

Sexual size dimorphism and timing of spring migration in birds

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Keywords:

migration;
natural selection;
passerine birds;
sexual selection;
sexual size dimorphism.

Abstract

Sexually selected traits are limited by selection against those traits in other fitness components, such as survival. Thus, sexual selection favouring large size in males should be balanced by higher mortality of larger males. However, evidence from red-winged blackbirds (*Agelaius phoeniceus*) indicates that large males survive better than small males. A survival advantage to large size could result from males migrating north in early spring, when harsh weather favours large size for energetic reasons. From this hypothesis we predicted that, among species, sex differences in body size should be correlated with sex differences in timing of spring migration. The earlier males migrate relative to females, the larger they should be relative to females. We tested this prediction using a comparative analysis of data collected from 30 species of passerine birds captured on migration. After controlling for social mating system, we found that sexual size dimorphism and difference in arrival dates of males and females were significantly positively correlated. This result is consistent with the hypothesis that selection for survival ability promotes sexual size dimorphism (SSD), rather than opposes SSD as is the conventional view. If both natural selection and sexual selection favour large adult males, then limits to male size must be imposed before males become adults.

Introduction

Darwin (1871) recognized that among birds and mammals, males are typically larger than females, and that the extent of that sexual size dimorphism (SSD) is related to the species' mating system. As competition to mate increases, and the reproductive rewards for success in mating competition become greater, SSD increases. Darwin proposed that large body size helps males win fights with other males over access to females. Although extensive research has supported Darwin's sexual selection hypothesis for SSD, it is also the case that substantial variation in SSD across species is unaccounted for by

variation in mating systems (Andersson, 1994). Here we examine the hypothesis that selection for survival of migratory passerine birds in harsh spring weather conditions favours large males, and thus promotes SSD (Weatherhead & Clark, 1994).

Sexual selection theory generally assumes that the mating advantage of a sexually selected trait is balanced by a survival disadvantage (Selander, 1965). Thus, a mating advantage associated with large body size in males should be balanced by higher mortality of large males. In apparent support of this prediction, comparative analyses of birds have shown that male mortality increases relative to that of females as SSD increases (Searcy & Yasukawa, 1981; Promislow *et al.*, 1992). However, Weatherhead & Clark (1994) pointed out that just because the collective mortality of males is higher than that of females in more dimorphic species, it does not necessarily follow that large size is detrimental to individual male survival. Higher male mortality could be a consequence of some male attribute other than large size that is associated with more intense sexual selection. In fact, it is possible to have

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higher male mortality relative to female mortality associated with SSD, and actually have a survival advantage of large size in males (Weatherhead & Clark, 1994).

Weatherhead & Clark (1994) based their argument on data they presented on size and mortality in red-winged blackbirds (*Agelaius phoeniceus*), a socially polygynous species with pronounced SSD. Consistent with an earlier study (Weatherhead *et al.*, 1987), they found that larger males had higher survival between years, contrary to the prediction from theory that natural selection should favour smaller males. They proposed that mortality patterns in male red-winged blackbirds could be explained by their behaviour in spring. Males migrate back to the breeding grounds well in advance of females, presumably to compete for territories. Weatherhead & Clark (1994) argued that harsh weather conditions when males first return to their breeding grounds are likely to expose males to pronounced energetic stress resulting in mortality. Because females are in more benign southern climes at that time, they do not confront similar stress, so overall mortality is higher for males than females at this time. However, among males, larger individuals cope better with energetic stress than smaller individuals, explaining why larger males survive better. If this explanation is correct, then natural selection actually promotes large size in adult male red-winged blackbirds, rather than opposes large size as is conventionally theorized (Selander, 1965).

