

4-20-2012

Migration Distance and Sexual Dichromatism: Cost of Migration is Correlated with Reduced Female Coloration in Wood Warblers

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**Migration Distance and Sexual Dichromatism: Cost of Migration is
Correlated with Reduced Female Coloration in Wood Warblers**

Richard Kendall Simpson III

A DEPARTMENT HONORS THESIS SUBMITTED TO THE
DEPARTMENT OF BIOLOGY AT TRINITY UNIVERSITY
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR GRADUATION WITH
DEPARTMENTAL HONORS

April 20, 2012

THESIS ADVISOR

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CURRICULUM AND STUDENT ISSUES

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Acknowledgements

I would like to thank my thesis committee: Troy Murphy, Michele Johnson, and David Ribble. I thank my thesis advisor Troy Murphy for all of his guidance, support, and many, many hours of dedication to this project; if it weren't for him, I would not be where I am today. I would like to thank Michele Johnson for all of her help in teaching me how to use R, which has become my new favorite tool, and for teaching me how to conduct proper evolutionary analyses. I thank David Ribble for all of his guidance throughout my entire time at Trinity, and for all of his work to get me to understand the importance of GIS technology and how it is properly used. I am also grateful to Kevin McIntyre for his help with statistical analysis. I am very grateful to Melanie Sweeney, Natasha Kopecky, Tiffany Pham, Aaron Rosenblatt, and Lucy Cevallos for their help with scoring dichromatism. I would again like to thank Melanie Sweeney for being wonderful and supporting me every step of the way, and also Steven Gore, Joe west, Jessica Rodriguez, Nicholas Dybdal-Hargreaves, Spencer Hayes, Adam Kosti, and my family for all of their moral support throughout this process. I would like to thank the Trinity University Biology Department and Trinity University. Finally I would like to thank my Daft Punk Pandora Radio station for keeping me awake and motivated during all of those long, long nights of writing.

Abstract

Avian sexual dichromatism has been observed to be greater at higher latitudes, and one of the long-standing explanations for the underlying evolutionary forces underlying this geographic pattern is the breeding latitude hypothesis, which focuses on changes in male ornamentation and posits that sexual selection for male ornamentation is stronger at higher latitudes. I offer an alternative hypothesis that focuses on how changes in female coloration can drive the evolution of sexual dichromatism. I propose that the costs of migration, including increased predation risk and high energetic costs, negatively select against elaborate plumage coloration, and that the distance a species migrates is positively related to these costs. Furthermore, because positive directional selection for ornamentation is generally greater on males than on females, I propose that the costs associated with longer migration have imposed stronger net negative selection on female ornamentation compared to male ornamentation. Specifically, I predict that migration distance is positively related to sexual dichromatism. To address both the breeding latitude and migration distance hypotheses, I tested how migration distance and breeding latitude predict sexual differences in plumage coloration among wood warblers (Parulidae) using independent contrasts to control for phylogeny. Both migration distance and breeding latitude independently predict sexual dichromatism, and based on model-selection analyses, my results indicate that migration distance has more predictive power than breeding latitude. Thus, these results provide evidence consistent with the mechanism that changes in female ornamentation have driven the evolution of sexual dichromatism. Furthermore, these results suggest that incremental increases in migration distances are associated with concurrent increases in the costs associated with ornamentation. Future studies of both migratory and non-migratory taxa should consider how

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costs associated with female ornamentation might contribute to the evolution of sexual dimorphism.

Keywords: female coloration, sexual dichromatism, wood warbler, migration distance, breeding latitude

Introduction

The evolution of sexual dimorphism has been the focus of biological study since the time of Darwin (1871). Sexual dichromatism is a specific case of dimorphism that concerns the difference in coloration between males and females. Sexual dichromatism studies have strongly focused on bird coloration, likely because there is a wide range of dichromatism found within avian taxa (see Bailey 1978). Sexual differences in coloration vary from subtle examples such as the American Robin, where the sexes share most of the same colors, to cases where males and females look like different species, such as in Peacocks. Furthermore, there are species in which there is no dichromatism, and these monochromatic species vary from species where both males and females are equally dull, such as flycatchers, to species like macaws, in which both sexes are similarly ornate. Although much research over the last few decades has established functional explanations for male coloration, such as vibrant male colors serving as mate-choice signals (reviewed in Badyaev and Hill 2003), or as signals of fighting ability (reviewed in Senar 2006), less attention has been paid to the underlying selective mechanisms acting on female coloration (but see Amundsen and Parn 2006 for review). Indeed, the vast majority of research on the evolution of sexual differences in ornamentation has focused on how selection has acted to exaggerate male ornamentation (Andersson 1994, Savalli 1995, Badyaev and Hill 1999, Badyaev and Hill 2003), yet little is known about how changes in female coloration influence the evolution of sexual dichromatism (but see Irwin 1994, Martin and Badyaev 1996, Burns 1998, Omland and Hoffmann 2006).

One of the most remarkable patterns of sexual dichromatism is that it varies dramatically with breeding latitude in North America (Bailey 1978). Northern temperate species tend to be highly sexually dichromatic — with ornamented males and drab females — whereas species

breeding at more southern latitudes tend to have similarly ornamented males and females (Badyav and Hill 2003). A positive correlation between latitude and drabness of females has been noted for many taxonomic groups, including warblers and blackbirds (Hamilton 1961, Hamilton and Barth 1962). The breeding latitude hypothesis, originally proposed by Hamilton (1961), proposes that this geographic pattern arises because the strength of sexual selection on males is greater at northern latitudes (also see, Hamilton and Barth 1962, Badyaev and Hill 2003). It has been hypothesized that the strength of sexual selection increases with latitude because of greater breeding synchrony (due to shortened breeding season at high latitudes), which increases the opportunity for extra-pair copulations (Stutchbury and Morton 2001, Spottiswood and Moller 2004). In addition, at northern latitudes there is greater male-male competition for territories due to shorter breeding seasons, as males have less time to establish territories and begin mating before the peak of the breeding season (Catchpole 1980, 1982). Furthermore, sexual selection can be greater at northern latitudes because there is high variation among males as to whether they breed with the early-arriving females, as these females can produce larger clutches or more clutches (Kirkpatrick et al. 1990). There is much evidence that sexual selection increases with breeding latitude. For example, song complexity (Irwin 2000) and song length (Collins et al. 2009) are greater among species breeding at higher latitudes or species that migrate (i.e., species that tend to breed at higher latitudes) (also see, Read and Weary 1992), and Fitzpatrick (1994) found that migratory birds are more colorful than non-migratory birds. As such, there is much theoretical and empirical support for increased sexual selection acting on males at higher latitudes, and this geographic pattern of the strength of sexual selection has often been cited to explain the geographic pattern in sexual dichromatism (for review, see Badyaev and Hill 2003). This hypothesis proposes that the differences in appearance of the sexes is driven

by increases in male ornamentation, yet does not consider how evolutionary changes in female ornamentation can also influence sexual dichromatism.

