

TARGETS OF SEXUAL SELECTION: SONG AND PLUMAGE OF WOOD WARBLERS

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Abstract.—Extant hypotheses predict that, in the face of sexual selection, avian song and plumage may evolve in a concerted fashion, in an antagonistic fashion, or in ways unrelated to each other. To test these ideas regarding which traits sexual selection targets, and the consequences for other traits, we analyzed patterns of song complexity and plumage dimorphism in 56 species of wood warblers (Parulinae). Overall, males of more dimorphic species sang shorter songs more often, but did not have more complex songs. However, when monomorphic species were excluded from the analysis, we found that the total time spent singing and repertoire size increased with plumage dimorphism. Monomorphic species are predominantly ground-nesters and the greater risk of nest predation for these species may constrain males from becoming more visually conspicuous. Thus, sexual selection may have been restricted to targeting song in these species. Even though song may have been the only target of sexual selection in ground-nesting species, overall, song in those species is not more complex than in species that nest above the ground. We propose that traits targeted by sexual selection evolve in concert, except when constrained by some ecological factor.

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In his theory of sexual selection, Darwin (1871) attributed the evolution of secondary sexual characters to the advantages they provide their bearers in the competition to mate. Although sexual selection is now widely accepted as the process underlying the evolution of sexual dimorphism, much remains at issue regarding the specific mechanisms involved in that process (Partridge and Harvey, 1986). Here we address the question of whether sexual selection is predictable in the trait(s) that it targets by analyzing patterns of sexual dimorphism in North American wood warblers (Parulinae).

A survey of avian taxa reveals not only great variation in degrees of sexual dimorphism, but also great variety in the features that have been targeted by sexual selection. In addition to the elaboration of nearly all aspects of plumage, one can also find examples of dimorphism in most other morphological traits. Behavioral traits have also been targeted by sexual selection, ranging from complex male song to elaborate courtship behaviors (Darwin, 1871; Searcy and Andersson, 1986). In short, virtually all traits that could have been targeted by sexual selection, have been, in most cases many times. Given that sexual selection has been rather catholic in the targets on which it has acted in birds, it is useful to ask whether there are patterns (and principles) regarding which traits are targeted and the extent to which they have been selected.

Kroodsma (1977) found that song complexity increased with the degree of polygyny in nine species of North American wrens (Troglodytidae). This result supports the general view that the elaboration of a secondary sexual trait should be proportional to the intensity of sexual selection (e.g., Wade and Arnold, 1980). Furthermore, these results suggest that, within a related group of species, sexual selection targets the same trait (e.g., song). If this pattern is general, we should expect that when more than one trait is targeted within a taxon (e.g., song and plumage), then both traits will be elaborated by sexual selection. Therefore, across members of the taxon, the degree of elaboration of the two traits will be positively correlated.

The traits sexual selection targets are not consistent between taxa, however. Catchpole (1980) found the opposite of what Kroodsma (1977) had reported for the relationship between song complexity and polygyny. In six species of *Acrocephalus* warblers, the two polygynous species sang shorter, less complex songs than their four monogamous counterparts (Catchpole, 1980). Subsequently, Catchpole and McGregor (1985) reported that, in five species of *Emberiza* buntings, the species with the least complex song was the only polygynous species and also exhibited the most pronounced size dimorphism. This result led Catchpole and McGregor (1985) to propose

that epigamic selection favors song development whereas male–male competition favors large size. Such a straightforward rule appears to have little generality, because both song and size can function in mate attraction and/or in male–male competition (Payne, 1984; Searcy and Andersson, 1986). However, the testable prediction from this hypothesis is that different secondary sexual traits should evolve in an uncorrelated fashion because different types of sexual selection are hypothesized to target different traits.

Another candidate for a general rule about the targets of sexual selection is the transfer hypothesis (Gilliard, 1956, 1969; Diamond, 1988). Prior to Gilliard's (1956) formalization of the hypothesis, Darwin (1871 p. 707) had stated:

"It is . . . remarkable that birds that sing well are rarely decorated with brilliant colours or other ornaments Hence bright colours and the power of song seem to replace each other. We can perceive that if the plumage did not vary in brightness, or if bright colours were dangerous to the species, other means would be employed to charm the females; and melody of voice offers one such means."

