.

Previous studies have demonstrated significant effects of small differences in wing length and shape on the foraging behavior of several species of birds (e.g., Andersson and Norberg 1981, Lifjeld and Slagsvold 1988). In this paper, we assess the relationship between reproductive success and intra-pair differences in wing length. This study differs from previous efforts by focusing on an aerial insectivore, the Tree Swallow

(*Tachycineta bicolor*), and on a species that feeds by gleaning and flycatching, the Collared Flycatcher (*Ficedula albicollis*).

MATERIALS AND METHODS

The study was carried out at the Creston Valley Wildlife Management Area in southeastern British Columbia, Canada (1986-1987), and on the island of Gotland, in southern Sweden (1991). Detailed descriptions of the study sites and methods are in Wiggins (1989) and in Pärt and Gustafsson (1989). Female swallows were captured on the nest and measured during incubation, typically 7-9 days following clutch completion. Male swallows were captured and measured while feeding young, 3-5 days following hatching. Both female and male flycatchers were captured and measured 5-9 days following hatching. Nestling swallows and flycatchers were weighed 16 and 13 days after hatching, respectively. At these times body mass has reached adult levels in both species. Nestling body mass of swallows was measured to the nearest 0.02 g with a portable electronic balance. Nestling flycatchers were weighed to the nearest 0.1 g with a Pesola scale. Adult wing length (flattened wing chord) was measured on a ruler to the nearest mm. Measurements of wing length were highly repeatable in both Tree Swallows (Wiggins 1989) and Collared Flycatchers (J. Merilä, pers. comm.).

Tree Swallows and Collared Flycatchers are sexually dimorphic in wing length and body mass. However, body mass is a difficult trait to measure in most species since it fluctuates both daily and seasonally and has low repeatability (e.g., Wiggins 1989). We used differences in wing length as an indicator of sexual dimor-

TABLE 1. Sexual differences in wing length (mm) among paired Tree Swallows ($n = 29$) and Collared Flycatchers ($n = 47$). Only unmanipulated pairs that fledged at least one young were used in the analysis.

Group	Mean wing length	SD	Range	Paired t	P
<i>T. bicolor</i>					
Female	115.8	2.4	110-121	6.8	<0.001
Male	121.1	3.0	117-127		
<i>F. albicollis</i>					
Female	81.2	1.6	79-86	5.8	<0.001
Male	83.3	2.0	79-87		

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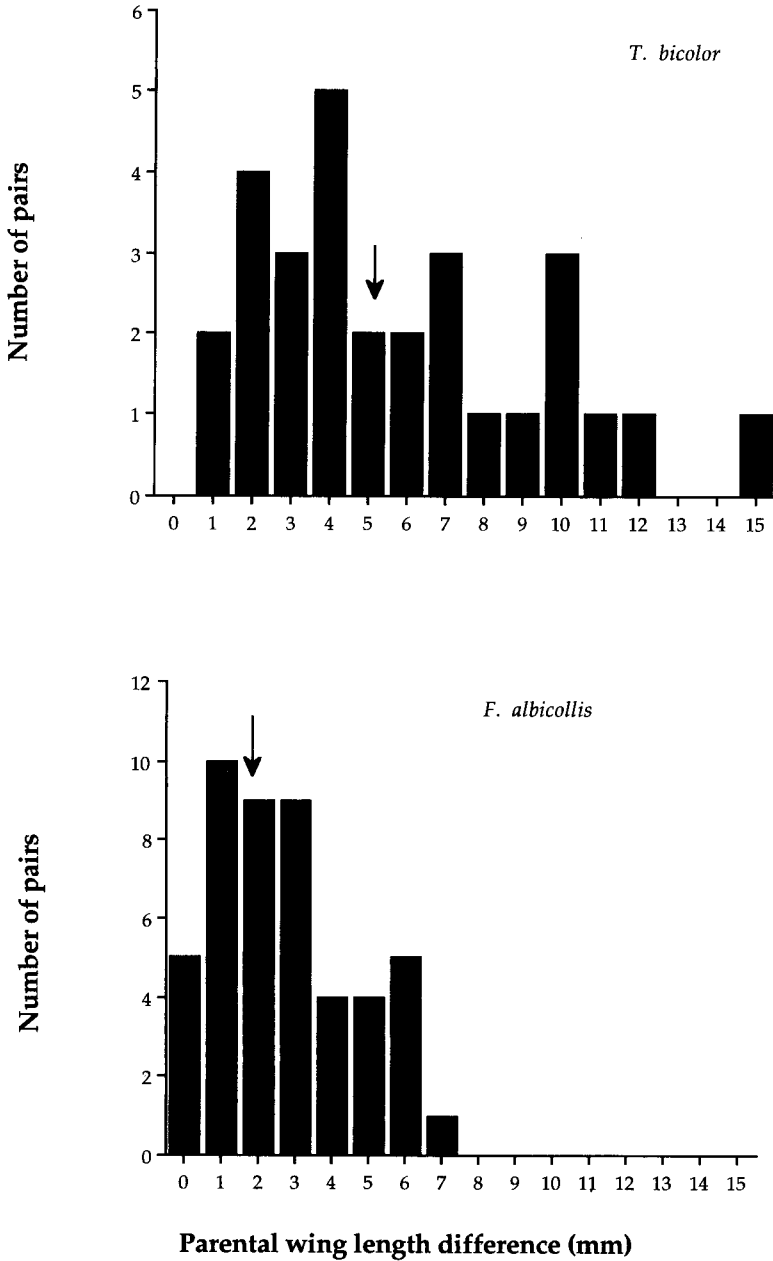


