

Sex and age-related wing size dimorphism in
monogamous North American passerines

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The occurrence of sex-related size dimorphism is a widespread phenomenon. It has been recorded in a large number of diverse faunal groups: lizards (Cooper and Vitt 1989; Carothers 1984; Fitch 1978; Vial and Stewart 1989), anurans (Sullivan 1984; Shine 1979; Woolbright 1983), turtles (Berry and Shine 1980), snakes (Shine 1978) and mammals (Ralls 1976a, 1977; Clutton-Brock et al. 1977; Myers 1978). It has also received a considerable amount of attention with respect to birds (Sigurjonsdottir 1981; Searcy 1979; Amadon 1959; Selander 1966; Selander 1972; Rising 1987; Ross 1979; Lack 1968; Ankney 1977). Among the avian groups where sexual dimorphism has been extensively studied are ones which possess unique characteristics: the reversed size dimorphism of raptorial birds (Newton 1979; Snyder and Wiley 1976; Amadon 1975; Storer 1966) and the polygynous and polyandrous mating systems of shorebirds (Jehl and Murray 1986). Less attention has been given to the passerines except where, once again, unique conditions prevail; Darwin's finches (Price 1984b; Boag and Grant 1978) or the polygamous mating systems of the Icteridae (Searcy and Yasukawa 1981; Searcy 1979). The development of current theories regarding sexual dimorphism have been greatly aided through research done on these groups of passerines (Verner and Wilson 1966; Orians 1969).

In spite of the importance that some groups of passerines have had in terms of research regarding the evolutionary causes of size dimorphism, there has not been a detailed survey of dimorphism encompassing the many different taxa of Passeriformes. The purpose of this paper, then, is to examine the prevalence of sex and age related size dimorphism in various species of North American passerines.

There are two main classes of hypotheses in the literature concerning the evolution of sexual dimorphism, where evolutionary pressures have differed between the sexes: natural selection and sexual selection (Rising 1987; Ebenman 1986; Price 1984b). Natural selection, termed more precisely in this case as the competition avoidance hypothesis (Searcy 1979), is the presence of increasing sexual dimorphism in some trophic character(s) which permits niche partitioning among the sexes and is thus, an adaptation to reduce competition between males and females for various resources, mainly food (Ebenman 1986; Price 1984b). There are many studies which have demonstrated ecological differences between males and females (eg. Selander 1966; Morrison 1982; Tiainen 1982; Franzreb 1983; Grubb 1982; Holmes 1986; Kodric-Brown and Brown 1978).

Sexual selection, as proposed by Darwin, is comprised of two types of selection pressures that could produce a sexual size dimorphism: female choice and inter-male competition (Berry and Shine 1980; Ralls 1977; Sigurjonsdottir 1981). Female choice (epigamic selection) arises when females choose males that possess a desirable trait of some kind, eg. body size (Berry and Shine 1980) or territory quality. Inter-male competition, for resources such as the food and territories which females desire, determines a males' relative fitness (Berry and Shine 1980). Since the ability of a male to

control these resources, and thus obtain mates, is dependant on his fighting ability, and success in intrasexual encounters increases with increased body size (Ebenman 1986; Berry and Shine 1980; Price 1984), there will be selection for larger males. Even though these two hypotheses are not mutually exclusive, intrasexual aggression between males appears to be considered the driving force in sexual selection (Rising 1987; Lande 1980; Ralls 1977; Cooper and Vitt 1989). Thus, the result of sexual selection is the development of characters in one sex that ensures successful mating (Partridge and Halliday 1984), to the extent that these characters might be otherwise maladaptive (Rising 1987).

Darwin's hypothesis that sexual selection has resulted in the evolution of sexual dimorphism has received a great deal of support (Wilbur et al. 1978; Halliday 1978; Wilson 1975; Trivers 1972; O'Donald 1980). Indeed, there are some who feel that 'there is no doubt that sexual selection can account for the origin and maintenance of sexual dimorphism' (Slatkin 1984).

There is some thought that the level of sexual selection in monogamous, territorial passerine species is weak (Searcy 1979), implying that sexual size dimorphism may not be strongly exhibited, or at least not to the extent present in polygynous species. A strong correlation between polygyny and sexual size dimorphism has been demonstrated in the Icteridae (Selander 1972; Orians 1961). In the majority of passerine species, males establish and maintain breeding territories which are advertised through singing and defended by aggressive inter-male competition. Males of these species are commonly larger than females (Rising 1987; Selander 1972). Again, the degree of sexual dimorphism is greater in species such as the icterids but is also present in monogamous species, where males compete for early breeding females (Price 1984). Thus, we can hypothesize that, due to the presence of epigamic selection and inter-male competition, monogamous passerines should exhibit a significant sexual size dimorphism, with males larger than females. Furthermore, the body size and degree of sexual size dimorphism in groups of closely related species, i.e. Anatinae (Sigurjonsdottir 1981), owls (Earhart and Johnson 1970), and grouse (Wiley 1974), are positively correlated (Sigurjonsdottir 1981; Lande 1980), a condition that should also prevail in monogamous passerines.

