

SEXUAL DIMORPHISM AND POPULATION SEX RATIOS IN JUVENILE SAVANNAH SPARROWS

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Abstract.—Savannah Sparrows (*Passerculus sandwichensis*) breeding on Kent Island, New Brunswick, Canada, are polygynous and sexually dimorphic in size. The sex of 7-d-old nestlings cannot be reliably identified by size alone, but juveniles begin to display clear sexual dimorphism in size by the time they reach independence, several weeks after leaving the nest. On average, juvenile males weigh 11% more and have 6% longer wings than juvenile females. A discriminant function analysis using wing length and mass correctly classified as male or female 94% of juveniles, whose sex was later confirmed when they returned to breed as yearlings. Juvenile population sex ratio did not differ significantly from 1:1 in any year of the 4-yr study, and return rates of juveniles were independent of sex. The consistently female-biased adult sex ratio in this population must therefore be due to the failure of some returning males to establish a permanent territory, the influx of young females from other populations, or greater mortality of males (compared to females) after 1 yr of age.

DIMORFISMO SEXUAL Y RAZÓN DE SEXOS EN JUVENILES DE *PASSERCULUS SANDWICHENSIS*

Sinopsis.—La población *Passerculus sandwichensis* reproduciéndose en la Isla de Kent, Nueva Brunswick, Canadá, es polígona y sexualmente dimórfica en tamaño. El sexo de pichones de 7 días de nacidos no se puede determinar confiablemente sólo por su tamaño, pero los juveniles empiezan a mostrar claro dimorfismo sexual en términos de tamaño por el tiempo en que adquieren independencia, varias semanas después de dejar el nido. Los machos juveniles promedian 11% más en peso y tienen alas 6% más largas que las hembras juveniles. Un análisis de función discriminante usando largo de ala y masa correctamente clasificó como macho o hembra un 94% de los juveniles, cuyo sexo se confirmó posteriormente cuando retornaron un año después para procrear. La razón de sexos de la población no difirió significativamente de 1:1 durante ninguno de los cuatro años que duró el estudio. Las razones de retorno de los juveniles fueron independientes del sexo de éstos. La razón de que consistentemente hayan más hembras adultas en esta población debe relacionarse a la inhabilidad de establecer territorios permanentes por parte de algunos machos que retornan, al influjo de hembras de otras poblaciones, o a una mortalidad superior de machos (sobre hembras) después del primer año de vida.

Sexual dimorphism in plumage and morphology is relatively common among adult birds, especially in polygamous species in which sexual selection is strong, or in species where the sexes have distinctive reproductive roles or feeding behavior (Hughes and Hughes 1986, Payne 1984, Selander 1972, Willson et al. 1975). Reliable cues for distinguishing males from females are unknown for many sexually monochromatic species, however. Moreover, it is often impossible to identify the sex of nestlings or juveniles without sacrificing young or performing laparotomies, even in species that are sexually dimorphic as adults. As a consequence, our ability to test certain theories of life history evolution, behavior and pop-

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ulation biology is limited. For example, describing the allocation of parental care to male versus female offspring, or estimating the cost of raising sons versus daughters, depends upon being able to recognize the sex of offspring (Gowaty and Lennartz 1985, Howe 1977), as does an understanding of the basic biology of juveniles, such as sex-related dispersal, foraging behavior, habitat selection or mortality (Breitwisch 1989, Cody 1985, Greenwood and Harvey 1982).

In Savannah Sparrows (*Passerculus sandwichensis*), sexual differences in plumage are subtle or non-existent (Stobo and McLaren 1975). Adult males are larger on average than females throughout their range (Wheelwright and Rising 1993). Given the fact that many populations of the species are known to be polygynous (Wheelwright et al. 1992), sexual selection based on male-male competition for females would be expected to lead to such sexual dimorphism in body size among adults. (The degree of sexual dimorphism within a particular population, however, appears to be unrelated to the existence of polygyny in that population [Rising 1987, Weatherhead 1980].) Moreover, because morphological differences are relatively slight and variable, no attempt has been made to distinguish the sexes of Savannah Sparrows other than by cloacal protuberances or brood patches (Canadian Wildlife Service 1984, Pyle et al. 1987), features that are useless in the non-breeding season or for immature birds.