FIGURE 1. Frequency distributions of intrapair differences in wing length in Tree Swallows (upper) and Collared Flycatchers (lower). Arrows indicate mean wing length difference.

phism, as wing length differences between the sexes may result in differential flight performance and, perhaps, differences in prey utilization. Although prey selection has been studied in Tree Swallows (Quinney and Ankney 1985), sexual differences in prey selection have not been reported.

Throughout the analyses only unmanipulated pairs

that fledged at least one offspring were considered. This analytical restriction was necessary since pair members that deserted or failed during the early nestling stage were not captured. Unmanipulated pairs of both species were chosen randomly during experimental work at both study areas. In addition, mean chick mass per brood was used as the indicator of offspring quality, as

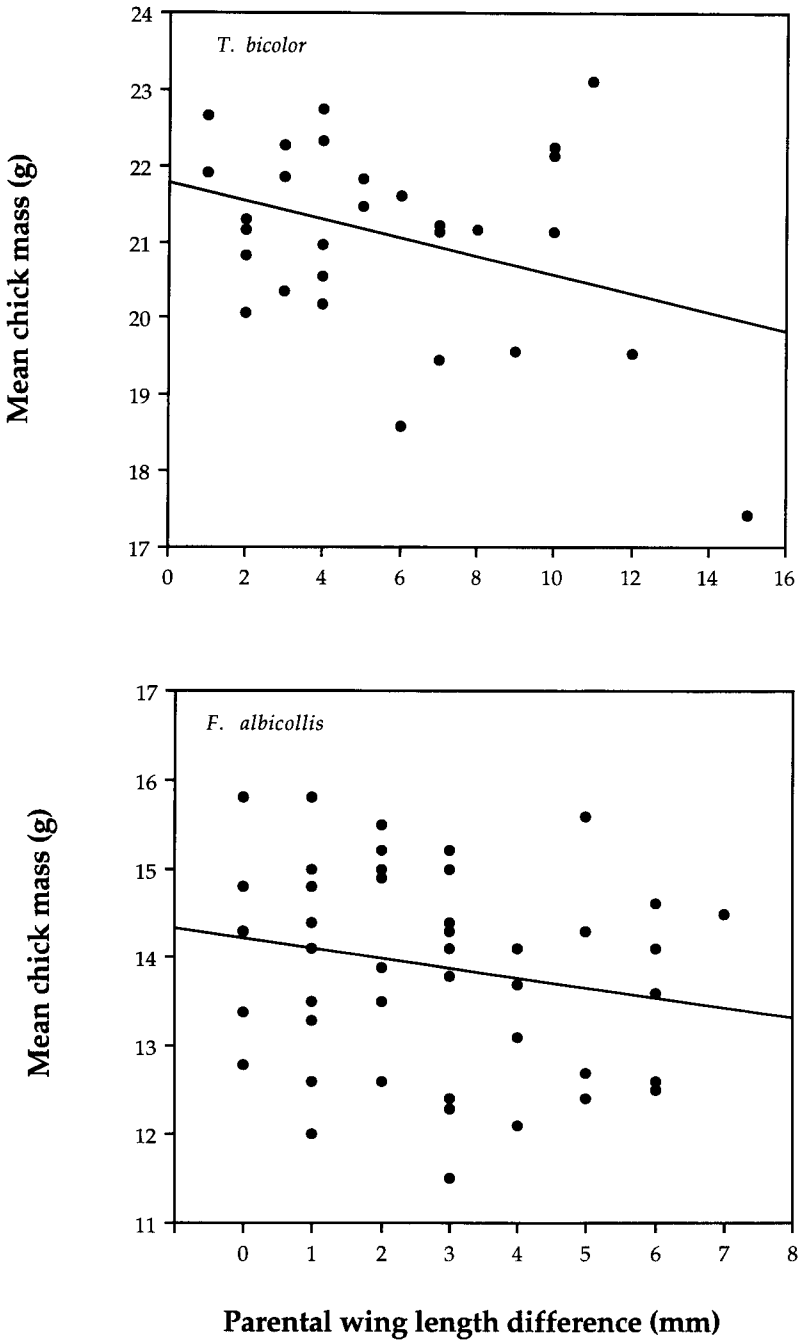


FIGURE 2. Regressions of mean chick mass per brood on parental wing length difference in Tree Swallows (upper) and Collared Flycatchers (lower). Regression equations are $Y = 21.8 - 0.12x$, $R^2 = 0.12$, $P = 0.07$, and $Y = 14.2 - 0.04x$, $R^2 = 0.04$, $P = 0.17$, respectively.

this measure did not vary significantly with brood size (Tree Swallows, analysis of variance (ANOVA), $F = 0.9$, $df = 5$, $n = 29$, $P > 0.1$; Collared Flycatchers, $F = 1.2$, $df = 5$, $n = 47$, $P > 0.1$). To control for date-related effects on breeding success, we measured fledging success as the residuals from the regression of fledging success on clutch initiation date. As there were no inter-year differences in Tree Swallow body size or fledging mass, data for the two years were pooled.

RESULTS