A second class of dimorphism among birds is that found between adults and their progeny. The existence of age-related size dimorphism has been well established among passerines (Sellers 1986; Bibby and Thomas 1984; Mueller et al. 1981; Norman 1983; Alatalo et al. 1984; Stewart 1963). Several researchers have postulated reasons for this difference, both for passerines (Tiainen and Hanski 1985; Sellers 1986; Alatalo et al 1984) and for other avian groups in which this phenomenon occurs, such as the raptors (Mueller et al 1979; Mueller et al 1981). What has not been reviewed in the literature is the degree of dimorphism among the age-sex classes for passerines and, a) whether there is a parallel in size dimorphism between age classes of males and females (HY and AHY) for each species, and b) if the degree of size dimorphism between adults and juveniles is constant over the range of body sizes.

Size dimorphism among juvenile passerines appears to have received little attention within the overall context of sexual selection. Growth in male and female passerine nestlings follows different developmental paths (Richter 1983) such that one sex is significantly larger at fledging (Bancroft 1984). Generally, adult size is achieved at fledging (Downhower 1976). If sexual selection favors larger body size in males then presumably this trait should be expressed from an early age (i.e. at full fledging). Thus, we should expect to find that species in which the adults are sexually dimorphic should rear young that, by the time they are fully fledged, are also significantly dimorphic. Also, the degree of dimorphism among juveniles should parallel that of the adults.

Methods

Size dimorphism is commonly studied by expressing morphological variables in terms of a male-female ratio (Rothstein 1973a; Searcy and Yasukawa 1981; Jehl and Murray 1986). The trait most often used with birds is wing length because it correlates well with the fat-free weight of a bird (Connell et al. 1960) and is, thus, a good indicator of overall body size (Hamilton 1961; Bahrman 1978; Van Balen 1967; Mueller et al. 1979; James 1970). It is also the least variable morphological trait that is easily and accurately measured on live birds (Lanyon 1960), as opposed to body weight, which fluctuates seasonally or even daily (Searcy 1979, 1979b; Freeman and Jackson 1990). Other researchers have found that the average wing length of some passerine species correlates well with their average weight (Grant 1986). All ratios used in this study refer to body size ratios using wing length.

Wing length data for the species discussed herein was obtained from the banding records of the Long Point Bird Observatory (at Port Rowan, Ontario) for the years 1986 to 1989 inclusive. The wings were measured as the unflattened wing chord of live birds caught in mist nets and heligoland traps. In many previous studies which used wing length measurements, data were obtained from Ridgway (1901-1908). The use of more recent banding records from a single locality is preferred because Ridgway's data lack the necessary detail for intraspecific comparisons and do not provide variance measures (Wiens and Rotenberry 1980).

All species are referred to by a standard four letter code; complete species names are provided in the appendix. Wing length comparisons were done using a Student's t-test.

Results

Adults

Fifty-two species were examined in this study, with at least one species from thirteen different families (table 1). Within this group, forty-seven species exhibited a significant sexual size dimorphism, with most of these results being highly significant

($P < 0.001$). The five species that did not exhibit a significant level of dimorphism do not belong to any particular taxonomic group.

The male:female size ratio ranged from 1.00 to 1.14, with the average being 1.05, thus, the mean intrasexual difference in wing length is approximately five percent.

To determine how the size of males and females relate to each other a regression analysis was performed on the wing lengths of all species. The result was highly significant ($r = .99$, $F = 3030.99$, $P < .001$), indicating a virtual 1:1 linear relationship of male and female size among passerines.

The amount of inherent variability within each species was examined through the use of a coefficient of variability (CV). The CV of males ranged from 1.10 to 4.07, with an average of 2.63. The CV of females ranged from 1.15 to 3.93, with an average of 2.57. Overall, there was no real difference in variability between these two groups ($t = 0.46$, $P = 0.65$) and there was no consistent pattern of intersexual dominance: in twenty-eight of the species the male had a greater CV, while the female CV was greater in the remaining twenty-four. The relationship of this index to other factors was also examined (see table 2). Male and female CV's were linearly related, however, in neither sex was the variability linearly related to wing length. A significant negative relationship does exist between the CV of both sexes and the male:female ratio. Thus, the more similar the males and females are in body size, the more variable their body sizes tend to be. This may be indicative of the degree to which wing length is inheritable; strongly inheritable for very dimorphic species, less so as the level of dimorphism decreases.