Among bowerbirds (Ptilorhynchidae), males of species that build the most ornate bowers have the least ornate plumage. Conversely, species that build simple bowers have more elaborate plumage. Gilliard (1956, 1969) proposed that, through the course of bowerbird evolution, female choice had gone from being based on male appearance to being based on the appearance of males' bowers. As a consequence, male plumage became less ornate as bowers became more so. If the transfer hypothesis has generality, one would predict an inverse relationship between the dimorphism in the character targeted by sexual selection and dimorphism in all other characters. For example, in taxa with elaborate song, plumage dimorphism should be relatively poorly developed.

In this paper, we examine the relationship between male song and sexual plumage dimorphism in North American wood warblers, to test the three hypotheses discussed above. If the degree of sexual dimorphism

in all traits is a straightforward consequence of the intensity of sexual selection, we predict a positive correlation between the development of song and plumage (i.e., both become better developed in the face of stronger sexual selection). If intersexual selection tends to target one trait for all members of a taxon, whereas intrasexual selection targets a different trait, then variation in either song or plumage can reflect the intensity of sexual selection, but there need not be a correlation between the development of the two. Finally, if the transfer hypothesis applies to wood warblers, then we should find a negative correlation between song complexity and plumage dimorphism. This negative relationship should hold regardless of the intensity of sexual selection. The fact that these opposing predictions can be supported from ideas extant in the literature points to the need for both theoretical and empirical treatment of this issue.

Fifty-seven species of wood warblers in 18 genera are found in North America. Although many parulines are known to hybridize (Bledsoe, 1988, and references therein), Avise et al. (1980) concluded that each of the 28 parulines they analyzed for enzyme polymorphism constituted "good" species.

Wood warblers are primarily insectivorous and most species occupy wooded habitat (Perrins and Middleton, 1985). Males are territorial (loose "coloniality" has been reported in few species [Harrison, 1984]), do not aid in incubation, but help feed and raise the young. Therefore, ecological factors should have less impact on our analysis than if we were comparing a more diverse group of species.

Although parulines are primarily monogamous, polygynous matings have been reported for 14 of 57 North American species (Ford, 1983; Petit et al., 1988). Only five of these species are known to mate polygynously with regularity (Ford, 1983). The degree of polygyny is one index of sexual selection intensity; thus we predicted that these species would exhibit the most complex songs, or the most dimorphic plumage, or both. Even the monogamous species, however, exhibit substantial variation in the development of male song and the extent of sexual plumage dimorphism. This variation

implies substantial variation in sexual selection. The bulk of our predictions focus on the patterns of coevolution of sexually selected traits, and these predictions do not require information regarding the intensity of sexual selection itself.

Our intention in this study is not to examine all possible factors that might influence the effect of sexual selection on various traits. However, predation seems one obvious factor to consider. As Darwin (1871) suggested in the quotation cited above, if bright colors become dangerous, sexual selection might be forced to target traits other than plumage. Wood warblers conveniently divide into species that nest on the ground and those that nest above ground. Because ground-nesting birds are subject to higher predator exposure than above-ground-nesting birds (Collias and Collias, 1984), and because the presence of a brightly colored male around the nest could increase the risk to the nest, we would expect ground-nesting species to be disproportionately monochromatic. In making this prediction, we assume that the female's plumage has been selected for its cryptic appearance and that any deviation from that appearance by males will make them more conspicuous.

MATERIALS AND METHODS

Plumage

E. H. Burt Jr. kindly provided data on plumage colors for 21 body regions for each sex of all paruline species. The percent of surface area of each of the body regions are given in Burt (1986 p. 113). Burt had assigned each body region to one of 14 colors. We calculated the percent body surface area where plumage color differed between the two sexes (hereafter PLUMAGE). This avoided problems with subjective estimates of how dimorphic two colors or shades are. However, as an alternative method we asked five panelists to assess sexual plumage dimorphism based on the whole bird rather than individual body regions. Panelists had neither seen Burt's plumage data, nor the song data. Panelists were asked to score sexual dimorphism of warblers on a one-to-five scale using illustrations in two field guides (Peterson, 1980; National Geographic Society, 1983). Monomorphic species

were not scored, nor were species where both sexes were not fully illustrated. To compare our objective dimorphism scores (based on Burt's data) with our panelists' subjective scores, we first arranged the objective data into five classes of equal range (0–0.17, . . . , 0.68–0.85). We then calculated Spearman rank correlations between the objective and subjective scores for each species.