As an alternative to the breeding latitude hypothesis, I offer a novel hypothesis that focuses on how changes in female coloration can account for the evolution of sexual dichromatism. I propose that the costs of migration (i.e., increased predation risk {Lindstrom 1989, 1990} and high energetic costs {Alerstam et al. 2003}), have led to a greater reduction in plumage ornamentation among females compared to males. Specifically, I hypothesize that the distance a species migrates is positively related to sexual dichromatism because of increasing exposure to these costs along lengthy migrations. Furthermore, females are expected to experience a stronger net negative selection than males, because even though both sexes are likely to experience similar costs along a migratory route, males are often under greater positive selection for sexual signaling than females (Andersson 1994). In other words, I hypothesize that sexual dichromatism arises when females migrate longer distances, because they experience a greater net costs associated with being colorful, either due to a greater risk of predation by visual predators along a long migratory route, or because the production of costly pigmentary coloration (McGraw and Hill 2001) may conflict with the energetic costs of migrating long distances. This migration distance hypothesis focuses on how changes in female ornamentation can lead to sexual differences in ornamentation; however it is not mutually exclusive with the breeding latitude hypothesis, as both positive selection (for increased male ornamentation) and negative selection (for decreased female ornamentation) can occur simultaneously.

In this study, I test the relationship between migration distance and sexual dichromatism among wood warblers (Parulidae). I also evaluate the breeding latitude hypothesis by testing whether warblers breeding at higher latitudes are more sexually dichromatic. Wood warblers

represent a diverse monophyletic group that varies greatly in sexual dichromatism, breeding latitude, and seasonal migration distances (del Hoyo et al. 2010, Winger et al. 2011). Of the 108 species in this clade, approximately half are migratory, and the distances migrated range from short distances (from Northern Mexico to South Central United States), to very long (from Brazil to Northern Canada) (Ridgely et al. 2007). Due to the high variability in migration distance, breeding latitude, and sexual dichromatism, and with the recently reconstructed phylogeny (Lovette et al. 2010), wood warblers provide a unique opportunity to study how migration distance and breeding latitude influence the evolution of sexual dichromatism.

Methods

Ranking Sexual Dichromatism

To quantify sexual dichromatism in wood warblers I used a human visual ranking system, following methods similar to Martin et al. (2010). I constructed a sexual dichromatism score for each species of warbler based on visual differences between males and females. I quantified plumage differences based on artistic renditions in the Handbook of the Birds of the World (HBW) (del Hoyo et al. 2010). Each species was categorized by a five-point scale starting at 0, representing monochromatic species, and dichromatism ranged between 1, representing a minimal degree of dichromatism, up to 4, which represented a high degree of dichromatism (Figure 1). When there was only one drawing for a species in the HBW, I considered the species monochromatic and assigned a score of 0. Because there are very few drab-monomorphic warblers, I combined both drab- and elaborate-monomorphic species into one category representing monomorphic taxa. For dichromatic species, I had five observers categorize dichromatism (on a 1-4 scale) based on photographs of the HBW plates that presented the male

and female of one species at a time. I removed the symbols representing sex from each photograph to prevent potential observer bias. All observers were unaware of the hypotheses being tested. For species with multiple sub-species, one subspecies was selected at random. To encourage detailed observation of plumage differences between the sexes, observers were asked to write down three visible differences for each male-female pair. Human evaluation of dichromatism has been found to be comparable to those created with objective readings taken with a spectrometer (Armenta et al. 2008), so I was confident in the use of human subjects to visually evaluate plumage differences. Observer scores were similar to one another (Intraclass correlation = 0.74, $F(47,188) = 15.53$, $P < 0.001$). A mean dichromatism score was computed for each species.

Measuring Migration Distance

Using GIS mapping software (DIVA-GIS) and species range maps downloaded from www.natureserve.org (Ridgely et al. 2007), I calculated migration distance for each species. I measured migration distance in two ways: 1) maximum distance: distance between the latitude of the most southerly point in the wintering-range to the latitude of the most northerly point of the breeding-range, 2) centroid distance: distance between the latitude of the centroid within the wintering range to latitude of the breeding range centroid. Using DIVA-GIS, centroids were determined by tracing the perimeter of the breeding, wintering, or year round range (see below), and calculating the center point of the polygon. All non-migratory birds were assigned a migration distance of 0. To measure the distances between coordinate points, I used the program Geographic Distance Matrix Generator, from the American Museum of Natural History (Ersts, version 1.2.3). For three species, it was questionable whether a species was migratory (i.e., only

subpopulations migrated, or altitudinal migrations occurred), and I identified them as non-migratory following the designations of Winger et al. (2011).

Assessing Breeding Latitude

Breeding latitude was assessed by two methods: 1) maximum latitude of the breeding-range, 2) centroid latitude of the breeding range. For non-migratory species, I assigned the centroid of the year-round range as the centroid breeding latitude, and took the most northerly point of the year-round range for the maximum-breeding latitude. For species that breed south of the equator, we positivized breeding latitudes ($n = 7$ species for maximum breeding latitude and $n = 21$ for centroid breeding latitude), because our measure is meant to represent the degree of seasonality (i.e., greater seasonality with greater latitude).