In our study of an isolated, polygynous population of Savannah Sparrows, we found that adult males and females can be distinguished in most cases on the basis of wing length. More surprisingly, juveniles begin to exhibit clear sexual dimorphism in body size within 2 wk of leaving the nest. In this paper we present data on body size of nestlings, independent juveniles, and adults. Using discriminant function analysis to distinguish males from females (Clark et al. 1991), we also describe juvenile population sex ratios over a 4-yr period. In contrast to the majority of passerine populations, the adult population sex ratio of Savannah Sparrows at Kent Island is consistently female-biased. By being able to distinguish males and females at the juvenile stage, we estimate first-year survival rates and determine the extent to which skewed breeding sex ratios are influenced by differential mortality of juveniles.

STUDY SITE AND METHODS

Our study site is the Bowdoin Scientific Station, located on Kent Island, an 80-ha island in the Bay of Fundy, New Brunswick, Canada (44°35'N, 66°46'W), where Savannah Sparrows nest in a range of open habitats. Breeding densities are high in the study site. For example, 12–29 adults have bred in a 1.2-ha field each year between 1987 and 1993. Nestlings remain in the nest for about 10 d, and fledglings stay with their parents for 10–25 d after leaving the nest (Dixon 1972, 1978; Wheelwright and Rising 1993). Depending upon the year, 15–33% of males are polygynous (Wheelwright et al. 1992).

Between 1988 and 1993, all breeding adults and all nestlings in the 6.2-

ha study area were banded under license with Canadian Wildlife Service aluminum bands, including a total of 2965 birds, of which 2493 were first banded as nestlings or juveniles. Nestlings were measured in the nest at 7 d of age; we used mist-nets to capture juveniles and adults. For the purposes of identifying the sex of juveniles, we measured them only after flight feather development appeared to be complete (longest rectrix 48 mm or longer, remiges and rectrices free of sheaths). The average age of measured juveniles was 38.6 d (± 9.1 SD; 27–95, $n = 372$ known-age individuals). Parental care typically terminates at about 23 d of age (Wheelwright and C. Freeman, unpubl. data). For all age classes the length of the unflattened wing was measured to 1 mm with a wing ruler. We measured the mass of each bird to 0.1 g with an electronic balance. Tarsus length was measured to 0.1 mm with dial calipers (proximal to distal end of the tarsometatarsus, with digits folded forward). All measurements of adults and juveniles were made by NTW. Adult males were recognized by their prominent cloacal protuberances, adult females by the presence of brood patches. In almost all cases, the identification of an adult's sex was later verified by observing its behavior (e.g., singing in males, incubation in females, sex-specific call notes, copulation position).

In contrast to some mainland Savannah Sparrow populations, in which birds banded as nestlings are rarely or never seen again (e.g., Bédard and LaPointe 1984, 1985), nestling and juvenile philopatry at Kent Island is quite high. Eleven percent of birds banded as nestlings and 26% of birds banded as fledglings were recaptured in subsequent years (Wheelwright and Schultz 1994). As a result, we could recapture birds when they were reproductively mature and relate their morphological measurements as juveniles to their sex as adults.

Statistical analyses were performed with Statview (Abacus Concepts, Inc. 1992) except for discriminant analysis, which used the multivariate general linear hypothesis (MGLH) procedure of Systat (Wilkinson 1989). Except where noted otherwise, descriptive statistics are given as means \pm 1 SD.