Song

We assessed song complexity within the parulines using data accompanying Borror and Gunn's (1985) sound recordings. Borror and Gunn provided data for 56 species. For species with both an aggressive call and a mate attraction call (Borror and Gunn, 1985), we used both to characterize the species' song because both are assumed to be products of sexual selection and are therefore relevant to the premise of this study.

We used male weights (Dunning, 1984) as a variable so we could control for the possible constraints size exerts on song production (e.g., Wallschläger, 1980). Data were checked for normality, and intra- and intergeneric variation were calculated to assure that taxonomic artifacts did not produce misleading results (Ridley, 1983; Clutton-Brock and Harvey, 1984; Felsenstein, 1985).

The Yellow-breasted Chat (*Icteria virens*) was excluded because its taxonomic affinities are unclear (Avise et al., 1980; Ingold et al., 1988), and because song data for this species are both difficult to quantify and are unusual for parulines (e.g., repertoire). Data for the two subspecies of Yellow-rumped Warbler (*Dendroica coronata*) were averaged. All raw data for this analysis are given in the Appendix. The variables chosen (mnemonics used later are in block letters) were:

1) Song DURATION (sec). Where Borror and Gunn (1985) did not give a value, we measured the average song length of the sonagrams depicted in their booklet. Where Borror and Gunn gave a range, the middle of the range was used.

2) Repeat RATE (per min). These data were taken from Borror and Gunn (1985) where given, otherwise they were obtained from Robbins et al. (1966). Where a range was reported, the middle of that range was used. When both references provided data

TABLE 1. A comparison of the variance of variables within large genera with the variance between the mean values of the remaining genera.

Variable	Variance without <i>Vermivora</i> 14 ≤ N ≤ 16	Variance within <i>Vermivora</i> only N = 9	Variance without <i>Dendroica</i> 14 ≤ N ≤ 16	Variance within <i>Dendroica</i> only 12 ≤ N ≤ 22
DURATION	0.12	0.23	0.12	0.12
RATE	— ^a	— ^a	2.50	3.35
TIME SINGING	— ^a	— ^a	1.82	4.67 ^b
PHONES	5.86	0.53 ^b	5.86	1.23 ^b
REPertoire	1.44	0.11 ^b	1.46	0.38 ^b
MIN FREQ	0.77	0.62	0.77	2.04 ^b
MAX FREQ	1.25	1.25	1.25	1.64
FREQ RANGE	0.76	0.88	0.76	0.86
PLUMAGE	0.04	0.03	0.04	0.05

^a N = 5, too small for test.

^b Variances different at P < 0.05; F-test for comparing variances.

for a species, we used the values from Borror and Gunn (1985) because a larger sample of sound recordings had accumulated by the time their analysis was conducted. There were minor differences in the values reported by these two authorities for seven of eight species; these species are indicated in the Appendix.

3) Total TIME SINGING (sec per min). The product of 1) and 2).

4) Number of types of PHONES per song. As defined by Lemon et al. (1981, 1983), a phone is an individual continuous sound. An individual phone type was distinguished based on a subjective evaluation of the pictorial representation in the sonagrams in Borror and Gunn (1985), and the maximum number of phones per song was used.

5) REPERTOIRE. We accepted Borror and Gunn's (1985) assessment of the maximum number of different "songs" a bird could sing. A "song" was defined as a distinct order of phones. One song type included all of AAAAB, AAABB, AABBB, etc., where each letter represents a distinct phone type. For a few species, a repertoire of phones rather than songs was given by Borror and Gunn. Presumably, a bird could interchange these phones in all possible permutations (e.g., 2 different phones per song; 5 different phones in "repertoire," $5 \times 4 = 20$ possible songs). In practice, a bird probably uses far fewer songs, but we have no data for this. We have estimated these repertoire sizes based on the brief discussion in Borror and Gunn (1985); these species are indicated in the Appendix. There are many problems with repertoire estimation

(Kroodsma, 1982), but we assumed that Borror and Gunn (1985) used consistent criteria.

6) and 7) MINimum and MAXimum FREQ (kHz). These values were based on the most extreme values given by Borror and Gunn (1985).

8) FREQUENCY RANGE. The difference between 6) and 7).

Mating System and Trait Elaboration

We compared plumage and song variables between species for which polygynous matings have been reported (Ford, 1983) and monogamous species.

Nest Height

We used information in Harrison (1978) to separate warblers into ground-nesting and above-ground-nesting species.