The relationship between body size and the degree of sexual size dimorphism was examined using regression analysis for different groups of species (summarized in table 3). The analysis started with the most generally related group (all species combined) and then examined the more closely related groups: the four families and subfamilies and the one well-represented genus, *Dendroica*. None of these groups, regardless of how closely related the species were, exhibited any significant relationship between body size and degree of sexual dimorphism, for either males or females.

Juveniles

Thirty-seven of the species listed in table 1, and one additional species, representing eleven families in total, were analyzed in approximately the same fashion as the adults (table 4). Of the thirty-two species of juveniles with adequate data for male-female comparisons, twenty-nine exhibited a significant sexual size dimorphism (most at $P < .001$) while three were non-significant. As with the adults, these three non-significant species were unrelated.

The juveniles were also quite similar to the adults in other ways. The male:female size ratios ranged from 1.01 to 1.14, with the average being 1.05. Again, the mean

intrasexual difference was about five percent. And body size showed a consistent intraspecific variation: the correlation between male and female wing lengths was again highly significant ($r=.98$, $F=964.2$, $P<.001$).

Wing length variability of juveniles was also measured by a coefficient of variability (CV). The CV of males ranged from 0.92 to 4.49, the mean being 2.72. Among the females, the CV was quite similar, ranging from 0.90 to 4.76, with a mean of 2.78. The overall variability between these groups was not significant ($t=0.37$, $P=0.71$) and there is no pattern of intersexual dominance for this variable: seventeen species have males with a greater CV while in the remaining fifteen species the higher CV values belong to the female. The relationship between CV and other factors is summarized in table 2. Male and female CV's are linearly related, but there is no significant relationship between the CV of each sex and their respective body sizes. There is a significant relationship, however, between the CV of each sex and the juvenile Male:female ratio. Thus, the closer the ratio is to unity, the more variable the body sizes of each sex are.

Adult-Juvenile Comparisons

Comparisons of body size among the age-sex classes were used to determine how similar juvenile and adult birds were by the time the juveniles were fully fledged.

The degree of sexual size dimorphism of adults compared to that of their juveniles revealed that there is a parallel dimorphism between the two age groups. All twenty-nine juvenile species listed in table 4 that exhibit a significant sexual dimorphism have adults that are also significantly dimorphic. And the male-female size ratio of the two age groups is very similar: in twenty-five species the size ratios of the two age groups vary by one percent or less (see also fig. 1). This trend is corroborated by regression analysis which showed a highly significant relationship between these two ratio variables ($r=.93$, $F=202.2$, $P=0.0$). Thus, the greater the degree of sexual size dimorphism in adults the greater the sexual size dimorphism of their progeny. Bear in mind that this is a general trend over all the species considered, and that some species deviate from this trend. For example, the three juvenile species that do not possess a significant size dimorphism have adults which do.

Another method of analyzing the data is to examine the adult:juvenile size ratio for each sex (see table 5). Among the thirty-six male species examined, only thirteen exhibited a significant age-related size dimorphism while the remaining twenty-three were non-significant. The average male adult:juvenile size ratio is 1.01 and the total ratio range is 0.96 to 1.07. Thus, adults are, on average, only one percent larger than juveniles and eight species of juveniles are actually larger than their adults, two of them significantly so. The female species exhibited results similar to those of the male species. Of the thirty-six female species, only fourteen possess a significant size dimorphism while twenty-two species are non-significant. The average female adult:juvenile size ratio is 1.00 and the

ratio range is from 0.98 to 1.07. On average, adult females are the same size as their female progeny. However, twelve species have juveniles that are larger than the adults and six of these are significant size differences. Only six species (all unrelated) possess a significant adult:juvenile size ratio for both males and females. Thus, there is no consistent pattern among the passerines with regards to age-related size dimorphism, except in the distribution of this ratio, where both sexes are quite similar (see fig. 2).

The intersexual relationship of these adult:juvenile ratios was examined for several groups of species using regression analysis (table 6). The only significant result was obtained when all the species were considered. When more closely related taxonomic groups were examined, no significant correlations were found. Thus, a viable trend between the adult:juvenile ratios of males and females is present only on a large scale, not among the more closely related groups.

The pattern of variability between the two age groups is quite similar. Analysis of the CV for each age-sex group (table 2) shows that, for both adults and juveniles, male and female CV's are significantly correlated, as is the relationship between CV and male:female ratio. In neither groups is the CV and wing length of either sex significantly related.

To determine if the degree of age-related size dimorphism is constant over a range of body sizes, the adult:juvenile ratio was compared to the adult size, again for various groups of species, using regression analysis. The results are presented in table 7. Analyzing all the species combined results in a significant correlation between the adult:juvenile ratio and adult body size of both males and females. If just the groups Emberizidae, Parulinae and Dendroica are considered, no significant results are obtained for either sex. Once again, this trend is present only on a large scale (all passerines) but not amongst the smaller taxonomic units.