Statistical Analysis

I used regression analysis to test whether migration distance and/or breeding latitude predicted sexual dichromatism. These analyses were run with and without phylogenetic controls. The phylogeny of wood warblers has recently been resolved using two mitochondrial DNA regions and six nuclear DNA loci (Lovette et al. 2010). This robust phylogeny contains 108 species of wood warblers, with only one polytomy, and the relationships were estimated using RaxML maximum likelihood analysis (Figure 2; provided by Irby Lovette). For the phylogenetically controlled analysis, I used the *ape* package in R (Paradis et al. 2004) to calculate independent contrasts for the two measures of migration distance, the two measures of breeding latitudes, and the sexual dichromatism scale. Independent contrasts are a powerful tool to control for phylogenetic relationships during regression analysis. The method involves taking

the difference in trait values between two sister taxa and weighting this difference by the branch lengths of those taxa (Felsenstein 1985). In addition, I tested whether there were categorical differences in dichromatism based on the presence or absence of migration using both a standard ANOVA and a phylogenetic ANOVA (Garland et al. 1993). To explore the relationship between my independent variables, I ran correlation analyses on migration distance and breeding latitude, both using species means (a non-phylogenetic analysis) and independent contrasts.

Because there were strong correlations between the independent contrasts of migration distance and breeding latitude (maximum distance versus maximum latitude, $P < 0.001$, $r = 0.84$; centroid distance versus centroid latitude, $P < 0.001$, $r = 0.62$), I used an Akaike's Information Criteria (AIC) analysis to parse out the predictive power of the breeding-latitude hypothesis versus the migration-distance hypothesis. AIC analysis is not biased by high degrees of collinearity (Burnham and Anderson 2002, Johnson and Omland 2004), and so is able to compare models containing both migration distance and breeding latitude. This analysis was performed using the *MuMIn* package in R (Barton 2012). The AIC analyses were generated from multiple regressions on two sets of analyses: one using the centroid distance and centroid latitude measures, and the other using the maximum distance and maximum latitude measures to predict sexual dichromatism. Models were evaluated based on their $\Delta AICc$ values, which are used to compare the top model to all other models, and I used a threshold value of $\Delta AICc < 2$ for models to assess which models were indistinguishable from the top model (following guidelines of Anderson et al. 2000). Evidence ratios (ER) from the models were used to determine the predictive power of each model compared to the top model, and the Akaike weights (w) were calculated to evaluate the likelihood that a given model was the strongest predictive model.

Results

Dichromatism in relation to presence and absence of migration

The presence of migration was associated with sexual dichromatism. The degree of sexual dichromatism was greater among migratory compared to non-migratory birds ($F(1,106) = 41.52$, non-phylogenetic $P < 0.001$; phylogenetic $P < 0.001$). Migratory wood warblers are on average 1.5 higher on the dichromatism scale than non-migratory birds (Figure 3), suggesting that the occurrence of migration plays a role determining the degree of sexual dichromatism.

Dichromatism in relation to migration distance

The two measures for migration distance predicted sexual dichromatism, both when analyzed using standard (non-phylogenetic) analyses (least squares regression: centroid: $F(1,106) = 42.73$, $P < 0.001$, $R^2 = 0.29$; maximum distance: $F(1,106) = 49.53$, $P < 0.001$, $R^2 = 0.32$; Figures 4,5) and with phylogenetic control (centroid: $F(1,106) = 26.53$, $P < 0.001$, $R^2 = 0.20$; maximum distance: $F(1,106) = 26.37$, $P < 0.001$, $R^2 = 0.20$; Figure 6,7). These results indicate that migration distance, when considered alone, predicts sexual dichromatism.

Dichromatism in relation to breeding latitude

The two measures of breeding latitude predicted sexual dichromatism, both when phylogeny was not considered (centroid: $F(1,106) = 54.83$, $P < 0.001$, $R^2 = 0.34$; maximum: $F(1,106) = 51.58$, $P < 0.001$, $R^2 = 0.33$; Figures 8,9) and in analyses with phylogenetic independent contrasts (centroid: $F(1,106) = 21.91$, $P < 0.001$, $R^2 = 0.16$, $P > 0.001$; maximum $F(1,106) = 20.46$, $P < 0.001$, $R^2 = 0.17$; Figure 10,11), thus indicating that breeding latitude, when considered alone, predicts sexual dichromatism.

AIC analyses using centroid measures

When using the AIC analysis to compare the centroid migration distance and centroid breeding latitude measures, the top model was the combination model, which included both migration distance and breeding latitude, and this model was supported with an Akaike's weight (w) of 0.66, indicating that it has considerable support as the top model (Table 1). The only other model with similar predictive power to the top model ($\Delta AIC < 2$) was the migration distance only model ($\Delta AICc = 1.48$), with a w of 0.32. Based on the evidence ratios, the combination model had 2.10 times more predictive power than the migration only model, while both the combination and migration distance only models had far more (20.46 times) predictive power than the breeding latitude only model, ($\Delta AICc = 6.04$, $w = 0.03$). The large difference between the top models (combination model and migration only model) and the next model (latitude only model) suggests that breeding latitude and migration distance together are much stronger predictors than breeding latitude alone.

AIC analyses using maximum measures

When using the AIC to compare the maximum distance and maximum breeding latitude measures, the top model was migration distance, with a w of 0.68 (Table 2). The other model with similar predictive power to the top model ($\Delta AIC < 2$), was the combination model with maximum distance and maximum breeding latitude ($\Delta AICc = 1.87$). This combination model had a w of 0.27, indicating has less predictive power than the migration distance only model. The migration distance only model had 2.55 times more predictive power than the combination model, but both models have over 10 times the predictive power of the breeding latitude only model. These

AIC analyses suggest that migration distance is the best predictor of sexual dichromatism, and that breeding latitude and migration distance together are much stronger predictors than breeding latitude alone.

Discussion

I found that breeding latitude and migration distance both independently predict sexual dichromatism, providing support for both the long standing breeding latitude hypothesis (Hamilton 1961, Hamilton and Barth 1962, Bailey 1978), and for the hypothesis that the cost experienced by females during migration are directly proportional to the distance they migrate. By using AIC model selection to assess the relative contribution of migration distance and breeding latitude to variation in sexual dichromatism, I show that migration distance and a combination model (with both factors) had more predictive power than the null model and the breeding latitude-only model. Although the results varied depending on whether I analyzed centroid distance or maximum distance (in the centroid distance analysis, the combination model was the top model, whereas in the maximum distance analysis, migration distance model was the top model), both analyses indicate that the migration distance model could not be distinguished from the combination model. Given that the combination model was one of the top models in both analyses, this suggests that two evolutionary forces may be working in tandem, although in opposite directions for the sexes: that females ornamentation is selected against because females experience increasing net costs to ornamentation with longer migratory distances, and that male ornamentation is under positive selection because of the increasing strengths of selection at higher latitudes (as proposed by the breeding latitude hypothesis, see Badyaev and Hill 2003). As such, our results support both hypotheses, and suggest that sexual dichromatism can evolve when

there is selection for a reduction in female ornamentation while at the same time there is concomitant selection for increased male ornamentation.