For the discriminant function analyses, we randomly divided into two approximately equal groups ($n = 83$ birds) our data set of juveniles that hatched in 1988–1990 and were subsequently recaptured and sexed as adults. The morphological data and sex identifications of one group were used to derive the function, which proved to be significant. Next, the function was applied to individuals of the other group to classify them as male or female and to verify the function's ability to distinguish the sexes. Third, the groups were recombined to derive a new function as above, taking advantage of the larger sample size. Finally, that function was applied to an independent set, juveniles that had hatched and been measured in 1991 and had returned in 1992. A similar procedure was followed for nestlings.

RESULTS AND DISCUSSION

Adult Savannah Sparrows are sexually dimorphic in body size on Kent Island, as in other populations (Rising 1987, Stobo and McLaren 1975).

TABLE 1. Morphological measurements of nestling, juvenile and adult Savannah Sparrows on Kent Island, New Brunswick. Nestlings were measured at 7 d of age, juveniles at 27–95 d of age. Sex for nestlings and juveniles was subsequently identified when they returned as reproductively mature yearlings. Data from 1988–1990 combined for nestlings and juveniles, 1987–1992 for adults. *P* values refer to results of two-tailed Mann-Whitney *U*-tests comparing sexes within age groups.

Age/Sex	\bar{x}	SD	Range	<i>n</i>	<i>P</i>
Wing length (mm)					
Nestling males	30.9	3.1	24–40	53	
Nestling females	29.5	3.6	21–36	40	
Juvenile males	69.2	1.5	64–73	77	<0.001
Juvenile females	65.1	1.5	62–69	68	
Adult males	68.6	1.7	64–73	255	
Adult females	64.7	1.7	57–70	220	
Mass (g)					
Nestling males	16.1	1.5	10.7–19.1	57	<0.001
Nestling females	14.6	1.4	10.8–16.5	41	
Juvenile males	18.9	1.1	16.6–21.4	62	<0.001
Juvenile females	17.0	0.9	14.1–18.7	56	
Adult males	20.1	1.3	15.8–23.4	194	<0.001
Adult females	18.9	1.9	15.5–25.2	146	
Tarsus length (mm)					
Nestling males	19.3	1.7	14.5–22.6	57	0.11
Nestling females	18.9	1.2	16.6–21.4	44	
Juvenile males	21.2	0.9	19.2–22.6	47	
Juvenile females	20.7	0.9	18.6–22.3	28	
Adult males	21.6	0.6	19.6–23.3	233	<0.001
Adult females	21.0	0.5	19.7–22.5	204	

Males and females differed significantly in wing length, mass and tarsus length (Table 1). There was, however, pronounced seasonal and diurnal variation in adult mass, especially during egg-laying, and males and females overlapped in mass, tarsus length and, to a lesser extent, wing length. Although Rising (1988) points out the limitations of using wing length as an indicator of body size, it is useful nonetheless for distinguishing the sexes. Sexual dimorphism in wing length in adults is probably widespread among other sparrow species (e.g., Piper and Wiley 1991).

More than 100 individuals measured as nestlings were recaptured the following year as breeding adults, at which point their sexes could be identified. Male nestlings averaged 10% heavier than female nestlings at 7 d of age (Table 1). There were no significant differences between male and female nestlings in wing or tarsus length, although males tended to have slightly longer wings and tarsi than females (Table 1).

By the time juveniles were at least 27 d old, their wings were fully developed and in fact were longer than their parents at the same time of year (Fig. 1, Table 1). The sex of juveniles (as determined when they were recaptured as breeding adults a year later) could be ascertained at an early age on the basis of wing length. The wings of juvenile males were