The assumptions on which Weatherhead & Clark's (1994) hypothesis is based seem sound. Larger males should be able to out-compete smaller males for food (e.g. Fretwell, 1969; Searcy, 1979; Eckert & Weatherhead, 1987a), and the smaller surface area to volume ratios of larger males should increase their heat retention and metabolic efficiency (Kendeigh, 1944). It is generally assumed that there are energetic costs associated with early migration (e.g. Kokko, 1999), and the importance of body size to surviving energetic stress is well established. Bergmann's rule, which states that larger individuals of a species are found in cooler climates, is well supported empirically, in particular by evidence that larger individuals within species winter farther north (Ketterson & Nolan, 1976). Thus, large size should also confer an advantage during cold weather on the breeding grounds. Our general goal in this study is to determine whether Weatherhead & Clark's (1994) hypothesis applies to migratory passerines generally.

Following Weatherhead & Clark (1994), we hypothesized that the earlier males migrate in the spring relative to females, the stronger selection should be for large size in males. Therefore, we predicted that among species, SSD should be positively correlated with the difference in migration dates of males and females.

Materials and methods

To test the prediction that SSD should be more pronounced in species in which differences in the

migration dates of the sexes are more pronounced, we used data on the timing of spring migration for 30 passerine species. We used data from Long Point Bird Observatory (42°33'N, 80°10'W) on the north shore of Lake Erie, Ontario, Canada. Birds were captured at Long Point during daily banding operations from mid-April to mid-June of 1960 through 1996. Details of capture methods can be found in Hussell (1981, 1982). We selected 30 species for analysis that had adequate sample sizes and could be sexed accurately by plumage characteristics (Pyle, 1997). The number of years of data used for each species ranged from 17 to 37 years. To calculate the difference in migration dates between the sexes for a given species, we first determined the mean capture date for each sex each year. We then calculated the overall mean capture date within sexes across years. We used the difference between the overall mean capture dates of the sexes (male minus female) as the sex difference in migration date for that species.

We used wing chord as our measure of body size. Wing chord measurements came from the same birds used to determine migration dates. We used the index suggested by Lovich & Gibbons (1992) to estimate SSD for each species. Mean wing chord of the larger sex was divided by mean wing chord of the smaller sex and the difference between this value and 1 was used as the sexual size dimorphism index (SSDI). Because males were larger than females for all species, the SSDI was always positive. This method overcomes many of the statistical problems associated with using ratios as an index of SSD (e.g. improper scaling, asymmetry around a central value) (see Lovich & Gibbons, 1992).

Several variables could have confounded our analysis of migration dates of the sexes relative to SSD. First, because polygynous species tend to be more sexually size dimorphic than monogamous species (e.g. Selander, 1972; Webster, 1992), we only included species classified as socially monogamous by Ehrlich *et al.* (1988). Although this step does not eliminate all the contribution of sexual selection to SSD, it should remove a substantial component of that contribution. For example, Webster (1992) found that variation in social mating system accounted for 72% of the variation in size dimorphism in New World blackbirds.

A second potentially important factor is migration distance. Sex differences in migration dates within species could be affected by differences in migration distance among species. Such a relationship could contribute to the predicted relationship between SSD and sex differences in migration – e.g. migrating further might promote sex differences in migration dates, and thereby promote SSD. Alternatively, migration distance could be correlated with some other factor that could also be related to SSD (e.g. body size), thereby confounding the relationship between SSD and sex differences in migration. Therefore, we conducted analyses both controlling for, and not controlling for migration distance. To

estimate migration distance for a species, we estimated the latitude of the centre of its complete wintering range and of the centre of its breeding range in Canada using range maps in DeGraaf & Rappole (1995) and National Geographic Society (1987). We restricted the breeding range to Canada because we assumed that birds caught on spring migration at the Long Point Observatory were going to breed in Canada. We calculated migration distance as the difference in latitude between these wintering and breeding midpoints measured from digital maps of North and South America using a geographical information system (GIS). The difference in timing of arrival between the sexes was negatively correlated with migration distance ($R^2 = 0.15$, $t = -2.26$, $P = 0.03$), so in analyses in which we controlled for migration distance we used residuals from this regression (hereafter 'corrected difference in migration date').