The positive relationship between migration distance and sexual dichromatism suggest that species that migrate further distances experience greater costs associated with migration (i.e., predation risk and energetic costs). Although we did not directly assess costs associated with migration, there is good evidence that migration is extremely costly in terms of energy use (Henderstrom and Alerstam 1997, see Alerstam et al. 2003 for review), and that birds are far more susceptible to predation during migration (Walter 1979, Lindstrom 1989, Lindstrom 1990, Sillett and Holmes 2002). The added costs of producing and maintaining coloration can further add to the stress of migration (Fitzpatrick 1994). Producing colorful traits, such as carotenoid-based plumage, is a costly because, once deposited in feathers, the carotenoids are unavailable for other physiological functions (Brush 1981, Hill and Montgomerie 1994, Hill 2000, 2002, McGraw et al. 2001, 2005). In addition, we propose that the expression of elaborate coloration on migration can lead to an increased risk of predation by visual predators (as seen in Caldwell 1986, Slagsvold 1995).

Previous studies on sexual dichromatism have found a link between the evolutionary patterns of sexual dichromatism and migration. Among *Icterus*, phylogenetic analyses indicate that there have been several gains and losses of migratory behavior (Kondo and Omland 2007), and these changes are correlated with the evolution of sexual dichromatism (Friedman et al. 2009). One proposed mechanism explaining the role of migration on the evolution of sexual dichromatism is that non-migratory species generally occur in the tropics, where both sexes are often involved in territorial defense, and where both sexes may use elaborate signals to mediate territorial conflict (i.e., female status signaling; Irwin 1994, Whittingham et al. 1992, Murphy et

al. 2009). This female status-signaling hypothesis posits that elaborate female traits will be lost in migratory species because females of migratory species are generally not territorial (Stutchbury and Morton 2001), and so there would be reduced positive selection to maintain female ornamentation (Murphy et al. 2009, Price et al. 2009). My results with wood warblers, which indicate that migrants are more dichromatic than non-migrants, are consistent with this status-signal hypothesis. It is relevant to note that the migration distance hypothesis is complementary to this female status-signal hypothesis, because it provides a possible mechanism for the loss of female ornamentation among migratory lineages where females no longer gain benefits from maintaining signals of status.

Most previous research on the evolution of sexual dichromatism has focused on changes in male ornamentation due to sexual selection, focusing on the link between dichromatism and breeding latitude (Hamilton 1961, Hamilton and Barth 1962, Bailey 1978, Badyaev and Hill 2003), or dichromatism and mating system (Irwin 1994, Dunn et al. 2001), and there have been few studies that have evaluated changes in female ornamentation. Results from comparative studies have demonstrated that female ornamentation is often more labile than male ornamentation (Irwin 1994, Burns 1998, Hofmann et al. 2008), suggesting that more attention needs to focus on selection pressures that act upon female characters. One such study by Martin and Badyaev (1996) focused on how nest location and predation risks among parulid warblers and carduline finches have selected against female coloration. They found that predation risk was negatively correlated with female ornamentation, yet they did not find a relationship between predation risk and male coloration (Martin and Badyaev 1996). Additionally, Irwin (1994) showed that among Icterine blackbirds, females are more likely to be colorful and similar to males (i.e., elaborate monomorphic) in monogamous species, and hypothesized that females of

these species were under direct selection to use colorful plumage to signal during territorial defense. The results presented here on how costs associated with migration are correlated with warbler sexual dichromatism add to the short list of studies on sexual dimorphism that have considered the role of selection on females.

One limitation of this study is that I do not know the ancestral character state of sexual dichromatism in wood warblers. Although I propose that sexual dichromatism in this group is driven, in part, by losses in female plumage coloration, this assumes that the ancestral species was elaborate-monochromatic with colorful plumages in both sexes (as hypothesized for wood warblers by Hamilton, 1961). However, if the ancestral character state of female wood warblers was dull (due to a monochromatic dull, or dichromatic ancestor), then the migration distance hypothesis is still applicable. Under this evolutionary scenario the cost of migration would maintain female dullness and prevent elaboration of female ornamentation. For example, migratory costs could potentially maintain female drabness even if there was positive selection on male ornamentation and strong genetic correlation between the sexes that would otherwise lead to the expression of non-adaptive ornamentation in the female (sensu, Lande 1980).

In this study I present a new hypothesis to explain the geographic variation in sexual dichromatism — and it is distinct in that it focuses on changes in female plumage coloration rather than male coloration. I found support for both the migration distance hypothesis and the long-standing breeding latitude hypothesis. I propose that the costs associated with long distance migration may depress female color, whereas in males, I propose that the increasing costs of long migration may be compensated by the increasing strength of sexual selection on male coloration at high latitudes. It has long been understood that male plumage coloration influences the evolution of sexual dichromatism due to varying strengths of sexual selection, but there is still

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much that is unknown about how female plumage coloration is driving this evolutionary and geographic pattern. I urge future research on sexual patterns in ornamentation to consider how changes in both males and females can lead to the evolution of sexual dichromatism.

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Table 1. Akaike's Information Criteria analysis on how centroid migration distance independent contrasts and centroid breeding latitude independent contrasts predict the sexual dichromatism independent contrasts of wood warblers. The combination model includes both the migration and latitude variables. The AICc is the value given to each model to determine which model has the strongest predictive power. The Δ AICc is the comparison of the AICcs from all subsequent models to the AICc of the top model. The Akaike's weight is the probability that the given model is the top model, and the evidence ratio is the comparison in predictive power of each model to the top model.