RESULTS

Plumage

Our five panelists showed considerable agreement in how they scored plumage dimorphism, particularly when using the same field guide. Spearman rank correlations between individual panelists' scores and the mean panelist score ranged from 0.77 to 0.93 within field guides ($N = 31$ for the National Geographic Society Guide; $N = 26$ for the Peterson Guide; all P 's < 0.01) and from 0.33 to 0.64 between field guides ($N = 21$, all P 's < 0.05). The mean panelist scores from the National Geographic Society Guide and the Peterson Guide were significantly correlated with our objective

dimorphism scores calculated using Burt's feather data ($r_s = 0.49$ and 0.55 , $P < 0.05$ and 0.01 , respectively). Because the subjective assessments of dimorphism based on overall appearance were significantly correlated with our objective scores, we use our scores (i.e., PLUMAGE) in all our analyses.

Song

To assess the accuracy and repeatability of our song measures, we compared DURATION, TIME SINGING, PHONES, and REPERTOIRE with the equivalent variables given by Weary and Lemon (1988). Weary and Lemon (1988) used a sample of 19 warblers, which are a subset of the Borror and Gunn (1985) data set. The only variable in our data set that was not significantly correlated with that of their data set was TIME ($r_s = 0.29$, $P = 0.11$; for the other variables, all r_s 's ≥ 0.52 , all P 's ≤ 0.01). Thus, in general our assessments were similar to those of Weary and Lemon (1988).

In comparative studies it is appropriate to use species values as long as the variation within genera is as great as that between genera (Ridley, 1983). Only the genera *Vermivora* ($N = 9$) and *Dendroica* ($N = 22$) were large enough to allow tests of intra- versus inter-generic variation. Only *Dendroica* had enough species with data to test for variation in RATE and TIME SINGING (12 *Dendroica* species with data versus 14 genera).

Of the eight song variables, four (TIME SINGING, PHONES, REPERTOIRE, MIN FREQ) varied significantly more between genera than within genera (Table 1), so analysis of these variables was done at the generic level (i.e., using mean values for each genus). Species values were used for the analysis of the other four song variables. PLUMAGE scores varied as much within as between genera (Table 1), so analyses could be done at either the specific or the generic level.

We wished to determine the correlation between PLUMAGE and each of the individual song variables. This first required determining whether each variable was normally distributed. PHONES, REPERTOIRE, and MIN FREQ were not normally distributed (Kolmogorov-Smirnov Goodness of Fit Test, all P 's < 0.01). Because

weight was also used in this analysis we tested it and found it not to be normally distributed ($P < 0.05$). Because the three song variables and weight could not be easily transformed (see also Read and Weary, 1990), we calculated Spearman rank correlations for these variables.

We found significant correlations between PLUMAGE and some song variables (Table 2). More dimorphic species sang shorter songs but sang at a higher rate, and their songs had both higher minimum and maximum frequencies. However, many of the variables that we intuitively expect to be products of sexual selection (e.g., TIME SINGING, PHONES, REPERTOIRE, FREQ RANGE) were not significantly correlated with plumage dimorphism.

We then retested the hypotheses using only the dimorphic warblers. This analysis revealed a correlation between REPERTOIRE and PLUMAGE ($r_s = 0.32$, $P = 0.02$). Furthermore the correlation between PLUMAGE and TIME SINGING became significant ($r_s = 0.31$, $P = 0.05$, $N = 30$) among dimorphic species. The remaining correlations between PLUMAGE and the song variables were consistent with those from the larger sample. However, aspects of song complexity (TIME SINGING, FREQ RANGE, PHONES, and REPERTOIRE) did not differ between monochromatic and dichromatic species (t -tests, all P 's > 0.05). Thus, when sexual selection only targeted song, it did not produce greater elaboration of that trait.

Because of the correlations among the non-PLUMAGE variables (Table 2), we used factor analysis (Kleinbaum and Kupper, 1978) to reduce the number of variables. The factor analysis did not include the 20 species with incomplete data sets. Thus, 8 of 15 sexually monochromatic species and 12 of 41 dichromatic species were excluded. We performed the analysis twice, using species values and generic values. Because the two results were similar, we only present the results of the former analysis here. Because FREQ RANGE and TIME SINGING are linear combinations of other variables, it was necessary to discard these two variables from the factor analysis.

Three factors were extracted, which together explained 72% of the variation in the

TABLE 2. Correlation matrix for each of the variables used in the analysis of the song and plumage. Variables for which correlations were calculated at the generic level are indicated. Maximum sample sizes for each variable are given in parentheses. Variables are defined in the text.