Phylogenetic relatedness also poses a potential problem for interspecific studies because closely related species may share a certain character state (e.g. SSD) through common ancestry rather than through independent evolution (Felsenstein, 1985; Harvey & Pagel, 1991; Ricklefs & Stark, 1996). Therefore, we conducted our central analysis with and without controlling for phylogenetic effects. To control for phylogenetic effects, we used Purvis & Rambaut's (1995) program that employs the independent contrasts method outlined by Felsenstein (1985) and modified by Harvey & Pagel

(1991). This method calculates differences (contrast scores) in the values of a trait between nodes and between adjacent pairs of taxa in a phylogeny. One then assesses whether contrast scores of the dependent variable are related to those of the independent variable. Purvis & Rambaut's (1995) program arbitrarily sets contrast scores for the independent variable as positive. Consequently, a positive score for the dependent variable indicates a positive relationship between the independent and dependent variables. Because the taxa that are compared do not share the same branch in the phylogeny, contrast scores are statistically independent of one another, and thus they can be analysed using standard regression techniques forcing the regression through the origin (Pagel & Harvey, 1988).

To construct the phylogeny, we used Sibley & Ahlquist (1990) to resolve the relationships between more distantly related taxa (*Carduelis*, *Pipilo*, *Tyrannus*), and several other sources to resolve relationships between more closely related taxa (Martin & Clobert, 1996: *Dendroica* spp., *Mniotilta*, *Piranga*, *Pheucticus*, *Poliophtila*, *Regulus* spp., *Setophaga*, *Vermivora* spp., *Wilsonia* spp.; Freeman & Zink, 1995: *Icterus* spp., *Euphagus*; Yezerinac & Weatherhead, 1995: *Icteria*, *Pheucticus*, *Piranga*; Avise *et al.*, 1980: *Dendroica* spp., *Mniotilta*, *Setophaga*, *Vermivora* spp., *Wilsonia* spp.). Computer programs provided by Purvis & Rambaut (1995) and Page (1997) were used to draw the dendrogram (Fig. 1).