Model	K	R²	AICc	ΔAICc	Akaike's Weight	Evidence Ratio
Combination	4	0.23	-25.89	0.00*	0.66	1.00
Migration Only	3	0.20	-24.40	1.48*	0.32	2.10
Latitude Only	3	0.17	-19.86	6.04	0.03	20.47
Intercept Only	2	0.00	-2.65	23.23	0.00	N/A

* = Δ AICc < 2.00

Table 2. Akaike's Information Criteria analysis on how maximum migration distance independent contrasts and maximum breeding latitude independent contrasts predict the sexual dichromatism independent contrasts of wood warblers. The combination model includes both the migration and latitude variables. The AICc is the value given to each model to determine which model has the strongest predictive power. The ΔAICc is the comparison of the AICcs from all subsequent models to the AICc of the top model. The Akaike's weight is the probability that the given model is the top model, and the evidence ratio is the comparison in predictive power of each model to the top model.

Model	K	R²	AICc	ΔAICc	Akaike's Weight	Evidence Ratio
Migration Only	3	0.19	-24.20	0.00*	0.68	1.00
Combination	4	0.20	-22.51	1.87*	0.27	2.55
Latitude Only	3	0.16	-19.27	4.84	0.06	11.725
Intercept Only	2	0.00	-2.65	20.81	0.00	N/A

* = $\Delta\text{AICc} < 2.00$

Simpson - Dichromatism and migration distance in warblers



1- Nashville Warbler



2- Golden-Winged Warbler



3- Cerulean Warbler



4- Bay-Breasted Warbler

Figure 1. The dichromatism scale from 1-4 for wood warblers, with 1 representing minimal differences between the two sexes and 4 representing a large amount of differences between the two sexes. These images are photos taken of the image plate drawings in Handbook of the Birds of the World (del Hoyo et al. 2010).

Simpson - Dichromatism and migration distance in warblers

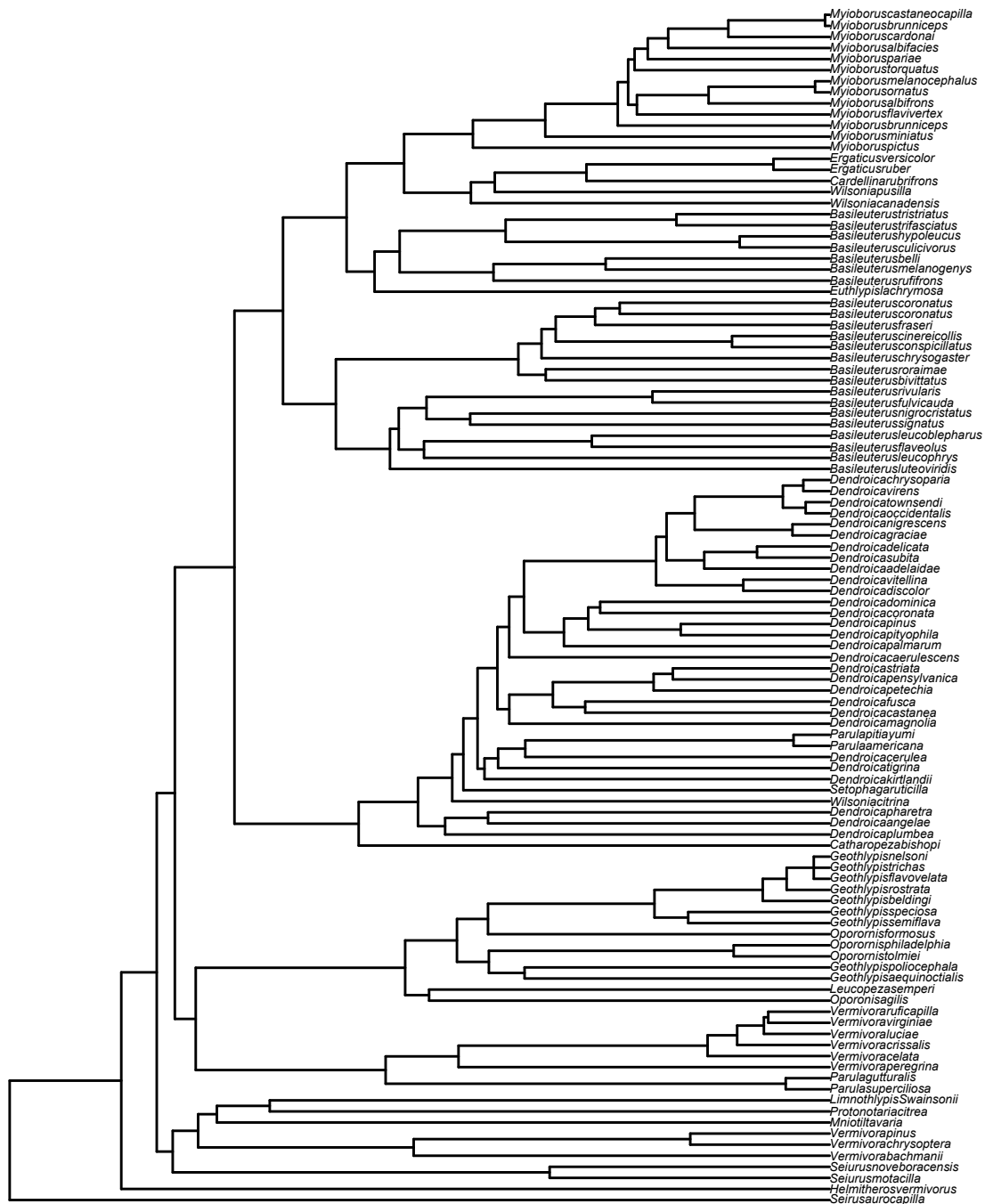


Figure 2. The phylogenetic tree of wood warblers redrawn from Lovette et al. (2010) figure 5.

The tree contains 108 species of wood warblers, and was created using mitochondrial and nuclear DNA and estimated using maximum likelihood analysis.