Discussion

Ninety percent of the monogamous species surveyed in this study were found to be sexually dimorphic. How indicative is this of passerines in general? A survey of avian breeding systems by Lack (1968) found that ninety-one percent of all passerines were monogamous. Within North America, Verner and Willson (1966) reported a similar trend, with 277 of 291 species of passerines (95%) being monogamous. If we assume, then, that the results of this study are representative of an overall trend, the large majority of North American passerines should exhibit a significant sexual size dimorphism. This trend is even more pervasive when we include the fourteen polygamous species, all of which are dimorphic, save for one, the long-billed marsh wren (Verner 1965).

The level of dimorphism between these two mating systems is quite different: the male:female ratio for monogamous species ranges from 1.00 to 1.14, while polygamous species generally range from 1.09 to 1.28 (Searcy and Yasukawa 1981). Why this

difference exists, and why monogamous species should have such low levels of dimorphism, if any at all, can be seen by considering some of the characteristics, and possible origin, of these two mating systems.

The exact origin and subsequent evolution of sexual dimorphism is a topic of great controversy that has given rise to many contrasting views (eg., Downhower 1976; Hedrick and Temeles 1989; Jehl and Murray 1986; Price 1984; Slatkin 1984, and others). One main concept concerns the role that mating systems have played in influencing the degree of sexual dimorphism. Mating systems are viewed as ecological adaptations to differing environmental conditions (Lack 1968). In an attempt to maximize their relative fitness, individuals will choose a particular mating system. Each system produces different levels of sexual selection due to such factors as the ability of some individuals to control access to resources (i.e. potential mates, nest sites) (Emlen and Oring 1977), the intensity of parental investment (Trivers 1972) and the occurrence of unbalanced sex ratios (Jehl and Murray 1986; Selander 1972). The end result is the presence of a sexual size dimorphism characteristic of each mating system. In some faunal groups there is a very strong correlation between mating systems and the degree of sexual dimorphism in body size (Selander 1972).

The probable origin of polygamy is nicely described by the Orians-Verner-Willson model (Orians 1969; Verner and Willson 1966). The condition required for this mating system is the environmental potential for one male to economically monopolize several mates (Orians 1969). The only habitats in which this is feasible are two-dimensional habitats (eg. marshes and prairies) where resources, such as nesting sites and foraging areas, are concentrated into a narrow vertical stratum (Verner and Willson 1966). Due to variances in territory quality and the limited number of those of high quality, females would tend to maximize their reproductive output by choosing to mate with an already mated male on a good territory rather than with an unmated male on a poor territory. The result is a polygamous mating system (Murray 1984; Emlen and Oring 1977).

The level of sexual selection in this mating system would be intense, with males competing for territorial control and females choosing mates based on both the quality of a males' territory and his breeding displays. As the reproductive rewards increased, there would be increased selection for larger body size among males, to ensure greater success in intra-male contests and epigamic displays (Searcy and Yasukawa 1981; Selander 1972). Sexual dimorphism would thus increase. In addition, polygamous males are freed from parental duties, so they can put more energy into intrasexual competition for resources, thereby reinforcing the selection for larger size (Emlen and Oring 1977).

Monogamous mating systems are thought to originate when neither sex can control members of the other sex by monopolizing resources (Emlen and Oring 1977). Thus, monogamy occurs when there is no environmental potential for polygamy (Emlen and Oring 1977; Mock and Fujioka 1990). This is the case in most habitat types where resources are not concentrated but spread over a broad vertical area (eg. forests). More males are able to obtain good quality territories and as a result, intramale competition is

not intense (Jehl and Murray 1986). Biparental care among monogamous species further decreases the ability of males to seek extra mates (Mock and Fujioka 1990). The overall effect is a decrease in the level of sexual selection, with a resulting low degree of sexual dimorphism relative to polygamous species. Another possible reason for these levels of sexual dimorphism is that, because they have fewer matings per year than polygamous species, selection in monogamous males may emphasize survival rather than sexual characters. This would enhance the probability of survival for the greatest number of breeding seasons possible (Selander 1972).

Given these conditions which do not appear to emphasize the need for large male size, why do monogamous species exhibit sexual dimorphism? Competition among males for breeding sites and breeding females, while not as intense as in polygamous species, will still result in the development of characters such as larger body size (Selander 1972; O'Donald 1980). And Mock and Fujioka (1990) have presented four possible sources of intrasexual variance in the reproductive success of males that could result in an increase in sexual dimorphism: cheating (through extra-pair copulations), variation in the quality of mates, the presence of unmated 'floaters' in a population and the use of infanticide.

