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Variation in wing length in relation to sex and age of Marsh Tits *Parus palustris*

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Abstract

Wing length of juvenile and adult Marsh Tits *Parus palustris* was measured during autumn and winter. Individuals later sexed during breeding were used to study a possible sexual dimorphism in wing length. Males of both juveniles and adults had significantly longer wings than females, the difference between the sexes being around 5.5 %. Using wing length as the only criterion, between 97.4 % and 88.6 % of juveniles and between 98.0 % and 93.4 % of adults can be unambiguously sexed during autumn/winter. Individuals measured during their second or later autumn/winter had significantly longer wings than those measured as juveniles. No evidence for selection against short-winged individuals was found. Each individual increased its wing length during the first complete moult. Hypotheses explaining an increase in wing length with age are discussed and I argue that the best explanation encompasses some sort of nutritional constraint during the nestling and/or early fledgling phase.

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Introduction

Many bird species are monochromatic, i.e. both sexes have more or less identical plumage. Although subtle plumage differences between the sexes have been noted in some of these species (e.g. Mosher & Lane 1972, Gosler & King 1989), other sex differences are often needed to sex these birds during autumn and winter. One such sex difference is the often observed sexual dimorphism in size (e.g. van Balen 1967). Wing length has been proposed to relate to overall size of an individual (van Balen 1967), thus this measure might be useful for sexing individuals of monochromatic species during the non-breeding season.

Another common feature of passerine wings is the increase in length with age, at least between juveniles and adults in their second winter or later. This increase in wing length may depend either on selection against short-winged juveniles, or on an increase in wing length of all surviving individuals during their first complete moult. Both processes will lead to a greater average wing length in adults than juveniles. Moreover, the shorter wing length of juveniles may be either a consequence of nutritional constraints on nestlings or fledglings (Slagsvold 1983) or an adaptive response to different wing length optima in juveniles and adults (Alatalo et al. 1984).

The aims of this study were (1) to outline a way to sex Marsh Tits *Parus palustris* during autumn and winter with the aid of wing length measurements, (2) to investigate the relation between wing length and age and, (3) to distinguish between some of the hypotheses explaining the commonly observed increase in wing length with age.

Methods

I have studied a population of Marsh Tits, 20 km east of Lund, southern Sweden since 1982. The Marsh Tit population bred in nestboxes within a 64 km^2 study area of small deciduous forests and groves interrupted by permanent pastures and agricultural fields.

During the breeding season all young from broods in the nestboxes and most of their parents were marked with an individual combination of colour-rings. During this time, I could easily sex the adults on the size and vascularization of the brood patch. In order to achieve reliable sex determination, only birds sexed during breeding entered the sex-specific analyses.

During the autumn and winters of 1982 - 1987, Marsh Tits were mistnetted, either using playback of song or feeding trays baited with sunflower seeds. I measured their wing length to the nearest 0.5 mm (using method (1) of Svensson 1984). All unbanded birds were colour-ringed for future identification.

The rectrices of juvenile Willow Tits *Parus montanus* and Crested Tits *P. cristatus* showed signs of feather wear from November and onwards (Laaksonen & Lehikoinen 1976). The degree of wear on rectrices and primaries are probably influenced by the amount of time and flying effort expended to meet the daily food requirements. Thus, factors such as quality of flock range and dominance status might result in differences between individuals in the degree and rate of feather wear. To avoid that this variation among individuals influence my measure of wing length, I restricted the analyses of wing lengths to individuals captured before 31 December each winter. Measures taken before 1 July, or on moulting adults, were omitted from the analyses since, before this date, the primaries of juvenile birds might still be growing.

Results

Sex differences: juveniles

Juveniles measured during their first autumn/winter showed a marked sexual dimorphism in wing length (Fig. 1). Males were the largest sex and had significantly longer wings ($\bar{x}$=65.73 mm; S.D.=1.06; N=35) than females ($\bar{x}$=62.36 mm; S.D.=1.08; N=43). Thus, males had 5.4% longer wing than females. In my study population, it seems reasonable to divide the sexes at a wing length of 64 mm (Fig. 1); individuals with a wing of 64 mm or shorter being females and those of 64.5 mm or longer being males. Only one male (2.9%) and one female (2.3%) had a wing length falling outside this dividing line.