Simpson - Dichromatism and migration distance in warblers

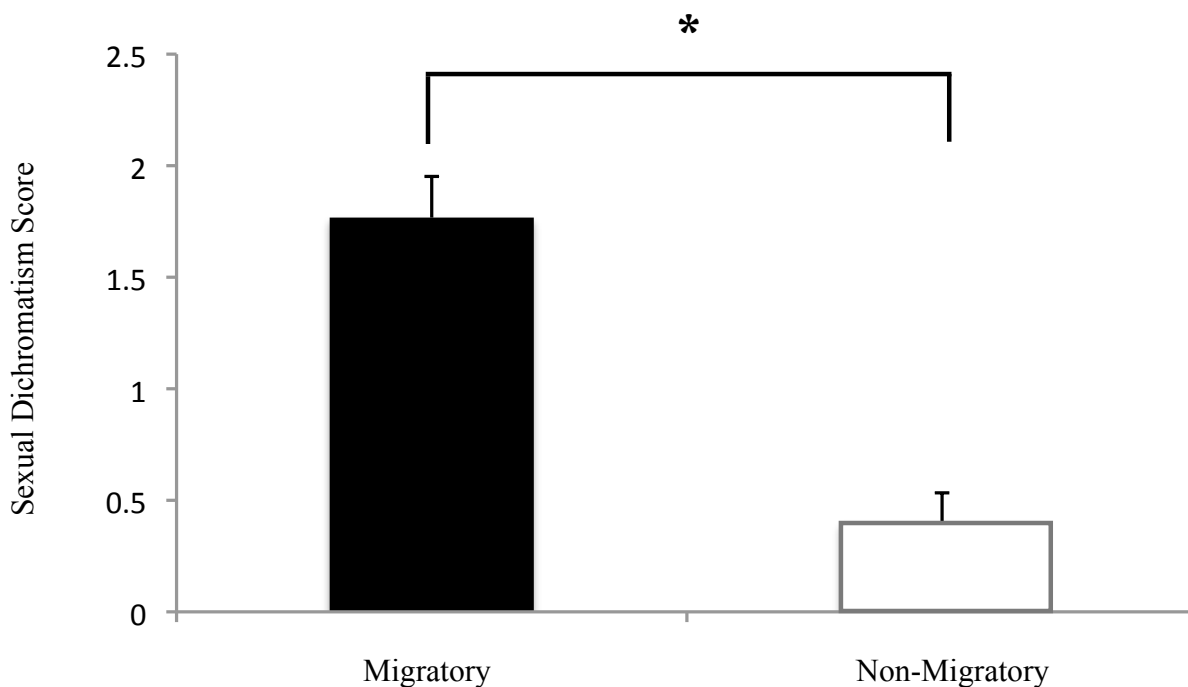


Figure 3. The mean sexual dichromatism score for migratory ($n = 49$) and non-migratory ($n = 59$) wood warblers, with the standard error represented in the error bars. The significance was tested using a phylogenetic ANOVA on sexual dichromatism ($F(1,106) = 41.52$). This was significant both when phylogeny was considered ($P < 0.001$) and in standard non-phylogenetic analysis ($P < 0.001$)

* = $P < 0.001$

Simpson - Dichromatism and migration distance in warblers

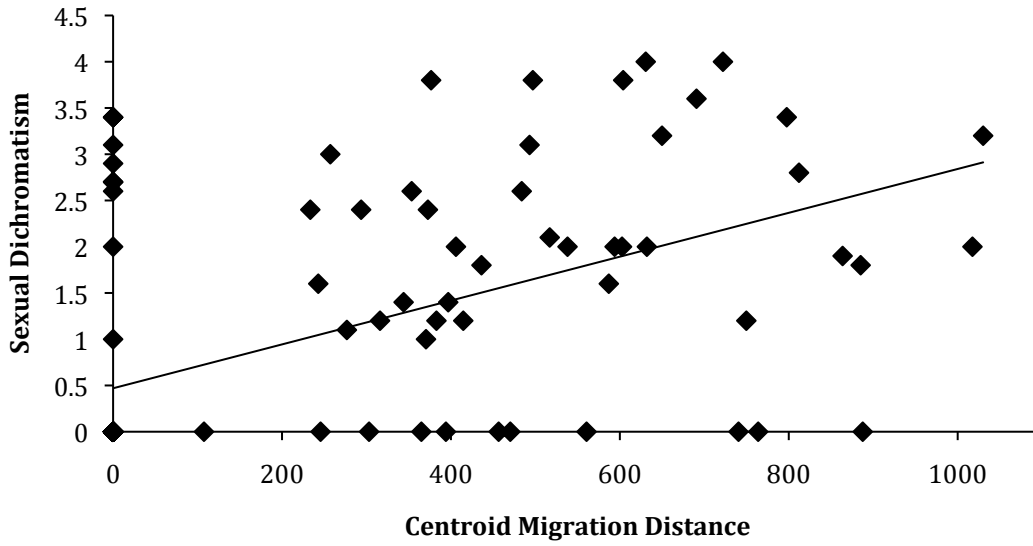


Figure 4. Centroid migration distance (m) and sexual dichromatism for wood warblers ($n = 108$). This data represents individual species means for migration distance and sexual dichromatism, and the trend line is based on a standard linear regression analysis ($P < 0.001$).

Simpson - Dichromatism and migration distance in warblers

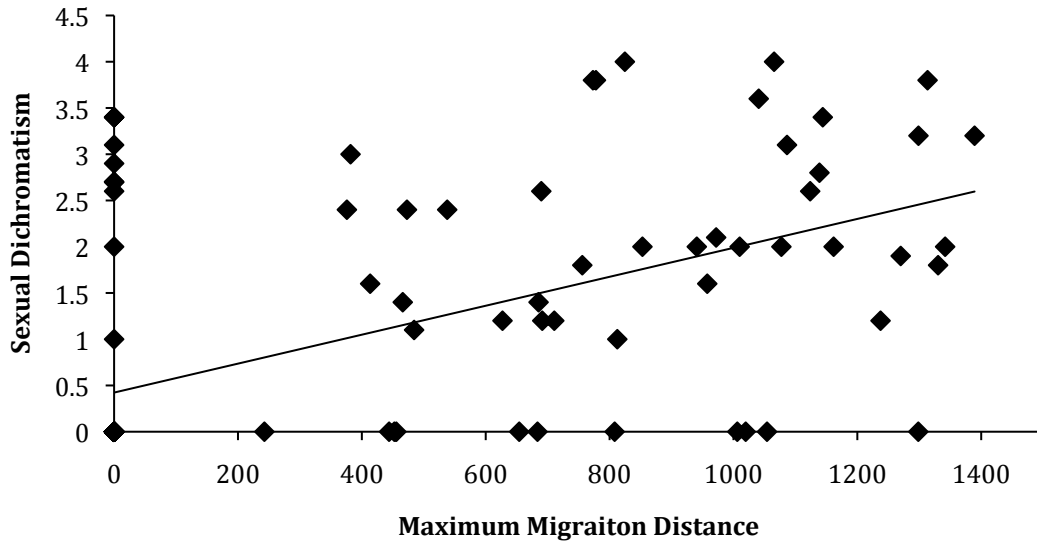


Figure 5. Maximum migration distance (m) and sexual dichromatism for wood warblers ($n = 108$). This data represents individual species means for migration distance and sexual dichromatism, and the trend line is based on a standard linear regression analysis ($P < 0.001$).