(Maximum <i>N</i>)	DURATION (56)	RATE (40)	TIME SINGING ¹ (15)	PHONES ^{1,2} (17)	REPERTOIRE ^{1,2} (17)	MIN FREQ ^{1,2} (17)
DURATION	—	-0.55**	0.52**	-0.07	-0.44	0.11
RATE		—	0.44*	0.10	0.36	0.14
TIME SINGING ¹			—	-0.11	-0.18	0.24
PHONES ^{1,2}				—	0.28	-0.14
REPERTOIRE ^{1,2}					—	0.15
MIN FREQ ^{1,2}						—
MAX FREQ						
FREQ RANGE						
Weight ²						
PLUMAGE						

Values significantly different from 0 (two tailed *t*-test) are indicated; * $P \leq 0.05$; ** $P \leq 0.01$.

¹ Correlations computed at the generic level.

² Variables for which Spearman rank correlations were used.

song data. Each factor can be readily interpreted based on the factor loadings of each variable (Table 3). Factor 1 reflects the sound frequency of songs. Factor 2 reflects the length of individual songs and how often they were sung, and Factor 3 represents the internal complexity of songs. The correlations between PLUMAGE and the first two factors (Figs. 1, 2) confirmed the results of the correlation analysis; more dimorphic species had songs with higher minimum and maximum frequencies, and sang shorter songs at a higher rate. However, they did not sing more complex songs in terms of PHONES or REPERTOIRE (Fig. 3).

Mating System and Trait Elaboration

We predicted that species with a higher frequency of polygyny would have the most developed sexually selected traits. The only trait for which the two groups differed was PHONES (Mann-Whitney $Z = -1.96$, $P =$

0.05), but it was the monogamous species that had the most PHONES, which is contrary to the prediction. When only the five regularly polygynous species were included in the comparison, no differences in song or plumage variables were detected.

Nesting Height

We predicted that the greater predation risk faced by warblers nesting on the ground would restrict the degree to which plumage dimorphism would develop due to sexual selection. Consistent with this prediction, ground-nesting species were significantly less dimorphic ($N = 21$, mean ± 1 SD dimorphism = $20 \pm 12\%$) than species nesting above ground ($N = 27$, mean ± 1 SD dimorphism = $34 \pm 24\%$; Mann-Whitney U Test, $Z = -3.58$, $P < 0.001$). At the generic level, the degree of dichromatism also increased with increasing mean nest height ($r_s = 0.67$, $P = 0.004$, $N = 14$).

The transfer hypothesis predicts that ground-nesting species should have more elaborate song because they are constrained in the evolution of bright plumage. However, ground-nesting species were not superior to above-ground-nesters for any song variables (*t*-tests, all P 's > 0.05) except DURATION ($t = 2.28$, $P = 0.03$).

DISCUSSION

Our analysis of plumage dimorphism and song in wood warblers revealed several relationships between the two features. Overall, males of more dimorphic species sang songs with higher minimum and maximum

TABLE 3. Factor loadings of the song variables following varimax rotation (Kleinbaum and Kupper, 1978) using all complete data records ($N = 36$) for all variables.

Variable ¹	Factor 1	Factor 2	Factor 3
DURATION	0.19	0.86	-0.05
RATE	0.14	-0.81	0.10
PHONES	0.01	-0.04	0.92
REPERTOIRE	-0.11	-0.29	0.84
MIN FREQ	0.90	-0.13	-0.09
MAX FREQ	0.93	0.04	-0.01
Weight	-0.09	0.48	-0.15

¹ Variables are defined in the text.

TABLE 2. Extended.

MAX FREQ (56)	FREQ RANGE (56)	Weight ² (56)	PLUMAGE (50)
0.09	0.16	0.05	-0.34**
0.14	0.05	-0.08	0.50**
0.18	0.19	-0.09	0.11
-0.03	-0.10	-0.24	-0.04
-0.20	-0.17	-0.24*	-0.16
0.64**	-0.01	-0.39*	0.39*
-	0.46**	0.07	0.33**
-	-	0.15	-0.03
-	-	-	-0.02

frequencies and sang shorter songs more often, but did not have more complex songs. However, when we restricted the analysis to dimorphic species, we found that repertoire size and time spent singing were positively correlated with the degree of plumage dimorphism.