Distributions of morphometric measures are often normally distributed. Therefore, knowing the mean and variance of the male and female distributions of wing lengths, respectively, it is possible to calculate the point on the x-axis where the two distributions intersect. I found this intersection point to be at a wing length of 64.1 mm. The proportions of the area under the male and female distribution curves that had x-values smaller or greater than 64.1 mm, respectively, was calculated to be 5.7% for both males and females. Thus, by fitting the data to a normal distribution, I found the division between the sexes to be at a wing length of 64.1 mm and that 88.6% of all individuals can unambiguously be assigned to the right sex on wing length alone.

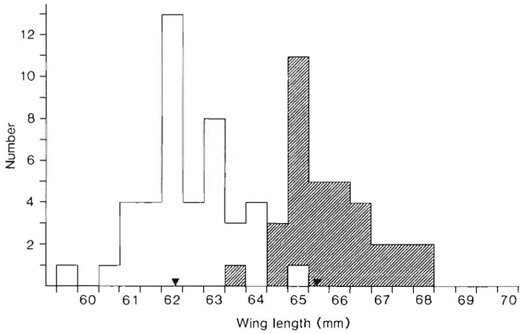

Fig. 1. Frequency distributions of male (hatched bars) and female (open bars) wing length in juvenile Marsh Tits. Males (N=35) and females (N=43) were measured during their first autumn or winter and subsequently sexed during breeding. Data from 1982 - 1987. The arrows indicate mean wing length for each sex. The difference between the sexes tested with t-test: t_{76}=13.85; P<0.001.

Fördelning av vinglängder hos hanar (fyllda staplar) och honor (ofyllda staplar) av entita. Hanar (N=35) och honor (N=43) mättes under deras första höst eller vinter och könsbestämdes vid efterföljande häckning. Data från 1982 - 1987. Pilarna anger medelvinglängden för varje kön. Skillnaden mellan könen testades med t-test. t_{76}*=13.85; P<0.001*

The sample above contained only juveniles that were found breeding the next breeding season and, thus, could be sexed on criteria other than wing length. Also when unsexed juveniles captured during autumn/winter were included, thereby greatly increasing sample size, the wing length distribution was clearly bimodal (Fig. 2).

To investigate whether the subsample of juveniles that succeeded in entering the breeding population constituted a random sample, with respect to wing lengths, of those juveniles alive during the preceding autumn/winter, I plotted the proportion of individuals in each wing length category in the two samples (Fig. 2). The two curves follow each other reasonably well and I conclude that the successful individuals were a random sample of those available with respect to wing length.

Sex differences: adults

A total of 50 individuals, sexed during breeding, were captured during their second autumn/winter or later. These adult birds also showed sexual dimorphism in wing length (Fig. 3). The wings of males ($\bar{x}$=66.55 mm; S.D.=1.21; N=30) were significantly longer (5.6%) than those of females ($\bar{x}$=63.00 mm; S.D.=0.73; N=20). Using a wing length of 64.5 mm as the division point between the sexes, all males and all but one female (95.0%) were correctly sexed.

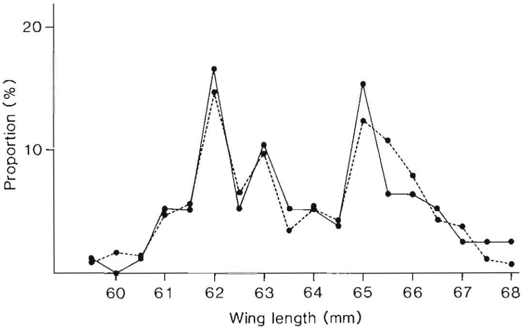

Fig. 2. Wing lengths of all juvenile Marsh Tits captured in autumn/winter (N=338; broken line) and of those that subsequently entered the breeding population (N=78; unbroken line). Data, expressed as percentages, from 1982 -1987.