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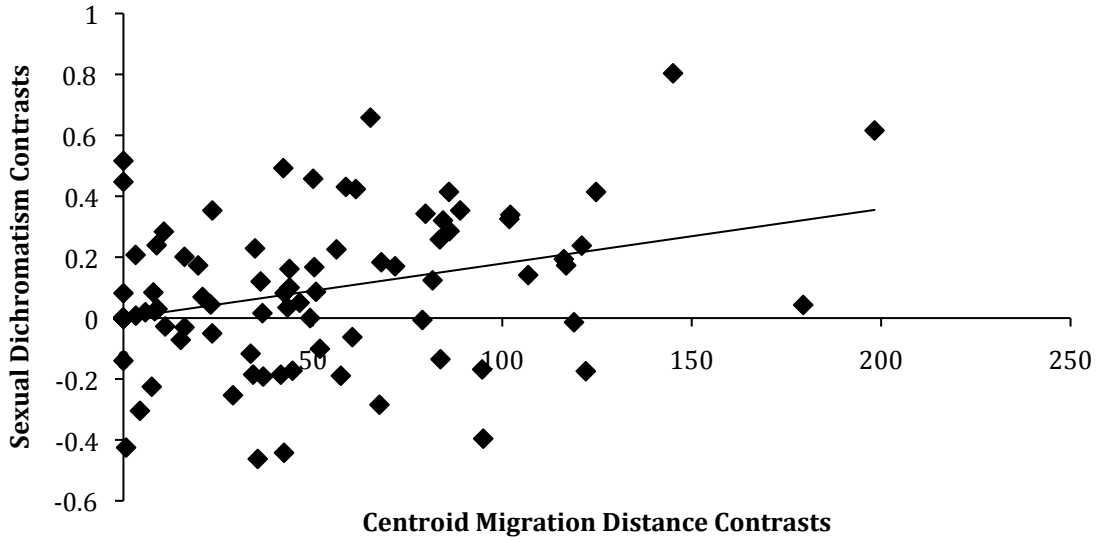


Figure 6. Independent contrasts of centroid migration distance and independent contrasts of sexual dichromatism for wood warblers ($n = 107$). The trend line is based on a standard linear regression analysis using positivized independent contrasts and forced through the origin ($P < 0.001$) (following Garland et al. 1992).

Simpson - Dichromatism and migration distance in warblers

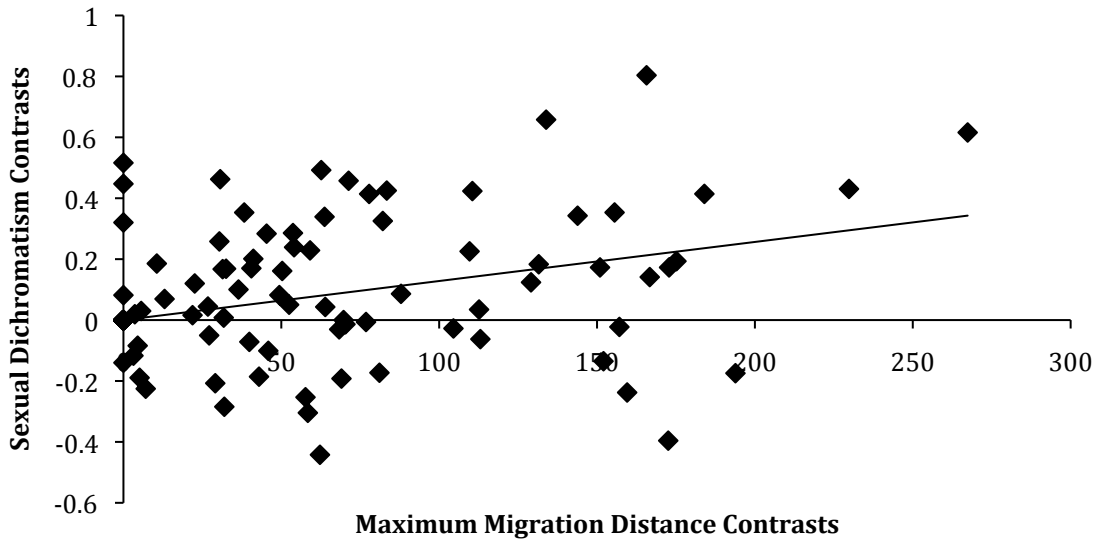


Figure 7. Independent contrasts of maximum migration distance and independent contrasts of sexual dichromatism for wood warblers ($n = 107$). The trend line is based on a standard linear regression analysis using positivized independent contrasts and forced through the origin ($P < 0.001$) (following Garland et al. 1992).