Both Tree Swallows and Collared Flycatchers showed significant intra-pair differences in wing length (Table 1), although the magnitude of the difference was especially pronounced in Tree Swallows (Fig. 1). There was no indication of assortative mating for wing length (Tree Swallows, $r_{29} = 0.11$, $P > 0.5$; Collared Flycatchers, $r_{47} = 0.12$, $P > 0.4$). Among Tree Swallows, there were no significant correlations between clutch initiation date and mean brood mass, female wing length or male wing length (Spearman rank correlations, all $P > 0.4$). However, among Collared Flycatchers, both mean brood mass ($r_{47} = -0.32$, $P = 0.03$) and female wing length ($r_{47} = -0.32$, $P = 0.03$) declined significantly over the course of the breeding season.

For both species, mean chick mass showed no significant relationship to parental wing length difference (Fig. 2). In addition, neither species showed a significant relationship between the residual number of young fledged (corrected for seasonal decline) and parental wing length difference (ANOVA, $P > 0.3$).

DISCUSSION

Gosler (1987a, 1987b) proposed that sexual dimorphism in the bill length of Great Tits was at least partly a result of selection favoring parents with dissimilar bill lengths. Tit parents with dissimilar bill lengths reared relatively heavy broods and, because fledging mass often correlates with subsequent fledging survival, this difference in chick mass likely had significant effects on offspring survival. However, Matthysen et al. (1991) found no relationship between parental morphology differences and offspring number or body mass in Great and Blue Tits. Furthermore, they found no evidence of reduced competition between pair members, as neither female nor male body mass was correlated with bill length difference. They suggested that other, non-adaptive explanations may be responsible for the sexual difference in breeding *Parus* bill lengths.