Vinglängd hos alla ungfåglar som fångades under deras första höst eller vinter (N=338; streckad linje) och hos de som lyckades överleva till häckningssäsongen (N=78; heldragen linje). Data från 1982 - 1987.

By assuming normally distributed data and applying the same calculations as with juveniles, I found the division between the sexes to be at a wing length of 64.3 mm. Under the same assumptions, 96.6% of the males and 96.8% of the females had wing lengths that did not overlap with that of the other sex. Thus, 93.4% of all adults can be correctly sexed on wing length.

Age differences

Individuals measured during their second or later autumn/winter had longer wings than those measured as juveniles (Figs. 1 and 3). The mean increase among males was 0.82 mm (t-test: t_{63}=2.92; P<0.01) and among females 0.64 mm (t-test: t_{61}=2.37; P<0.05). This increase in average wing length in the population might be achieved in two different ways. Selection might act against short-winged individuals resulting in only the long-winged ones of each sex surviving to their second autumn/winter. Alternatively, each individual is able to grow longer primaries following its first complete moult.

In order to test the second hypothesis, I compared the wing lengths of the same individual during its first and second autumn/winter. Small sample sizes precluded a test on each sex separately, although males seemed to increase their wing length more than females (Fig. 4). The combined data showed, however, a significant increase in wing length by on average 0.65 mm between the first and second winter (paired t-test: t_{16}=2.18; P=0.044).

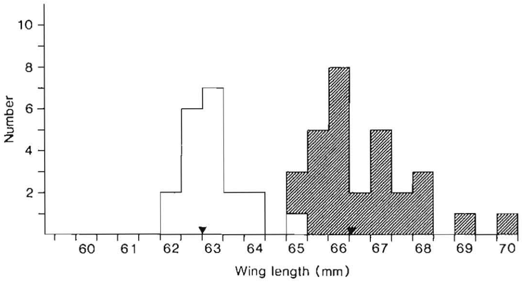

Fig. 3. Frequency distributions of male (hatched bars) and female (open bars) wing length in adult Marsh Tits. Males (N=30) and females (N=20) were measured during their second or later autumn/winter. Sex was determined during breeding. Data from 1982 - 1987. The arrows indicate mean wing length for each sex. The difference between the sexes tested with t-test: t_{48}=11.80; P<0.001.

Fördelning av vinglängder hos hanar (fyllda staplar) och honor (ofyllda staplar) av entita. Hanar (N=30) och honor (N=20) mättes under deras andra eller senare höst/vinter. Kön bestämdes vid deras häckningsförsök. Data från 1982 - 1987. Pilarna anger medelvinglängd för varje kön. Skillnaden mellan könen testades med t-test: t_{48}*=11.80; P<0.001*

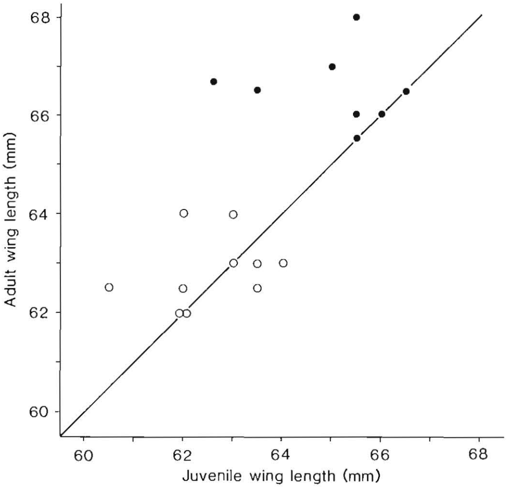

Fig. 4. Relationship between wing length of the same individual measured as a juvenile and as an adult, i.e. during its first and second autumn/winter, respectively. Data for 7 males (●) and 10 females (○). The line denotes unchanged wing length between the two times of measurements.