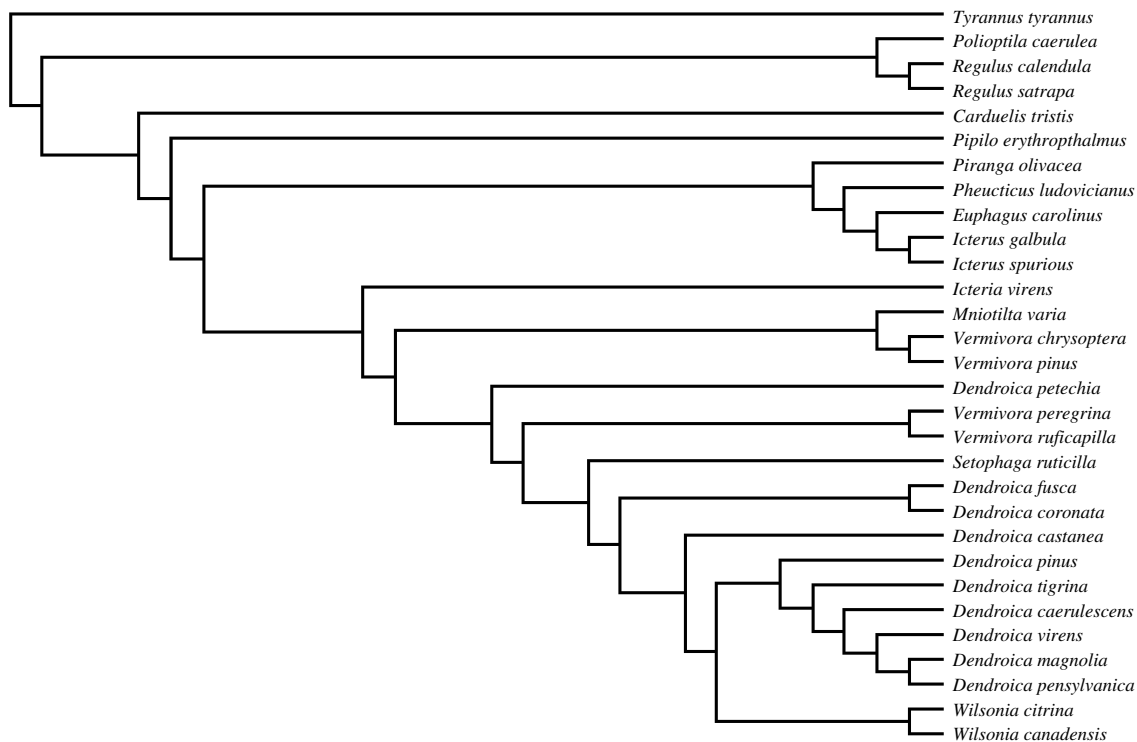


Fig. 1 Phylogeny used to generate independent contrasts.

Because we used several sources to construct the phylogeny, and those sources used different molecular techniques to establish ancestry, we did not have information on units of expected change among taxa in the phylogeny (i.e. branch lengths). We performed our analyses using two different assumptions regarding branch lengths. First, we set all branch lengths as equal. Secondly, we set branch lengths proportional to the number of species radiating from them (see Grafen, 1992; Purvis & Rambaut, 1995). This latter method weights contrast scores and provides a gradual model of evolution. Qualitatively, all our results were the same (i.e. significance and direction of relation) using the two different assumptions. Because Purvis *et al.* (1994) found that estimating branch lengths relative to the number of species tended to inflate error rates, whereas using equal branch lengths did not, we only present the results obtained using equal branch lengths.

For all regressions, we checked that contrasts were adequately standardized by verifying that there were no correlations between the absolute magnitude of the contrasts and the standard deviations of the contrasts (all $P > 0.11$) (see Garland *et al.*, 1992; Purvis & Rambaut, 1995). Regressions were performed using Statistica (StatSoft, 1993) and SAS (1996) software.

Results

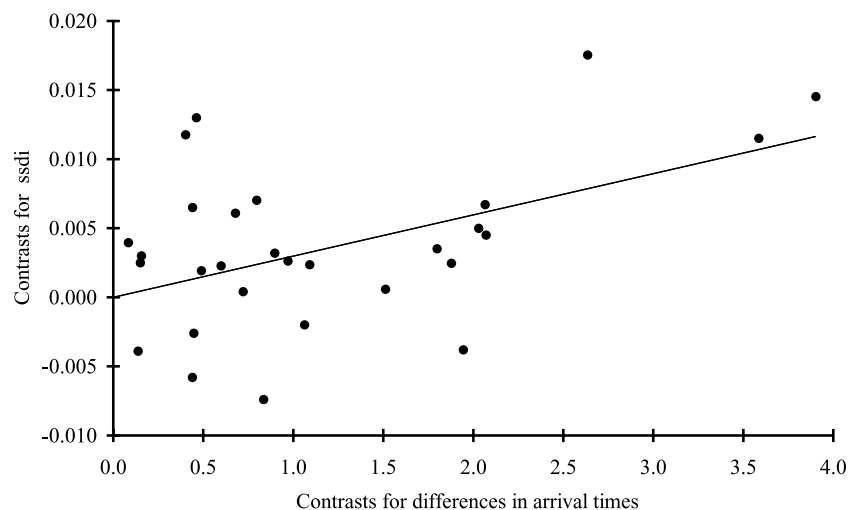
Among the 30 species, SSDI values ranged from 0.021 to 0.073 and differences in overall mean capture dates between the sexes ranged from 0.5 to 12.7 days (Appendix 1). Without controlling for phylogeny, we found that, as predicted, when SSDI was larger the greater the difference in arrival times between males and females ($R^2 = 0.26$, $t = 3.10$, $n = 30$, $P = 0.004$). To control for phylogeny we generated 29 contrast scores for SSDI and the difference in arrival date and repeated

the preceding analysis. Again as predicted, species in which males arrive earlier than females are more sexually size dimorphic than those species in which males arrive more synchronously with females ($R^2 = 0.48$, $t = 5.10$, $n = 29$, $P < 0.0001$, Fig. 2). Given the similarity of these results, hereafter we only present analyses in which we controlled for phylogeny.