Another aspect that has played a central role in the study of sexual dimorphism is differential niche utilization between the sexes. Many authors feel that sexual size dimorphism (in trophic or secondary sex characters) can arise through the intersexual partitioning of resources (Sigurjonsdottir 1981; Robins 1971; Williamson 1971). Slatkin (1984) has proposed several ecological mechanisms that may have been capable of originating sexual dimorphism: differences in sex-specific interactions with the environment, and intersexual competition for limiting resources. Other researchers, however, have tried to temper this view by arguing that the only force acting differentially on the sexes is sexual selection (Power 1980; Jehl and Murray 1986). The forces of natural selection may then act secondarily as an agent to maintain and/or modify the degree of dimorphism (Jehl and Murray 1986). The influence of both forms of selection pressures have made it difficult to determine the primary cause of sexual dimorphism (Lande 1980), a situation that has given rise to much controversy in the literature.

Intersexual body size differences have been shown to be statistically significant and have ramifications in terms of sexual selection theory. But should the actual size variations have a differential effect on the sexes? This is a logical question given that the data provided in table 1 show that the largest difference in wing length between males and females is only fourteen millimetres, with the average being three to four millimetres (or 5%). An increase in wing length results in a corresponding increase in surface area (Blem 1975) and thereby reduces the wing loading, but it also affects the wing beat and body weight (Faaborg 1988; Welty and Baptista 1989). Thus, in some species, differences in wing length may have a profound effect on maneuverability and consequently, foraging ability and predator avoidance. For example, a twenty percent increase in wing length among raptors is equivalent to a doubling in weight (Hamilton

1961), a situation that certainly affects foraging ability (Mueller et al. 1981). The extent of this effect would vary greatly among the Passeriformes, given the wide variety of body shapes and foraging methods that exist within this group.

Several researchers have shown that it is this variation in maneuverability as a function of wing length that has resulted in juveniles of many species having shorter wings than their adults (Sellers 1986; Mueller et al. 1979; Mueller et al. 1981). However, this study has found that this characteristic is not as widespread among the passerines as was previously thought. Several possible reasons may account for this. The data used for this study were collected from migrating individuals. George (1973) felt that the purpose of the first pre-basic wing molt was to equip newly fledged birds with an adult-sized wing prior to migration. Measuring first year birds before and during fall migration could very well produce different results. The magnitude of the difference in wing length in many species could be restricted because of the limitations imposed by the principals of flight (Mueller et al. 1981). Thus, wing shape may be more important than wing length (Alatalo et al. 1984). And, as the results in table 5 indicate, those species with significant wing length differences do not belong to any particular taxonomic group(s). It may be that many species in the Passeriformes do indeed follow this trend but they are, no doubt due to some life history related reason, randomly distributed.

One trait in which virtually all juveniles are quite similar to their parents is in their level of sexual dimorphism. The fact that a significant dimorphism has developed by the time they have fledged is indicative of a trait that is highly inheritable. This is further evidenced by the parallel in dimorphism ratios that exists between the adults and juveniles.

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Table 1. Wing length data for adult passerines