Samband mellan vinglängd hos samma individ, uppmätt dels som ungfågel dels som gammal fågel, dvs. under individens första respektive andra höst/vinter. Data från 7 hanar (●) och 10 honor (○). Den diagonala linjen visar oförändrad vinglängd mellan de två mättillfällena.

Discussion

Sexual dimorphism

Male Marsh Tits had significantly longer wings than females, a pattern that seems to be general among tits (Table 1). Many studies report a large degree of overlap between the sexes, making wing length of limited value as a method to sex individuals. As seen from Table 1, the best candidate for successful sex determination based on wing length, would be the Marsh Tit which has the largest sexual dimorphism. Also, the overlap between the sexes was relatively small and a large proportion of the Marsh Tits could be correctly sexed on wing length alone.

Variation with age

The smaller wings of juveniles compared with older birds found in this study also seems to be a general pattern among tits: Great Tit *Parus major* (van Balen 1967, Haftorn 1976, Winkel 1980, Alatalo et al. 1984), Blue Tit *P. caeruleus* (Stewart 1963, Winkel 1980), Willow Tit *P. montanus* (Haftorn 1982), Crested Tit *P. cristatus* (Laaksonen & Lehikoinen 1976) and Coal Tit *P. ater* (Winkel 1980, Alatalo et al. 1984). All of these studies report differences in the mean wing lengths of juvenile and adult birds. Thus, the increase in wing length with age might either be intra-individual, i.e. the wing of each individual increases during the first complete moult, or inter-individual, i.e. the short-winged juveniles in each sex die before they become adults. In the Marsh Tit there seems to be no such selection against short-winged juveniles. Increased wing length after the first complete moult, can explain most of the recorded difference between juveniles and adults at the population level. Furthermore, those juveniles that succeed in entering the breeding population seem to be a random sample of the winter population with respect to wing length. This is not surprising in the case of the Marsh Tit, since both establishment success and dominance has been shown to be unaffected by wing length (Nilsson & Smith 1988, Nilsson 1989a).

Why, then, do the wings become longer after the first complete moult? Either it may be adaptive for juveniles to have a shorter wing than adults (Alatalo et al. 1984) or the shorter wings of juveniles may be a consequence of nutritional constraints during the feather growth of nestlings or newly fledged young (van Balen 1967, Slagsvold 1983, Hogstad 1985).

The short wing of juveniles improve manoeuverability and as a consequence has been suggested to be important when it comes to predator avoidance (Alatalo et al. 1984). The longer wings of adults should instead minimize energy consumption during sustained flight. Although the interpretation of wing lengths in juveniles is reasonable, it is harder to understand why the adults of a sedentary species should have wings better designed for fast and sustained flight than those of juveniles. Since juveniles disperse during their first summer before becoming established in year-round territories (Marsh Tit, Nilsson 1989b) or may migrate (Great and Blue Tits, e.g. Ulfstrand 1962, Smith & Nilsson 1987), their need of adaptations for sustained flight ability should be greater than that of adults.

Table 1. Sex difference in mean wing length in some tit species, expressed as a percentage of the female wing length. The difference was calculated as the mean for age categories and sites within each study.

Skillnader i medelvinglängd mellan hanar och honor, uttryckt som procent av honans vinglängd, för några olika mesarter. Skillnaderna är uträknade som medel för ålderskategorier och olika områden inom en studie

	Difference *Skillnad*	N	Source *Källa*
Marsh Tit *Parus palustris*	5.5 %	128	This study
	5.3 %	11	Gosler & King (1989)
Willow Tit *P. montanus*	4.4 %	117	Haftorn (1982)
Great Tit *P. major*	4.4 %	535	Haftorn (1976)
	4.3 %	130	Alatalo et al. (1984)
	4.3 %	2773	van Balen (1967)
	3.7 %	493	Winkel (1980)
Blue Tit *P. caeruleus*	4.0 %	200	Winkel (1980)
Black-capped Chickadee *P. atricapillus*	3.3 %	94	Gochfeld (1977)
Coal Tit *P. ater*	3.3 %	321	Winkel (1980)
	3.2 %	35	Gosler & King (1989)

Therefore, among sedentary bird species, I think that the reason for shorter wings in juveniles than in adults is nutritional constraints during the growth of the wing. This may, for example, be due to a lowered growth priority of the wing feathers during their first summer compared to the time of their first complete moult when only feathers are grown (Hogstad 1985). The wing is also one of the last structures that attain adult or near adult size in juveniles (Slagsvold 1983). Thus, besides energy, time may also be limiting for the growth of the wing since selection for early independence and early dispersal, has been found among juveniles in many tit species (e.g. Nilsson 1989b, Perrins & McCleery 1989).