Polygynous species showed no greater elaboration of song or plumage than monogamous species. A species' mating system should provide a good index of sexual selection intensity. However, few of the warbler species in our analysis have been studied in sufficient detail to determine the degree of polygyny in their mating systems. Without detailed knowledge of the mating system, it is not possible to estimate sexual selection intensity accurately (Payne, 1984; Weatherhead and Shutler, 1989). Thus, this part of the analysis should be considered preliminary.

Paradoxically, our results provide some support for both of the two diametrically opposed hypotheses we were testing. If sexual selection has targeted more than one trait in a taxon, we predicted that those traits should evolve in concert. Thus, if sexual selection favored more complex song, it should also favor more dimorphic plumage. The positive correlations between song rate, the amount of time spent singing, and repertoire size, and the degree of plumage dimorphism for dimorphic species is consistent with this hypothesis. However, the transfer hypothesis, which predicted a negative relationship between targets of sexual selection, was supported by the difference between ground-nesting species and those

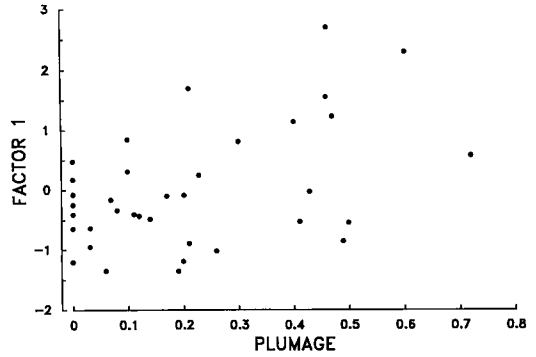


FIG. 1. The correlation between PLUMAGE and Factor 1 (sound frequency of songs) ($r_s = 0.33$, $P = 0.02$, $N = 36$).

nesting above ground. The data were consistent with the interpretation that, due to higher predation pressure on ground-nesting species, sexual selection is constrained from targeting plumage. This has resulted in little plumage dimorphism being observed among those species, presumably making song the single target of sexual selection. More complete support to the transfer hypothesis would be provided if the extent of song complexity among ground-nesting warblers is positively correlated with the intensity of sexual selection.

Other attempts to find general principles governing how sexual selection targets different traits have been sought. As mentioned previously, Catchpole and McGregor (1985) found that the one polygynous species among five species of buntings had the least complex song, but the greatest size

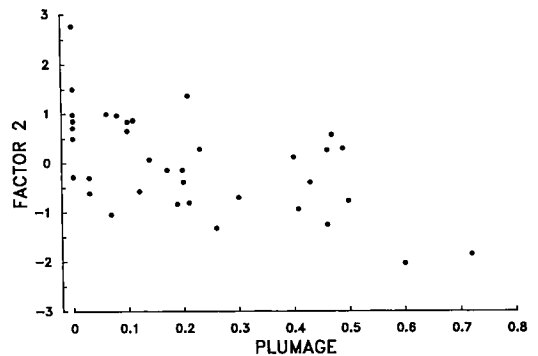


FIG. 2. The correlation between PLUMAGE and Factor 2 (song length and repeat rate of songs) ($r_s = -0.56$, $P < 0.001$, $N = 36$).

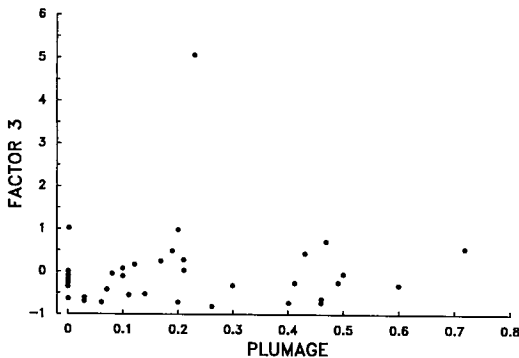


FIG. 3. The correlation between PLUMAGE and Factor 3 (song complexity) ($r_s = 0.06$, $P = 0.36$, $N = 36$). The outlier is the Canada Warbler.

dimorphism. This observation led to the proposal that epigamic and intrasexual components of sexual selection target different traits. Our results suggest that song and plumage can evolve in concert and two reviews (Payne, 1984; Searcy and Anderson, 1986) suggest that song, size, and plumage can be involved in inter- and intrasexual competition. It seems that principles derived from small numbers of species may have less likelihood of generality.