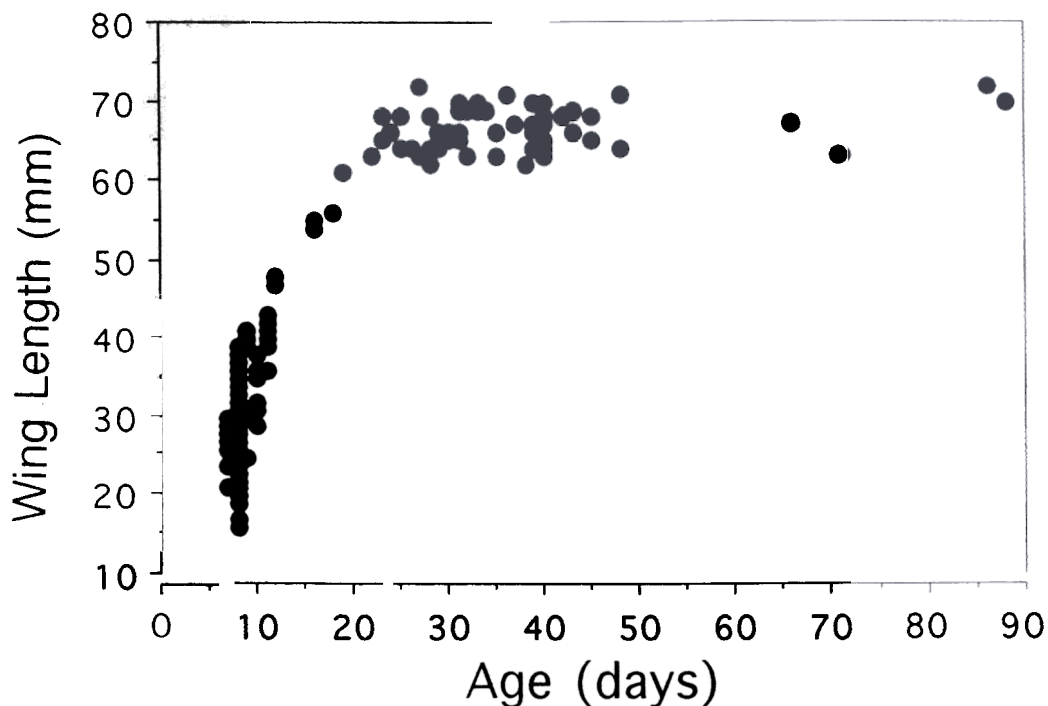


FIGURE 1. Growth in wing length of juvenile Savannah Sparrows ($n = 338$). By 27 d of age, juveniles are independent of their parents and development of remiges and rectrices is complete.

on average 6% longer than those of females (Table 1), although there was some overlap in the distributions of wing lengths of males and females (Fig. 2). On average juvenile males were also significantly heavier than females (11%) and had longer tarsi (2%) (Table 1). The distinctive juvenile plumage of Savannah Sparrows varies among individuals (Wheelwright and Rising 1993), but we found no association between coloration and sex.

In this population, juveniles with wing lengths exceeding 70 mm could be considered with confidence to be males, whereas those with wing lengths less than 65 mm were in virtually every case females (Fig. 2). Using mass as well as wing length allowed the sexes of most juveniles of intermediate wing size to be identified (Fig. 2). Discriminant function analysis, applied to successively larger subsets of the data (see Methods), resulted in the correct classification of more than 93% of individuals in each case (χ^2 test: $P < 0.0001$). Adding tarsus length to the equation did not improve the probability of correctly classifying juveniles to sex, so it was ignored. The final discriminant analysis, based on the entire sample of 119 juveniles, produced the following equation:

$$D = 1.567(\text{wing length in mm}) + 1.232(\text{mass in g}) - 127.192,$$

where D is the discriminant score. If $D > 0$, a juvenile was classified as a male; $D \leq 0$ indicated a female. When applied to the entire sample, the