For both Tree Swallows and Collared Flycatchers, we found no relationship between parental wing length difference and the number or condition of offspring. However, such a relationship rests on the assumption that for aerial insectivores, wing length differences are functionally similar to bill length differences among gleaning *Parus* species. Whereas Gosler (1987b) presented evidence of a link between prey size selection and bill length in Great Tits, we have no similar data for Tree Swallows or Collared Flycatchers. Lifjeld and Slagsvold (1988) manipulated the size and shape of female Pied Flycatcher (*Ficedula hypoleuca*) wings and found associated shifts in prey choice. Møller (1989) showed that manipulations of tail length in Barn Swallows (*Hirundo rustica*) had significant effects on prey choice. However, these studies involved extreme ma-

nipulations that likely disrupted the natural scaling of wing and tail lengths to overall body size. Nonetheless, in many species of raptors there is strong sexual dimorphism in wing size and prey choice (see references in Newton 1979). Several authors (e.g., Selander 1966, Andersson and Norberg 1981, Lundberg 1986, Newton 1986, Korpimäki 1987) have proposed that the body size/wing loading differences between male and female raptors are an adaptation to widen the diversity of available prey, and therefore reduce competition between pair members. Thus, we might expect that within-pair differences in wing length among swallows and flycatchers would lead to differential prey utilization.

In conclusion, while Gosler's studies (1987a, 1987b) suggest a causal relationship between sexual dimorphism in bill morphology and breeding success, the results of this study suggest that for small aerial insectivores, the degree of within-pair sexual dimorphism in wing length is not correlated with breeding success. The almost ubiquitous pattern of small but significant sexual dimorphism in passerine wing length (male > female) may be due to other factors (e.g., male territorial defense, differential timing of migration) selecting for differential flight performance between the sexes. A robust assessment of these ideas will likely come only from studies with sample sizes large enough to avoid potential Type II errors. Alternatively, the wing length dimorphism may simply be a correlated response to selection for an overall difference in body size between the sexes.

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NEW INFORMATION ON KITTLITZ'S MURRELET NESTS¹

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Key words: Alaska; *Brachyramphus brevirostris*; Kittlitz's Murrelet; nest-site characteristics; Russia.

Kittlitz's Murrelets (*Brachyramphus brevirostris*) are alcids that nest solitarily in remote areas of Alaska and the Russian Far East (AOU 1983, Day et al. 1983). Because of their low nesting density, the extreme difficulty of finding their nests, and the fact that areas used for nesting (talus slopes) are of such little interest to ornithologists that they rarely are surveyed, only 17 nests of this species have ever been located (Day et al. 1983). Although the sample size was small, the analysis presented by Day et al. (1983) suggested that this species was adapted to nesting in rocky, poorly vegetated scree slopes that occur at high elevations in the southern part of their range and at low elevations in the northern part of their range. Since that paper was published, only three new nests of this species have been found. This paper reports on the nesting habitat and nest-site characteristics of these new nests and com-

pares them with those discussed previously; each nest is named for the mountain on which it was found.

The Mt. Griggs nest (~58°21'N, 155°08'W) was found in Katmai National Park, Alaska, on 2 July 1979 (Table 1; P. Shearer photo, on file at the University of Alaska Museum [UAM]). In the photo, a Kittlitz's Murrelet chick sitting in a nest was similar in size and plumage characteristics to a six-day-old chick that had been photographed (E. P. Bailey, photo) in the Frosty Peak nest (see Day et al. 1983 for names of nests). The nest was 39 km from Katmai Bay (the nearest salt water that would be available to adults for feeding) and 5.6 km from Knife Creek, which is a roiling, dangerous river in the Valley of the Ten Thousand Smokes. The nest was situated at the base of a moderately sized (~0.3 m diameter) rock. From the photograph, this site does not appear to be sheltered from the weather but does appear to be well sheltered from debris rolling downhill.

The Broken Mountain nest (58°17'N, 155°10'W) was found in Katmai National Park, Alaska, on 23 July 1986 (Table 1; T.E.C. Keith, photo, on file at UAM). The chick in this nest appears to be the same age or a little older (i.e., ~6–10 days old) than the Bailey bird

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