It is possible that the three highest contrast scores (see Fig. 2) accounted for the positive relationship between SSDI and differences in arrival time. We repeated this analysis excluding the three contrasts with high values for both SSDI and differences in arrival time and the regression remained significant ($R^2 = 0.17$, $t = 2.27$, $n = 26$, $P = 0.03$), so the overall result was not simply a function of these three values.

Migration distance did appear to have the potential to affect our results. In addition to the correlation between migration distance and the difference in timing of arrival between the sexes reported above, the further that species migrated, the later males arrived in the spring ($R^2 = 0.50$, $t = 5.25$, $n = 30$, $P = 0.0001$). However, controlling for migration distance had little effect on the relationship between SSDI and sex differences in arrival date ($R^2 = 0.44$, $t = 4.69$, $n = 29$, $P < 0.0001$). To assess whether having a more northern breeding range (and thus harsher spring weather) might affect the relationship between SSDI and sex differences in arrival date, we repeated the analysis including the midpoint of each species' breeding latitude in Canada as a variable. Breeding latitude did not contribute significantly to the analysis ($t = 0.71$, $n = 29$, $P = 0.49$). Hereafter we only present analyses in which migration distance was not controlled, except where doing so qualitatively altered our results, and we do not consider breeding latitude as a separate variable any further.

We examined whether absolute arrival times of males explained more variation in SSDI than did sex differences



in arrival times. We found that contrasts for mean male arrival date were significantly negatively associated with contrasts for SSDI ($R^2 = 0.22$, $t = -2.78$, $n = 29$, $P = 0.01$), indicating that species in which males arrived later were less dimorphic. Although this result also supports our hypothesis, male arrival date explained less variation in SSDI than sex differences in arrival date (22 vs. 48%).

Our hypothesis that sex differences in timing of migration explains variation in SSD relies on the assumption that large size in males is advantageous early on the breeding grounds. We found no evidence that males of species that arrived earlier on the breeding grounds were larger than males of species that arrived later ($R^2 = 0.03$, $t = -0.89$, $n = 29$, $P = 0.38$). However, when we controlled arrival date for migration distance by using residuals from the regression of arrival date on migration distance ('corrected male arrival'), we found a significant negative association between contrasts for mean male size and corrected male arrival ($R^2 = 0.23$, $t = -2.87$, $n = 29$, $P = 0.008$, Fig. 3). Thus, controlling for migration distance, males of species that arrived earlier were larger.

Our analyses included taxa that are quite distantly related. To determine whether the relationship between SSDI and sex differences in arrival time occurred within a more closely related group, we repeated our central analysis using data only from warblers, the most speciose group in our sample (19 species). Although the relationship between contrast scores for SSDI and sex differences in arrival time was positive, it was not significant ($R^2 = 0.16$, $t = 1.81$, $n = 18$, $P = 0.087$). If we control for migration distance, the relationship becomes significant ($R^2 = 0.24$, $t = 2.29$, $n = 18$, $P = 0.04$). Thus, the relationship between SSDI and sex differences in arrival appears to hold, albeit weakly, within taxonomic groups.

Finally, if selection favours large size on the breeding grounds early in the spring, the same selection pressure could act on females and result in selection for overall larger size in birds that migrate early. Because SSD has been shown to increase with body size (e.g. Webster, 1992), it is possible that the relationship we found between SSDI and arrival time simply reflects a relationship between body size and SSDI. However, we found no relationship between contrast scores for sex differences in arrival time and female size ($R^2 = 0.01$, $t = 0.61$, $n = 29$, $P = 0.55$), male size ($R^2 = 0.03$, $t = 1.01$, $n = 29$, $P = 0.32$), or mean species size (i.e. mean of male and female size) ($R^2 = 0.02$, $t = 0.81$, $n = 29$, $P = 0.42$). Furthermore, we found no relationship between contrast scores for SSDI and mean species size ($R^2 = 0.02$, $t = -0.79$, $n = 29$, $P = 0.44$). Thus, the relationship between SSDI and sex differences in arrival time is not confounded by a relationship between SSDI and body size.