Species	Male				Female				Ratio	P
	N	Mean	SD	CV	N	Mean	SD	CV		
YBFL	52	68.6	1.0	1.47	30	62.0	1.1	1.79	1.11	***
LEFL	135	64.2	1.3	2.03	130	58.4	1.2	2.06	1.10	***
TRES	24	118.0	2.1	1.80	34	111.2	3.2	3.00	1.06	***
BARS	36	118.4	2.6	2.21	14	115.8	2.7	2.37	1.02	**
RBNU	121	66.9	1.4	2.10	79	65.1	1.4	2.16	1.03	***
WBNU	6	89.7	1.0	1.16	9	89.2	1.0	1.15	1.00	ns
GCKI	50	57.6	1.5	2.62	71	55.5	1.2	2.17	1.04	***
RCKI	844	58.5	1.5	2.56	427	55.7	1.3	2.34	1.05	***
SWTH	110	100.6	1.9	1.89	7	89.3	2.3	2.67	1.13	***
AMRO	45	129.4	3.9	3.03	102	123.2	2.7	2.20	1.05	***
GRCA	35	88.1	3.1	3.54	7	87.3	3.1	3.68	1.01	ns
CEDW	16	93.4	1.9	2.07	21	92.7	2.9	3.17	1.00	ns
EUST	46	126.9	3.4	2.69	44	123.7	2.8	2.28	1.03	***
REVI	32	82.4	0.9	1.10	31	75.5	1.8	2.40	1.09	***
TEWA	93	64.0	1.9	2.98	101	60.1	1.9	3.17	1.07	***
NAWA	221	58.6	2.1	3.59	149	56.2	1.6	2.85	1.04	***
YWAR	119	61.5	2.2	3.58	100	58.7	1.7	2.90	1.05	***
CSWA	135	61.5	2.5	4.07	67	60.1	1.9	3.17	1.02	***
MAWA	787	58.9	2.4	4.07	321	56.7	2.1	3.70	1.04	***
CMWA	75	66.0	1.9	2.89	72	63.7	2.2	3.46	1.04	***
BTBW	51	63.7	1.8	2.84	69	60.5	1.7	2.82	1.05	***
YRWA	279	72.2	2.2	3.05	258	68.5	2.0	2.92	1.05	***
BTNW	61	61.4	2.2	3.60	54	59.3	1.4	2.37	1.04	***
BLBW	36	67.4	1.9	2.84	57	64.1	1.3	2.04	1.05	***
PIWA	12	69.0	1.9	2.81	7	67.1	1.4	2.16	1.03	*
BBWA	64	72.9	2.3	3.17	39	70.0	2.1	3.02	1.04	***
BLPW	29	72.2	1.9	2.66	29	69.3	1.7	2.48	1.04	***
BAWW	95	68.8	2.2	3.21	69	65.9	1.7	2.59	1.04	***
AMRE	100	61.3	2.0	3.27	92	58.7	2.3	3.93	1.04	***
OVEN	44	78.0	1.4	1.81	19	68.5	1.0	1.48	1.14	***
MOWA	64	61.4	1.5	2.45	42	58.4	1.7	2.93	1.05	***
COYE	343	55.1	1.8	3.27	202	52.5	1.8	3.43	1.05	***
WIWA	290	54.1	1.8	3.33	47	51.7	0.9	1.75	1.05	***
CAWA	135	64.2	1.9	2.97	81	61.6	1.7	2.77	1.04	***
YBCH	14	75.0	2.2	2.99	10	74.4	1.8	2.48	1.01	ns
SCTA	15	94.2	2.2	2.37	9	90.1	2.1	2.4	1.05	***
NOCA	33	93.5	2.0	2.16	48	90.1	2.6	2.90	1.04	***
RBGR	131	100.1	3.0	3.00	105	98.1	3.0	3.06	1.02	***
INBU	17	66.8	1.5	2.28	12	63.8	1.4	2.24	1.05	***
RSTO	77	85.5	3.0	3.52	56	81.3	3.0	3.71	1.05	***
SOSP	34	65.1	1.5	2.32	11	61.6	1.7	2.82	1.06	***
WTSP	469	74.9	1.0	1.34	109	66.8	0.9	1.35	1.12	***
DEJU	217	78.9	1.0	1.27	441	71.3	1.0	1.40	1.11	***
COGR	388	140.6	3.3	2.35	406	126.5	3.5	2.77	1.11	***
BHCO	144	108.5	3.3	3.05	81	97.7	2.3	2.36	1.11	***
NOOR	118	91.6	2.9	3.17	47	87.9	2.5	2.86	1.04	***

PUFI	26	81.6	1.8	2.23	11	78.1	1.8	2.36	1.04	***
HOFI	12	77.3	1.9	2.51	12	76.0	1.8	2.42	1.02	ns
PISI	25	73.9	2.2	3.01	12	69.5	1.9	2.79	1.06	***
AMGO	125	71.4	1.8	2.53	102	69.2	1.6	2.32	1.03	***
EVGR	34	111.5	2.4	2.17	47	109.0	2.5	2.31	1.02	***
HOSP	14	77.1	1.5	1.98	11	73.8	1.4	1.94	1.04	***

CV: coefficient of variation

Ratio: male:female

P: results of t-tests between male and female wing lengths

* P<0.05

** P<0.01

*** P<0.001

ns - non significant

Wing length was measured in mm.

Table 2. Regression analysis of wing length variability for the different age-sex classes

<u>Regression</u>	<u>Adult</u>			<u>Juvenile</u>		
	<u>r</u>	<u>F</u>	<u>P</u>	<u>r</u>	<u>F</u>	<u>P</u>
Male CV vs female CV	.63	34.3	0.0	.53	12.9	.001
M:F vs male CV	-.38	9.4	.004	-.65	23.8	0.0
M:F vs female CV	-.29	5.6	.021	-.55	14.7	.001
Male CV vs male WL	-.24	4.3	.05	-0.0	.13	.72
Female CV vs female WL	-0.0	.09	.76	.23	2.98	.09

CV= coefficient of variation
 WL= wing length
 M:F= male:female ratio

r= correlation coefficient
 F= F statistic
 P= significance level

Table 3. Results of regression analysis between body size (male and female wing length) and degree of sexual size dimorphism (male:female ratio).

