Brief report

Why do juvenile Moustached Warblers have shorter wings?

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1. Introduction

The morphology of a species reflects a compromise between different selective pressures. For example, foraging behaviour, sexual selection or migratory habits impose selective forces that sometimes act in opposite directions (James 1982). In many species, adults have longer wings than young birds (see Jenni & Winkler 1994, Norman 1997), although the reasons for these differences remain largely unknown. Three hypotheses have been proposed to explain this pattern. Some authors have suggested that young individuals are more food constrained during the growth of feathers than adults, and wing length is probably influenced by food availability (van Balen 1967, Slagsvold 1982). Alternatively, young individuals could benefit from shorter wings through increased manoeuvrability, and thus a better ability to escape predators, whereas for more experienced older birds a longer wing allowing faster migration could give greater benefits (Alatalo et al. 1984, Hedenström & Alerstam 1998). A third, largely unexplored explanation, for the shorter wing length of young birds could be differential mortality with fewer short-winged than long-winged juveniles surviving, resulting in a greater adult mean wing length.

We used recaptures of individuals ringed in a wintering population of Moustached Warblers *Acrocephalus melanopogon* to test two of these three hypotheses suggested as explanations of the occurrence of age-related differences in the wing length of most passerines.

2. Material and methods

Regular ringing was carried out in the Filipines Marsh in the Llobregat Delta Nature Reserves (north-east Spain, 41°19′N, 02°01′E) from February 1992 to February 1998. Ringing efforts were variable during the first three seasons. However, from autumn 1994 onwards, ringing efforts were standardised: twenty 12 m long mist-nets were placed in the same positions during the daylight hours on six consecutive days, during six different sampling periods from October to the end of March (during the winter of 1994–95 from November to the end of April). To avoid including individuals on passage in the analyses, we only considered birds trapped between mid-November and the third week in February (see description of local phenology in Gutiérrez et al. 1995), and measured by the same person (JF). Wing, tarsus length and body mass of trapped individuals was

recorded.

The complete adult and juvenile post-breeding moult undertaken by this species in the breeding areas before migration did not allow age to be reliably assessed in winter on the basis of plumage characteristics (e.g. Leisler 1972, Baker 1997), since all individuals had finished the complete summer moult before arriving at the study area. The presence of tongue markings was used to identify first winter birds, as this is a characteristic only present in birds born in the previous breeding season (Cramp 1992). As some juveniles may even lose their tongue markings from June onwards (Cramp 1992), only data from individuals showing such markings when first captured were considered in the analyses. The species does not breed regularly in the area (Gutiérrez et al. 1995), and ringing recoveries, while not ruling out other origins, suggest a French origin for at least part of the wintering population (Aymi 1991, and own data). Data were analysed using t-tests because the variables studied were normally distributed, and the variances of the groups considered were homogeneous (as judged from Levene's test). Tarsus length was also included in these analyses because it is a good estimator of body size, attain its definitive length in the first months of life (Rising & Sommers 1989, Gosler et al. 1998) and is not directly related to flight performance. The differences in wing and tarsus length between individuals controlled and not controlled in following seasons were analysed separately with ANCOVA controlling for the other morphological variable.

The Moustached Warbler was chosen for this study because it shows a high year-to-year fidelity to wintering areas and therefore enabled us to test the different hypotheses with a longitudinal approach (by following individuals through time) rather than comparing young and old birds captured simultaneously (see, for example, Alatalo et al. 1984, Slagsvold 1982, Norman 1997). Additionally, due to the moult patterns of the species, feather growth occurs during the same period and under similar conditions in yearlings and adults (Cramp 1992), unlike other species studied up to now, in which feather growth in yearlings occurs mostly in the nest, and adult moult occurs some time later (see Alatalo et al. 1984,

Norman 1997 and references therein). Values reported are means ± standart deviations unless otherwise stated.

3. Results

3.1. Does wing length increase with age?

Individuals ringed as yearlings that were retrapped one year after first capture had longer wings when recaptured than during their first year of life (mean±SD, 58.2 mm ± 0.76 vs. 57.3 mm ± 0.84, paired t-test $t_7 = 5.35$, $P = 0.001$).

3.2. Is wing length correlated with the probability of recapture in the next year?

Yearlings recaptured at least one season after marking had longer wings on the first capture than individuals that were not recaptured (57.5 mm ± 0.71 vs. 56.1 mm ± 1.45, n = 8 and 24, ANCOVA controlling for tarsus length, $F_{1,29} = 6.63$, $P = 0.015$).

3.3. Do these changes also occur in tarsus length?

As expected, tarsus length did not increase from juvenile to adult (20.4 mm ± 0.63 vs. 20.4 mm ± 0.56, t-paired test $t_6 = 0.32$, $P = 0.76$). Neither was there any difference in tarsus length between juveniles recaptured and those not recaptured in later seasons (20.4 mm ± 0.58 vs. 20.4 mm ± 0.63, n = 8 and 24, ANCOVA controlling for wing length, $F_{1,29} = 0.34$, $P = 0.56$).

4. Discussion

Wing morphology has been shown to be affected by a variety of selective pressures such as migration distance (Mulvihill & Chandler 1990) or sexual selection (Hedenström & Møller 1992). According to our results, the age-related differences in wing length in the Moustached Warbler are the result of two different processes operating

in the same direction: a lower return rate of short-winged individuals and an age-related increase in wing length. These differences were only detected in wing length but not in tarsus length, a character unrelated to flight performance.