Discussion

Contrary to the prevailing view that large size should be detrimental to male survival in sexually dimorphic birds, Weatherhead & Clark (1994) proposed that in migratory species, large size may be beneficial, by helping males survive harsh spring weather. From this hypothesis we predicted that if selection has favoured large size in males relative to females within a species because it allows them to survive harsh spring weather, then the larger the size of males relative to females, the earlier they should migrate relative to females. We tested this hypothesis using data on timing of migration for birds crossing Lake Erie into Canada and found that, as predicted, sex differences in migration were significantly correlated with sex differences in size (i.e. SSD).

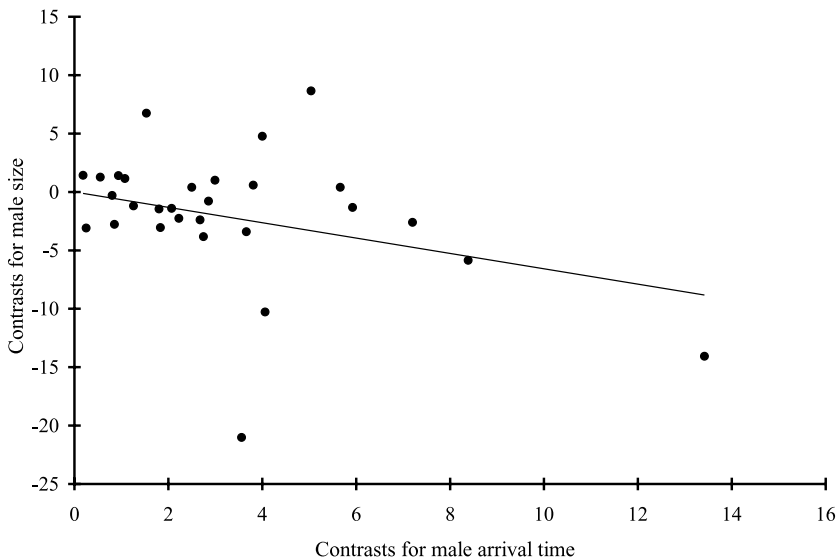


Fig. 3 Relationship between contrast scores for male size and adjusted male arrival date.

Francis & Cooke (1986) carried out a similar analysis with 18 species of warblers (including 13 species used in our study). In contrast to our study, they failed to find a significant relationship between the degree of SSD and differences in male and female migration times. We found that sex differences in migration timing not only increased with SSD across all the species we analysed, but also that this relationship held just among warblers, albeit weakly. The difference between the two studies does not appear to be a consequence of how they were conducted. Although Francis & Cooke (1986) did not control for phylogeny, doing so in our study had only minor effects on our results. However, Francis & Cooke (1986) used data collected over only 4 years, whereas we used data collected over 37 years. Thus, the greater power to detect significant patterns in our data may explain the difference between the results of the two studies.

Although our results are consistent with the migration-timing hypothesis, can they also be explained by other hypotheses? The most obvious alternative is that sex differences in both body size (SSD) and timing of migration are products of the same sexual selection pressure. Thus, in species with pronounced sexual selection on males, that selection favours larger males and also favours males that migrate early relative to females, because both attributes enhance a male's success at competing for territories or other resources attractive to females. One reason to consider this alternative less plausible is that we limited our analysis to species identified as socially monogamous. Variation in mating systems accounts for a substantial amount of variation in SSD produced by sexual selection (e.g. Webster, 1992). However, socially monogamous species are also subject to sexual selection. Darwin (1871) proposed that individuals choosing mates first should obtain superior mates and thus produce more offspring, and there is substantial evidence that early breeding females are in better condition and produce more young (reviewed by Price *et al.*, 1988). The resulting sexual selection pressure should favour earlier migration by males, even in monogamous species (Kokko, 1999; Morbey & Ydenberg, 2001). Thus, the species in which this sexual selection pressure is strongest will exhibit the largest difference between the sexes in the timing of migration. What is unknown, however, is the extent to which that same sexual selection pressure directly favours increased size in males (e.g. because large males compete more successfully for territories). Experimental evidence from red-winged blackbirds indicates that size has no effect on whether or not a male is successful in obtaining a territory (Eckert & Weatherhead, 1987a; Shutler & Weatherhead, 1991), or on the quality of the territory obtained if the male is successful (Eckert & Weatherhead, 1987b), but the generality of that result remains to be determined.