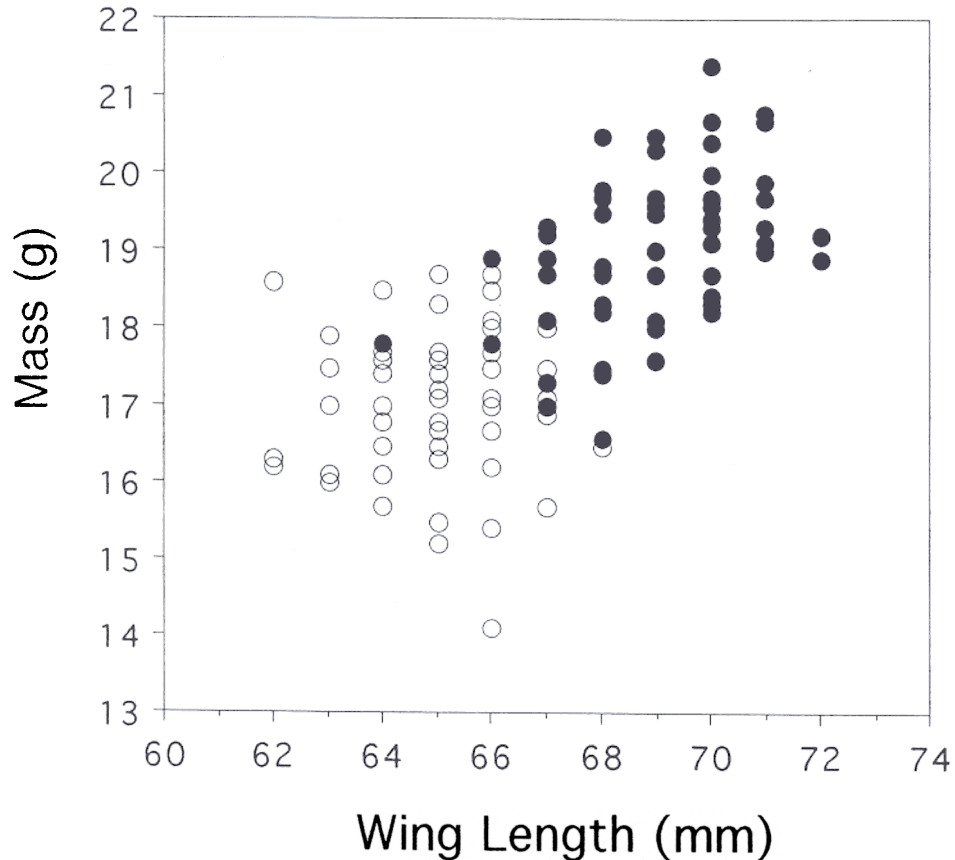


FIGURE 2. Wing length versus weight in juvenile Savannah Sparrows older than 27 d. Open circles represent females; solid circles represent males. Once the development of remiges and rectrices is complete, the sex of 94% of juveniles can be correctly identified using wing length and mass.

function correctly classified 112/119 juveniles (94.1%; χ^2 test: $P < 0.0001$). Every juvenile female was correctly classified; seven short-winged males were incorrectly classified as females.

Discriminant analysis on nestlings, using, as above, one portion of the data set to derive the function and verifying it with an independent set, demonstrated that size could be used to differentiate most males and females at only 7 d of age (χ^2 test: $P < 0.0001$), but the function incorrectly assigned sex in the case of about 25% of nestlings. Using all morphological measurements, the equation was:

$$D = -0.125(\text{wing length in mm}) + 0.814(\text{mass in g}) \\ + 0.444(\text{tarsus length in mm}) - 0.535$$

($D > 0$ for males, $D \leq 0$ for females). A function based on nestling mass alone ($D = 0.797[\text{mass in g}] - 0.463$) was equally successful, correctly classifying to sex 70/93 nestlings. Male and female nestlings were equally likely to be misclassified.

We attempted to estimate the population sex ratio of independent ju-

TABLE 2. Estimated sex ratio of independent juvenile Savannah Sparrows at Kent Island, New Brunswick. Sex assigned on the basis of discriminant function (see text). Sex ratios were not significantly different from 1:1 in any year (chi squared goodness-of-fit test: $P > 0.28$) or in all years combined ($P = 0.84$).