We purposely restricted our analysis to song and plumage in warblers because these are the most obvious targets of sexual selection in this group. However, sexual size dimorphism is very pronounced in some groups of birds and therefore an important target of sexual selection in some circumstances. We also only considered one possible ecological constraint on sexual selection, although there are almost certainly others that are important. While we have demonstrated how two targets of sexual selection coevolve in the face of one constraint, a comprehensive theory must consider all major targets of sexual selection and all the ecological factors that may constrain the extent to which sexual selection can act on those targets.

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APPENDIX

Raw data for each species for all variables used in the analysis of Borror and Gunn's (1985) data. Nomenclature follows the American Ornithologists' Union (1983). Weights are for males where values for both sexes were reported by Dunning (1984).

Common name, Species name	DURA-TION	RATE	TIME SINGING	PHONES	REPER-TOIRE	MIN FREQ	MAX FREQ	FREQ RANGE	PLUMAGE	Weight
Bachman's Warbler, <i>Vermivora bachmanii</i>	1.75	—	—	2	1	5	8	3	0.36	—
Blue-winged Warbler, <i>V. pinus</i>	1.4	7	9.8	3	1	4	9	5	0.30	8.4
Golden-winged Warbler, <i>V. chrysoptera</i>	1.2	8	9.6	2	1	5	10	5	0.46	8.7
Tennessee Warbler, <i>V. peregrina</i>	2.75	8 ¹	22	3	1	3	9	6	0.10	10.2
Orange-crowned Warbler, <i>V. celata</i>	1.3	—	—	2	1	3.5	7	3.5	0.18	9.0
Nashville Warbler, <i>V. ruficapilla</i>	2	5	10	3	1	3.5	8	4.5	0.10	8.9
Virginia's Warbler, <i>V. virginiae</i>	2	3.5	7	3	1	3	7	4	0.08	7.8
Colima Warbler, <i>V. crissalis</i>	1.5	—	—	1	1	3.5	7	3.5	0	9.7
Lucy's Warbler, <i>V. luciae</i>	1.75	—	—	3	22	3	7	4	0	6.6
Parula Warbler, <i>Parula americana</i>	1.4	6.5	9.10	3	2	3	7	4	0.11	8.6
Tropical Parula, <i>P. pitayumi</i>	1.4	—	—	3	2	3	7.5	4.5	0.06	7.2
Yellow Warbler, <i>Dendroica petechia</i>	1.3	6 ¹	7.8	4	3	3	8	5	0.20	9.8
Chestnut-sided Warbler, <i>D. pensylvanica</i>	1.4	6.5	9.1	4	2	3	8	5	0.43	9.8
Magnolia Warbler, <i>D. magnaolia</i>	1	6.5	6.5	4	1	3	7	4	0.41	8.9
Cape May Warbler, <i>D. tigrina</i>	1	10	10	2	2	7	10	3	0.60	11.0
Black-throated Blue Warbler, <i>D. caerulescens</i>	1.3	—	—	2	1	3	6	3	0.77	10.5
Yellow-rumped Warbler, <i>D. coronata</i>	1.6	9	14.4	2.5	2	2.75	6.75	4	0.50	12.6
Black-throated Gray Warbler, <i>D. nigrescens</i>	1.4	—	—	4	2	3	6	3	0.19	8.8
Townsend's Warbler, <i>D. townsendii</i>	1.3	—	—	3	2	4	8	4	0.24	9.1
Hermit Warbler, <i>D. occidentalis</i>	1.6	—	—	3	2	3.5	8	4.5	0.48	9.5
Black-throated Green Warbler, <i>D. virens</i>	1.4	5	7	3	2	3.5	7.5	4	0.17	8.8
Golden-cheeked Warbler, <i>D. chrysoparia</i>	1.8	—	—	4	2	3	8	5	0.50	10.2
Blackburnian Warbler, <i>D. fusca</i>	1.8	5	9	4	2	4	10	6	0.47	10.0
Yellow-throated Warbler, <i>D. dominica</i>	2.2	5	11	2	1	3	7	4	0	9.4
Grace's Warbler, <i>D. graciae</i>	1.75	—	—	2	22	3	7	4	0.24	8.1
Pine Warbler, <i>D. pinus</i>	1.8	5.5	9.9	1	2	3	6	3	0.49	11.9
Kirtland's Warbler, <i>D. kirtlandii</i>	1.1	7.5	8.25	3	3	2	6	4	0.19	13.8
Prairie Warbler, <i>D. discolor</i>	2.0	3.5 ¹	7	1	1	3	7	4	0.11	8.0
Palm Warbler, <i>D. palmarum</i>	1.5	—	—	1	1	3	8	5	0	10.3
Bay-breasted Warbler, <i>D. castanea</i>	0.9	—	—	2	1	5	9	4	0.29	13.1
Blackpoll Warbler, <i>D. striata</i>	1.75	5.5	9.63	1	1	8	10	2	0.46	13.0
Cerulean Warbler, <i>D. cerulea</i>	1.4	—	—	3	2	3	8	5	0.82	9.5
Black-and-white Warbler, <i>Mniotilta varia</i>	2.3	4	9.2	3	1	6	9	3	0.21	11.0
American Redstart, <i>Setophaga ruticilla</i>	1.05	9.5	9.98	3	3	3.5	9	5.5	0.72	8.5
Prothonotary Warbler, <i>Protonotaria citrea</i>	1.7	7	11.9	1	1	4	10	6	0.40	15.0
Worm-eating Warbler, <i>Helminthos vermivora</i>	1.9	5	9.5	1	1	3.5	8	4.5	0	13
Swainson's Warbler, <i>Limnothlypis swainsonii</i>	1.5	6.5	9.75	4	1	3	8	5	0	18.9