<u>Group</u>	<u>N species</u>	Male			Female		
		<u>r</u>	<u>F</u>	<u>P</u>	<u>r</u>	<u>F</u>	<u>P</u>
All species	52	0.0	0.29	0.59	0.0	0.12	0.74
Muscicapidae	4	0.0	0.23	0.68	0.0	0.11	0.77
Parulinae	21	0.11	1.25	0.28	0.0	0.0	0.98
Emberizinae	8	0.34	1.89	0.22	0.52	3.64	0.11
Fringillidae	5	0.0	0.87	0.42	0.22	1.21	0.35
Dendroica	11	0.0	0.19	0.68	0.0	0.0	0.95

r= correlation coefficient

F= F-statistic

P= significance level

Table 4. Wing length data for juvenile passerines

Species	Male				Female				Ratio	P
	N	Mean	SD	CV	N	Mean	SD	CV		
YBFL	6	68.0	0.6	0.92	47	61.8	1.1	1.79	1.10	***
LEFL	98	63.6	1.1	1.73	178	59.3	1.3	2.20	1.07	***
EAKI	---	----	---	----	10	110.6	2.6	2.41	----	--
RBNU	86	67.1	1.8	2.69	58	65.5	1.5	2.30	1.02	***
RCKI	363	58.1	1.4	2.41	424	55.6	1.5	2.70	1.04	***
SWTH	122	100.0	1.3	1.30	20	89.6	0.8	0.90	1.12	***
EUST	8	118.6	3.3	2.87	10	115.6	3.7	3.28	1.03	ns
REVI	34	81.6	0.9	1.11	99	74.3	0.9	1.21	1.10	***
TEWA	33	65.3	0.6	0.93	54	59.5	0.8	1.35	1.10	***
NAWA	91	58.4	1.8	3.09	98	55.9	1.3	2.33	1.04	***
YWAR	270	61.8	1.4	2.27	214	59.1	1.6	2.71	1.05	***
CSWA	78	61.7	2.1	3.41	20	59.1	1.1	1.88	1.04	***
MAWA	145	58.7	1.7	2.90	94	56.2	1.3	2.32	1.04	***
CMWA	229	66.1	1.8	2.73	260	64.1	1.4	2.19	1.03	***
BTBW	80	63.2	1.5	2.38	91	60.8	1.7	2.80	1.04	***
YRWA	339	72.1	2.1	2.91	353	67.7	1.4	2.07	1.06	***
BTNW	42	61.3	2.0	3.28	20	60.8	2.5	4.16	1.01	ns
BLBW	49	67.2	3.0	4.49	61	64.8	2.4	3.72	1.04	***
BBWA	98	72.2	2.1	2.92	66	69.4	1.6	2.31	1.04	***
BLPW	---	----	---	----	30	69.3	2.1	3.06	----	--
BAWW	115	67.2	2.2	3.28	98	65.3	1.9	2.92	1.03	***
AMRE	161	60.6	1.7	2.81	173	58.9	1.9	3.23	1.03	***
OVEN	6	78.3	1.2	1.60	10	68.4	0.8	1.20	1.14	***
MOWA	6	60.8	1.0	1.71	13	58.9	2.2	3.81	1.03	*
COYE	65	54.9	1.7	3.11	---	----	---	----	----	--
WIWA	98	54.2	1.6	2.96	73	52.1	1.2	2.31	1.04	***
CAWA	56	63.5	2.2	3.48	77	61.3	1.6	1.00	1.04	***
NOCA	28	89.6	3.9	4.39	29	87.3	3.1	3.58	1.03	*
RSTO	---	----	---	----	9	80.7	1.2	1.53	----	---
RBGR	23	100.7	2.5	2.51	23	97.5	2.8	2.90	1.03	***
WTSP	98	74.8	1.2	1.61	47	66.7	1.1	1.66	1.12	***
DEJU	53	78.8	1.0	1.28	78	71.5	0.9	1.26	1.10	***
COGR	---	----	---	----	62	124.4	5.9	4.76	----	---
BHCO	30	107.8	3.0	2.81	22	96.4	3.5	3.71	1.12	***
NOOR	21	91.7	2.9	3.20	16	89.4	1.8	2.05	1.03	**
HOFI	17	77.0	1.9	2.50	---	----	---	----	----	---
AMGO	60	71.1	1.9	2.68	64	69.4	1.8	2.60	1.02	***
HOSP	12	74.0	1.9	2.62	27	73.2	2.1	2.90	1.01	ns