Year	# males	# females	Males : females
1988	43	46	0.93
1989	68	76	0.89
1990	110	87	1.26
1991	70	73	0.96
All years combined	291	282	1.03

venile Savannah Sparrows and test for sex-specific survival and philopatry using the discriminant function to determine the sex of all juveniles, including individuals whose sex could not be confirmed because they failed to return as adults. We assumed that juvenile males and females were equally likely to be captured in mist-nets, a reasonable assumption given that juveniles were captured shortly after being attended by their parents, and differential dispersal by sex was restricted by being on an island (Greenwood and Harvey 1982). In every year of the study, as well as when all years were combined, the juvenile sex ratio did not differ significantly from 1:1 (Table 2). Unbiased sex ratios are typical of the few bird species for which juvenile sex ratios are known (Breitwisch 1989, Clutton-Brock 1986; see also Rising 1988). On the other hand, adult sex ratios on Kent Island were consistently and significantly female-biased in all years of the study (Wheelwright et al. 1992), in contrast to the more common pattern of male-biased adult sex ratios found in monogamous bird species (Breitwisch 1989, Smith et al. 1982). The fact that we found no difference in return rates of juveniles as a function of sex suggests that the skewed adult sex ratio was not simply caused by differential mortality or dispersal of juvenile males hatched on Kent Island. Rather, it must have been due to some combination of the following three factors: (1) the failure of returning males to establish a permanent territory (that is, they returned as yearlings and were recorded as having survived, but they were less likely than females to remain); (2) the influx of females from other populations; or (3) greater mortality rates of males (compared to females) after 1 yr of age. The first explanation seems unlikely given a high degree of philopatry of both males and females (Wheelwright and R. Mauck, unpubl. data) and the fact that no adults that previously bred on Kent Island have ever been recovered elsewhere. The second explanation, greater female dispersal, seems promising in light of female-biased dispersal in other bird species (Greenwood and Harvey 1982), even though at the scale of the Kent Island Archipelago, males and females do not differ in the distance between their natal nest and first territory (Wheelwright and R. Mauck, unpubl. data). A preliminary analysis shows no consistent difference between the sexes in adult mortality.

One of the implications of this study is that sexual selection for in-

TABLE 3. Survival (based on returns as breeding adults) as a function of sex of independent juvenile Savannah Sparrows at Kent Island, New Brunswick. Sex assigned on the basis of discriminant function (see text). Differences between the sexes in survival were not significant in any year (chi squared test of independence: $P > 0.35$) or in all years combined ($P = 0.38$). n refers to original sample size.

Year	% males surviving	n	% females surviving	n
1988	20.9	43	28.3	46
1989	27.6	76	23.5	68
1990	21.8	110	26.4	87
1991	15.7	70	23.3	73
All years combined	21.7	299	25.2	274

creased male body size at one life stage, reproductive maturity, can presumably cause as a pleiotropic consequence differential growth rates of the sexes beginning at a much earlier age. The fact that juvenile males averaged 6% heavier and 11% longer-winged than females at the termination of parental care also suggests a greater energetic cost of producing sons than daughters and raises questions about optimal allocation to male and female offspring (Fiala and Congdon 1983, Slagsvold et al. 1986). Nonetheless, our findings that population sex ratios were unbiased just after the termination of parental care provided no evidence that Savannah Sparrows adaptively adjust offspring sex ratio to equalize parental investment in sons and daughters (Howe 1977).

The discriminant functions were not improved by using tarsus length to distinguish the sexes, which raises the question of the value of measuring tarsus length in field studies for such a purpose (J. Bédard, pers. comm.). This conclusion and the precise functions described above, however, should not be applied uncritically to other Savannah Sparrows populations. Nonetheless, their success in discriminating juvenile males from females within 2 weeks of fledging suggests that we should examine other populations of Savannah Sparrows, as well as those of other polygamous species presumed to be sexually monomorphic until adulthood, in an attempt to understand population sex ratios and sex-specific mortality rates.

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