Extra-pair mating can also be an important cause of sexual selection in socially monogamous species (e.g. Yezerinac *et al.*, 1995). However, unlike competition for social mates, which may favour larger males, competition for success at extra-pair mating seems likely to favour attributes such as larger testes for sperm competition, or more elaborate plumage to signal quality (Birkhead, 1998). Furthermore, because competition for extra-pair matings occurs after birds have started to nest, it seems less likely than competition for social mates to be related to timing of migration. Thus, a link between timing of migration and SSD seems unlikely to arise as a result of sexual selection associated with extra-pair mating.

Weatherhead & Clark's (1994) energetic hypothesis and the alternative hypothesis discussed above need not be considered mutually exclusive. The reason that males expose themselves to harsh spring weather must ultimately be attributable to mating competition (Kokko, 1999). Thus, competition for nest sites or territories could favour both large size and early migration in males, and early migration could in turn also favour large males. Thus, the two mechanisms favouring large size in males would be additive. However, this is different from the conventional view in two ways. First, timing of migration is added as a direct (and potentially more important) contributor to selection promoting SSD. Secondly, if natural selection acts to promote SSD, then natural and sexual selection would be acting in concert. This is different from the view that a trait favoured by sexual selection should be opposed by natural selection (Darwin, 1871; Selander, 1972; Andersson, 1994).

If the migration-timing hypothesis is correct, the following predictions should apply. First, SSD should be more pronounced in species that migrate than in close relatives that do not migrate (or do not migrate as far), but that are otherwise ecologically similar. Secondly, within species, larger males should migrate earlier than smaller males. However, this pattern should be more pronounced in species that are more sexually size dimorphic if that dimorphism is at least in part a function of selection on male ability to survive cold weather. This analysis would have to control for age of birds, because juveniles tend to arrive later than adults in the spring (Ketterson & Nolan, 1983), and wing wear differs between juveniles and adults, which may bias analyses where wing chord is used as a measure of body size (Francis & Wood, 1989). The analysis would also have to take into account the possibility that not just the costs, but the benefits of early migration may differ among males (e.g. Forstmeier, 2002). Finally, more data are needed on survival relative to body size in sexually size-dimorphic species to determine whether a net survival advantage to large size in adult males occurs in species other than red-winged blackbirds (Weatherhead & Clark, 1994). These data must

assess survival over the long term, because individual mortality events can potentially select for large size, small size, or neither, depending on specific circumstances (Weatherhead *et al.*, 1984). If the net effect of mortality events over time is better survival of larger males, or even just no disadvantage to large size, then natural selection would not be acting against large size in adult males and may even favour large size.

Finally, if these additional tests support the hypothesis that natural selection favours rather than opposes large size in males of migratory birds, it will not refute the general hypothesis that sexual selection is balanced by natural selection (Darwin, 1871). That hypothesis must be true if sexual selection is to be prevented from exaggerating traits indefinitely. However, those tests would mean that natural selection against large size in males of migratory birds is imposed prior to adulthood (Clutton-Brock *et al.*, 1985; Weatherhead & Teather, 1991), a prediction also in need of testing.