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Sammanfattning

Variation i vinglängd i relation till kön och ålder hos entita Parus palustris

Många fågelarter uppvisar inga eller mycket små skillnader i dräktkaraktärer mellan könen. I ett försök att definiera vinglängdsgränser för hanar och honor som med någorlunda säkerhet kan användas för könsbestämning, fångade jag entitor under höst och vinter, 1982 - 1987. Jag analyserade sedan vinglängder för fåglar som fångades mellan 1 juli och 31 december.

Hanar fångade under sin första vinter hade signifikant längre vinge (medel=67.73 mm) än lika gamla honor (medel=62.36 mm). Detta betyder att hanarnas vinge var 5.4 % längre än honornas. Från figur 1 verkar det rimligt att påstå att individer med en vinglängd av 64 mm eller kortare är honor och de som har en vinge på 64.5 mm eller mer är hanar. Används detta värde som gräns mellan könen, kommer endast en hane (2.9 %) och en hona (2.3 %) på fel sida om skiljelinjen.

Storleksmått är oftast normalfördelade. Förutsätter man detta kan man räkna ut ett teoretiskt värde på överlappet mellan hanens respektive honans vinglängdsfördelningar. Med denna metod fann jag att 88.6 % av alla ungfåglar fångade under hösten/vintern kan könsbestämmas korrekt med hjälp av vinglängden.

Vid en analys av entitor som fångades under sin andra eller senare höst/vinter, fann jag likaså en signifikant längre vinge hos hanar (medel=66.55 mm) än hos honor (medel=63.00 mm). Skillnaden mellan könen uppgick i detta fall till 5.6 %. Använder man 64.5 mm som gränsvärde mellan könen fann jag att inga hanar och endast en hona (5.0 %) skulle ha bestämts till fel kön på vinglängden. Det teoretiskt uträknade överlappsvärdet mellan hanens och honans fördelningar blir i detta fall 6.6 %.

Individer som mättes under sin andra eller senare höst/vinter hade signifikant längre vinge än ungfåglar som mättes under deras första höst/vinter. Hanarnas vinglängd ökade med 0.82 mm och honornas med 0.64 mm. Denna ökning i vinglängd med åldern kan bero på två saker: antingen dör kortvingade individer i större utsträckning än långvingade eller också tillväxer vingen på varje individ under den första kompletta ruggningen. För att testa den andra av dessa förklaringar analyse-

rade jag förändringar i vinglängd för 17 individer som var mätta både under sin första och andra höst/vinter. Dessa individer ökade i genomsnitt sin vinglängd med 0.65 mm från sin första till sin andra höst/vinter. Detta betyder att nästan hela ökningen i populationens vinglängd kan förklaras med att alla överlevande individer, under sin första kompletta ruggning, växer ut pennor som är längre än ungfågelpennorna.

Den individuella ökningen av vinglängden med åldern kan antingen bero på att unga och gamla fåglar har olika vinglängds optima, och att skillnaden mellan ålderskategorier alltså är adaptiv, eller på en näringsmässig begränsning under botiden eller familjeflockstiden. Jag finner det föga troligt att unga och gamla individer hos en stannfågel skulle ha olika optimala vinglängder. Med tanke på att unga entitor är tidspressade för att lyckas etablera sig och att vingen är en av de sista strukturerna som blir färdigväxt, kan man istället tänka sig att ungfåglarna prioriterar andra aktiviteter än att låta vingen växa ut till full längd.