CV: coefficient of variation

Ratio: male:female

P: results of t-tests between male and female wing lengths

* P<0.05

** P<0.01

*** <0.001

ns - non significant

Wing length was measured in mm

Table 5. Wing length comparisons among the age-sex classes

Species	Male		Female	
	Ratio	P	Ratio	P
YBFL	1.01	ns	1.00	ns
LEFL	1.01	***	0.98	***
RBNU	0.99	ns	0.99	ns
RCKI	1.01	***	1.00	ns
SWTH	1.01	*	0.99	ns
AMRO	----	---	1.00	ns
EUST	1.07	***	1.07	***
REVI	1.01	***	1.02	**
TEWA	0.98	***	1.01	ns
NAWA	1.00	ns	1.01	ns
YWAR	0.99	ns	0.99	*
CSWA	1.00	ns	1.02	**
MAWA	1.00	ns	1.01	**
CMWA	0.99	ns	0.99	ns
BTBW	1.01	ns	1.00	ns
YRWA	1.00	ns	1.01	***
BTNW	1.00	ns	0.98	*
BLBW	1.00	ns	0.99	*
BBWA	1.01	ns	1.01	ns
BLPW	0.96	***	1.00	ns
BAWW	1.02	***	1.01	*
AMRE	1.01	**	1.00	ns
OVEN	0.99	ns	1.00	ns
MOWA	1.03	ns	0.99	ns
COYE	1.00	ns	----	---
WIWA	1.00	ns	0.99	*
CAWA	1.01	*	1.00	ns
NOCA	1.04	***	1.03	***
RSTO	----	---	1.01	ns
RBGR	0.99	ns	1.01	ns
WTSP	1.00	ns	1.00	ns
DEJU	1.00	ns	0.99	ns
COGR	1.03	*	1.02	**
BHCO	1.01	ns	1.01	ns
NOOR	0.99	ns	0.98	*
HOFI	1.00	ns	----	---
AMGO	1.00	ns	0.99	ns
HOSP	1.04	***	1.01	ns

Ratio: adult:juvenile

P: result of t-test between adult and juvenile wing lengths

* P<0.05

** P<0.01

*** P<0.001

ns - non significant

Table 6. Regression analysis between adult:juvenile size ratios of males and females.

<u>Group</u>	<u>N species</u>	<u>r</u>	<u>F</u>	<u>P</u>
All species	34	0.59	18.4	0.0
Emberizidae	4	0.62	2.92	0.23
Parulinae	18	0.0	0.0	1.0
Dendroica	10	0.0	0.29	0.61

r= correlation coefficient

F= F-statistic

P= significance level

Table 7. Results of regression analysis between adult body size and the adult:juvenile size ratio for each sex.

<u>Group</u>	<u>N species</u>	Male			Female		
		<u>r</u>	<u>F</u>	<u>P</u>	<u>r</u>	<u>F</u>	<u>P</u>
All species	34	0.43	8.56	0.006	0.56	16.03	0.0
Muscicapidae	4	0.0	0.06	0.83	0.45	1.76	0.32
Parulinae	18	0.0	1.01	0.33	0.0	0.85	0.37
Dendroica	10	0.0	0.53	0.49	0.0	0.30	0.59

r= correlation coefficient
 F= F-statistic
 P= significance level

Appendix A

Common names of the species used in this study and membership of those specific taxonomic groups discussed in the text

YBFL	Yellow-bellied Flycatcher
LEFL	Least Flycatcher
EAKI	Eastern Kingbird
TRES	Tree Swallow
BARS	Barn Swallow
RBNU	Red-breasted Nuthatch
WBNU	White-breasted Nuthatch
GCKI	Golden-crowned Kinglet
RCKI	Ruby-crowned Kinglet
SWTH	Swainson's Thrush
AMRO	American Robin
GRCA	Gray Catbird
CEDW	Cedar Waxwing
EUST	European Starling
REVI	Red-eyed Vireo

TEWA	Tennessee Warbler	Dendroica	Parulinae
NAWA	Nashville Warbler		
YWAR	Yellow Warbler		
CSWA	Chestnut-sided Warbler		
MAWA	Magnolia Warbler		
CMWA	Cape May Warbler		
BTBW	Black-throated Blue Warbler		
YRWA	Yellow-rumped Warbler		
BTNW	Black-throated Green Warbler		
BLBW	Blackburnian Warbler		
PIWA	Pine Warbler		
BBWA	Bay-breasted Warbler		
BLPW	Blackpoll Warbler		
BAWW	Black and White Warbler		
AMRE	American Redstart		
OVEN	Ovenbird		
MOWA	Mourning Warbler		
COYE	Common Yellowthroat		
WIWA	Wilson's Warbler		
CAWA	Canada Warbler		
YBCH	Yellow-breasted Chat		

SCTA	Scarlet Tanager	Emberizinae
NOCA	Northern Cardinal	
RBGR	Rose-breasted Grosbeak	
INBU	Indigo Bunting	
RSTO	Rufous-sided Towhee	
SOSP	Song Sparrow	
WTSP	White-throated Sparrow	
DEJU	Dark-eyed Junco	

COGR	Common Grackle
BHCO	Brown-headed Cowbird
NOOR	Northern Oriole

PUFI	Purple Finch	Fringillidae
HOFI	House Finch	
PISI	Pine Siskin	
AMGO	American Goldfinch	
EVGR	Evening Grosbeak	

HOSP	House Sparrow
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