APPENDIX. Continued.

Common name, Species name	DURA-TION	RATE	TIME SINGING	PHONES	REPERTOIRE	MIN FREQ	MAX FREQ	FREQ RANGE	PLUMAGE	Weight
Ovenbird, <i>Seiurus aurocapillus</i>	2.75	3.3	8.98	1	1	3	9	6	0	19.4
Northern Waterthrush, <i>S. moveboracensis</i>	1.75	5.5	9.63	4	1	2.5	7	4.5	0	17.8
Louisiana Waterthrush, <i>S. motacilla</i>	2	5.31	10.6	3	1	2	8	6	0	19.8
Kentucky Warbler, <i>Oporornis formosus</i>	1.7	3.51	5.95	1	1	2	6	4	0.06	14.3
Connecticut Warbler, <i>O. agilis</i>	1.2	6	7.2	2	1	2	6.5	4.5	0.20	15.2
Mourning Warbler, <i>O. philadelphia</i>	1.2	61	7.2	2	1	2	7	5	0.03	13.0
MacGillivray's Warbler, <i>O. tolmiei</i>	1.4	71	9.8	2	1	2.5	7	4.5	0.03	10.4
Common Yellowthroat, <i>Geothlypis trichas</i>	1.5	5	7.5	2	1	3	7	4	0.14	10.3
Gray-crowned Yellowthroat, <i>G. poliocephala</i>	2.5	6	15	10	1	2.5	6.5	4	0.15	—
Hooded Warbler, <i>Wilsonia citrina</i>	1.13	7	7.91	4	2	2.5	6.5	4	0.21	10.8
Wilson's Warbler, <i>W. pusilla</i>	1.3	7.5	9.75	3	1	3	7.5	4.5	0.07	7.3
Canada Warbler, <i>W. canadensis</i>	1.5	7	10.5	16	52	3	8	5	0.23	10.6
Red-faced Warbler, <i>Cardellina rubrifrons</i>	1.75	—	—	10	42	3	7.5	4.5	0	9.8
Painted Redstart, <i>Myioborus pictus</i>	1.75	6	10.5	2	42	3	5	2	0	7.9
Slate-throated Warbler, <i>M. miniatus</i>	1.6	5	8.75	3	52	3	6.5	3.5	0	—
Fan-tailed Warbler, <i>Euthlyis lachrymosa</i>	1.45	—	—	3	1	3	7	4	0	—
Golden-crowned Warbler, <i>Basileuterus culicivorus</i>	2	7.5	10.88	3	1	2.5	6	3.5	0	—
Rufous-capped Warbler, <i>B. rufifrons</i>	2	7	14	5	52	3.5	8	4.5	0	—
Olive Warbler, <i>Peucedramus taeniatus</i>	1.25	9	11.25	2	1	2.5	6	3.5	0.26	11.0

¹ The value shown for Borror and Gunn (1985) differs from that of Robbins et al. (1966).

² A repertoire was not given by Borror and Gunn (1985), so REPERTOIRE was estimated from PHONES and the discussion in Borror and Gunn (1985).