Whether a lower return rate reflects a lower survival rate has important implications for these results. No data have been published on the winter site-fidelity of the Moustached Warbler, although our own data suggest a very high fidelity to wintering areas. 19.7% of the birds trapped during the winter were retrapped in following seasons, and a preliminary analysis using capture-recapture models suggest a winter-to-winter local survival (fidelity) of 33% (SE = 5) (unpublished data). This estimate is in the line of other survival rates estimated for other similar species such as the Reed Warbler *Acrocephalus scirpaceus* (0.52 ± 0.04 SE - 0.54 ± 0.07, Dobson 1990; first-year 0.32 ± 0.06, adults 0.59 ± 0.07, Baillie & McCulloch 1993) or the Sedge Warbler *Acrocephalus schoenobaenus* (0.35 ± 0.09 - 0.38 ± 0.05, Dobson 1990; first-year 0.24 ± 0.06, adults 0.36 ± 0.09, Baillie & McCulloch 1993). In these studies, survival was calculated on the basis of ringing recovery information and, as such, reflect survival and not just fidelity to the study area (also known as local survival, see, for example, Cuadrado et al. 1995). This suggests that the lower return rates of short-winged individuals reflect a lower survival of short-winged yearlings.

Migration patterns and foraging behaviour are two of the factors proposed as selective pressures shaping wing morphology (Marchetti et al. 1995). Larger bodied individuals could also perform better when competing with conspecifics for food or territory as shown in other passerines (Garnett 1981, Lundberg et al. 1981, Yom-Tov & Ollason 1976) and better withstand low temperatures and starvation during adverse conditions (Biebach 1977, Reiss 1989, Brown & Brown 1998). Lower survival of short winged individuals could also be explained by other factors like poor nutrition, resulting in both a lower feather growth and survival. Consequently, we can not infer causality from our results because the relationship between wing length and return rate could be produced by some uncontroled factor operating both over wing length and survival.

The age-related increase in wing length could be the result of food constraints on young birds during feather growth. However, young and adult Moustached Warblers undertake a complete moult at the end of summer (Leisler 1972). This suggests that in the Moustached Warbler, age-related differences in wing length could be related to food constraints well after the nestling period, and independence from parents. The poorer foraging skills of young passerines (reviewed by Marchetti & Price 1989), and the use of the best foraging areas by adults (Marchetti & Price 1989, Desrochers 1992), could limit the amount of resources available to yearlings during feather growth. This hypothesis is also supported by the different studies that have demonstrated experimentally the effect of food availability on growth rate and feather size (Grubb 1991, Waite 1990).

Unfortunately, we lack information on wing shape to test the adaptive hypothesis proposed by Alatalo et al. (1984). They noticed that juvenile passerines use to have shorter and more slotted wings than adults, and suggested that these differences were due to intense selection in juveniles for more rounded wings and increased maneuverability to escape predators. A lower survival rate of short-winged individuals does not support this adaptive hypothesis, but detailed information of changes in flying performance with age and wing shape would be necessary to fully test this hypothesis.

In conclusion, our results show that the age-related increase in the wing length in the Moustached Warbler is the result of two processes operating in the same direction: the lower survival rate of short-winged yearlings and the growth of longer wings by older individuals.

anonymous reviewers comments inproved an earlier draft of this manuscipt.

Selostus: **Miksi nuorilla osmankää-mikerttusilla on lyhyet siivet?**

Lajin morfologiaan vaikuttavat erilaiset valinta-paineet. Monilla lintulajeilla aikuisilla yksilöillä on pidemmät siivet kuin nuorilla linnuilla. Selitykselle havainnolle on esitetty kolme hypo-teesiä: 1) nuorilla linnuilla on ravintopulaa sulki-en kasvuaikana ja ravinnon saatavuus vaikuttaa siiven pituuteen, 2) nuorille linnuille on hyötyä lyhyemmistä siivistä esimerkiksi niiden paetessa petoja ja 3) lyhytsiipisten ja pitkäsiipisten yksi-löiden välillä on eroja kuolleisuudessa; vähem-män lyhytsiipisiä nuoria lintuja selviää hengissä täysikasvuisiksi ja tämä johtaisi aikuisten lintu-jen suurempaan keskimääräiseen siiven pituuteen. Artikkelin kirjoittajat selvittivät rengastettujen osmankäämikerttusten takaisinpyynnillä eri hypoteesien paikkansa pitävyyttä Espanjan koil-lisosissa. Osmankäämikerttusten siiven pituus kasvoi iän myötä. Toisaalta siiven pituus korreloi positiivisesti yksilön uudelleen pyynnin onnistu-misen kanssa seuraavana vuonna. Nilkan pituu-dessa ei havaittu vastaavia eroja. Kirjoittajien mukaan ikäluokkien väliset erot siiven pituudes-sa johtuivat kahdesta eri prosessista, jotka vaikut-tivat samaan suuntaan: 1) lyhytsiipisten nuorten lintujen suuremmasta kuolleisuudesta ja 2)ikään liittyvästä siiven pituuden kasvusta.

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