Acknowledgments

Data were collected at Long Point Bird Observatory, a programme of Bird Studies Canada. We thank the thousands of volunteers and many staff members who have helped to collect the data over the past 40 years. Financial support for the field operations at Long Point was provided by the W. Garfield Foundation, the Ontario Ministry of Natural Resources, and private donations from hundreds of Bird Studies Canada supporters. We thank D.J. Bender, K.W. Dufour, and two anonymous reviewers for commenting on earlier drafts of this manuscript, and D.J. Bender and G.P. Brown for help with statistical analyses. Financial support for this analysis was provided by a Natural Sciences and Engineering Research Council of Canada (NSERC) operating grant to PJW and a NSERC post-graduate scholarship to KJK.

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Received 13 February 2002; accepted 23 March 2002

Appendix 1 Mean wing lengths (mm) of male and female migrants, their sexual size dimorphism indexes (SSDI) and the difference in arrival on the breeding grounds (days) between males and females.

Species	Wing length (mm)		SSDI	Male – female arrival (days)
	Males (n)	Females (n)		
<i>Carduelis tristis</i>	71.3 (1377)	68.7 (1217)	0.038	3.0
<i>Dendroica caerulescens</i>	63.7 (303)	60.2 (364)	0.058	6.1
<i>Dendroica castanea</i>	73.2 (231)	69.5 (197)	0.053	4.4
<i>Dendroica coronata</i>	72.1 (1749)	68.4 (1244)	0.054	7.5
<i>Dendroica virens</i>	62.1 (401)	59.3 (303)	0.047	7.6
<i>Dendroica magnolia</i>	58.9 (3381)	56.2 (2010)	0.048	4.2
<i>Dendroica pensylvanica</i>	61.8 (641)	59.7 (329)	0.035	3.0
<i>Dendroica petechia</i>	61.5 (1301)	58.8 (949)	0.046	2.6
<i>Dendroica pinus</i>	70.3 (48)	67.4 (25)	0.043	3.3
<i>Dendroica fusca</i>	67.6 (222)	63.8 (242)	0.060	6.4
<i>Dendroica tigrina</i>	66.1 (231)	63.6 (288)	0.039	4.6
<i>Euphagus carolinus</i>	116.1 (31)	107.6 (28)	0.079	12.7
<i>Icteria virens</i>	75.1 (77)	73.5 (64)	0.022	5.1
<i>Icterus galbula</i>	91.4 (904)	87.7 (332)	0.042	0.5
<i>Icterus spurius</i>	77.9 (27)	74.1 (25)	0.051	5.1
<i>Mniotilta varia</i>	68.6 (630)	65.5 (368)	0.047	7.8
<i>Pheucticus ludovicianus</i>	100.5 (1362)	98.0 (832)	0.026	1.4
<i>Pipilo erythrophthalmus</i>	85.0 (751)	80.8 (556)	0.052	8.0
<i>Piranga olivacea</i>	94.6 (213)	91.2 (176)	0.037	1.7
<i>Polioptila caerulea</i>	52.1 (78)	50.6 (71)	0.030	5.0
<i>Regulus calendula</i>	58.3 (4495)	55.5 (4234)	0.050	11.5

Appendix 1 Continued

Species	Wing length (mm)		SSDI	Male – female arrival (days)
	Males (n)	Females (n)		
<i>Regulus satrapa</i>	57.5 (1252)	55.3 (1334)	0.040	8.0
<i>Setophaga ruticilla</i>	61.3 (621)	58.5 (737)	0.048	3.4
<i>Tyrannus tyrannus</i>	115.1 (150)	112.7 (122)	0.021	3.8
<i>Vermivora chrysoptera</i>	62.4 (36)	58.5 (20)	0.067	7.4
<i>Vermivora peregrina</i>	64.4 (213)	60.0 (278)	0.073	4.0
<i>Vermivora pinus</i>	59.6 (47)	57.1 (43)	0.044	0.7
<i>Vermivora ruficapilla</i>	58.3 (835)	55.7 (548)	0.047	4.4
<i>Wilsonia canadensis</i>	64.1 (565)	61.1 (406)	0.049	3.7
<i>Wilsonia citrina</i>	66.4 (53)	63.0 (44)	0.054	5.7