Simpson - Dichromatism and migration distance in warblers

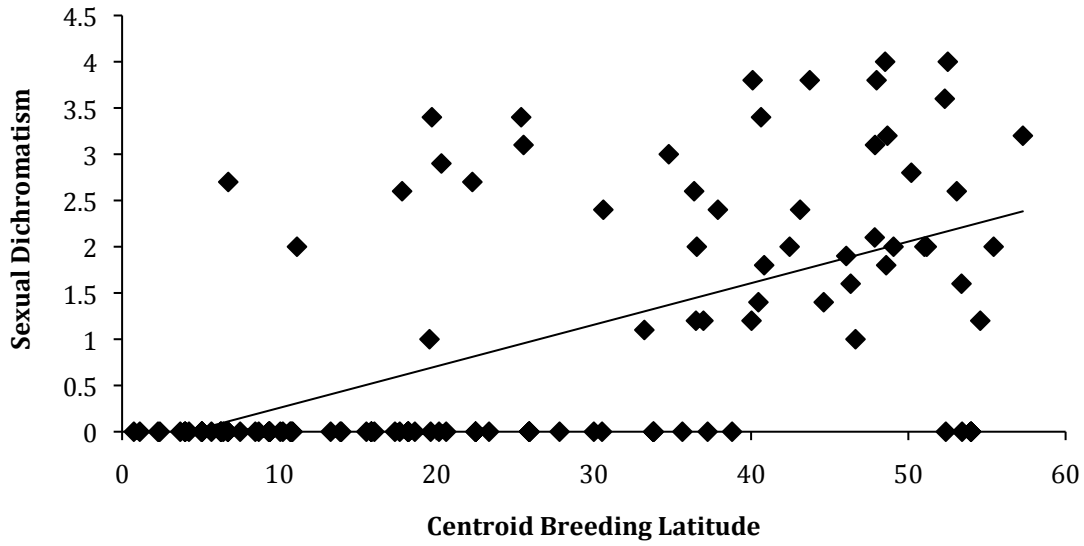


Figure 8. Centroid breeding latitude and sexual dichromatism for wood warblers ($n = 108$). All latitudes were made to be positive distances from the equator. This data represents individual species means for breeding latitude and sexual dichromatism, and the trend line is based on a standard linear regression analysis ($P < 0.001$).

Simpson - Dichromatism and migration distance in warblers

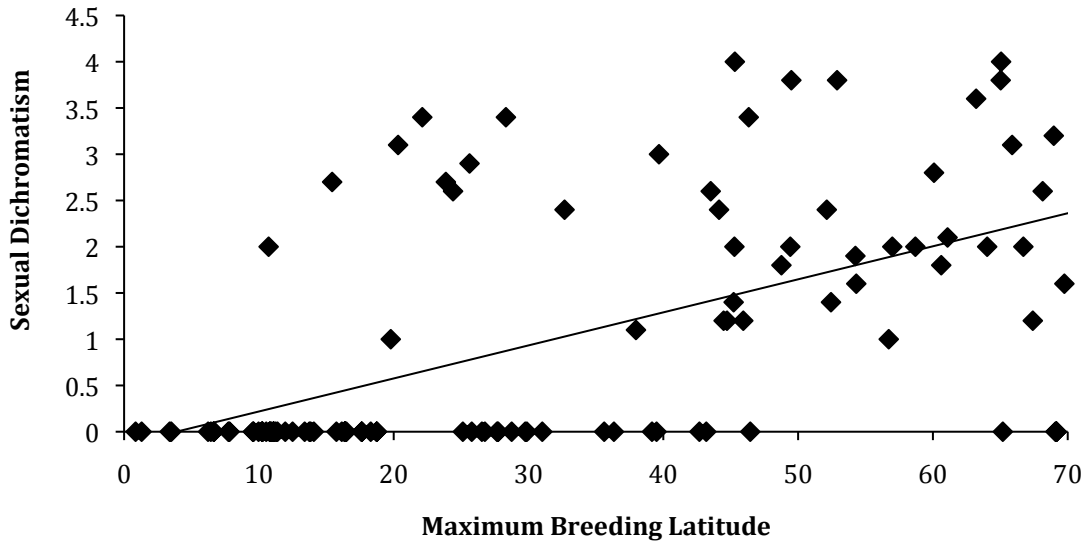


Figure 9. Maximum breeding latitude and sexual dichromatism for wood warblers ($n = 108$). All latitudes were made to be positive distances from the equator. This data represents individual species means for breeding latitude and sexual dichromatism, and the trend line is based on a standard linear regression analysis ($P < 0.001$).

Simpson - Dichromatism and migration distance in warblers

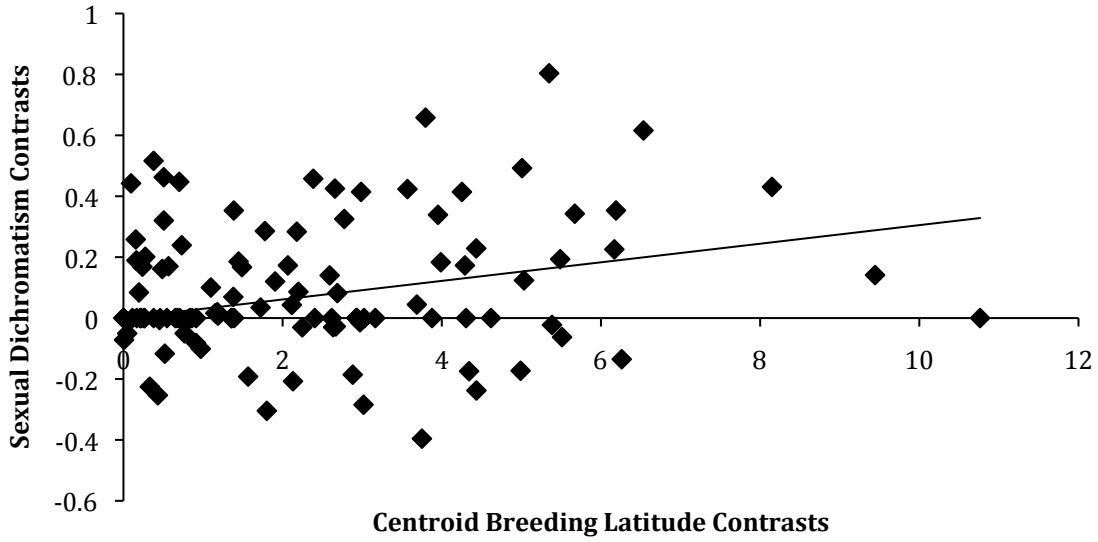


Figure 10. Independent contrasts of centroid breeding latitude and independent contrasts of sexual dichromatism for wood warblers ($n = 107$). The trend line is based on a standard linear regression analysis using positivized independent contrasts and forced through the origin ($P < 0.001$) (following Garland et al. 1992).

Simpson - Dichromatism and migration distance in warblers

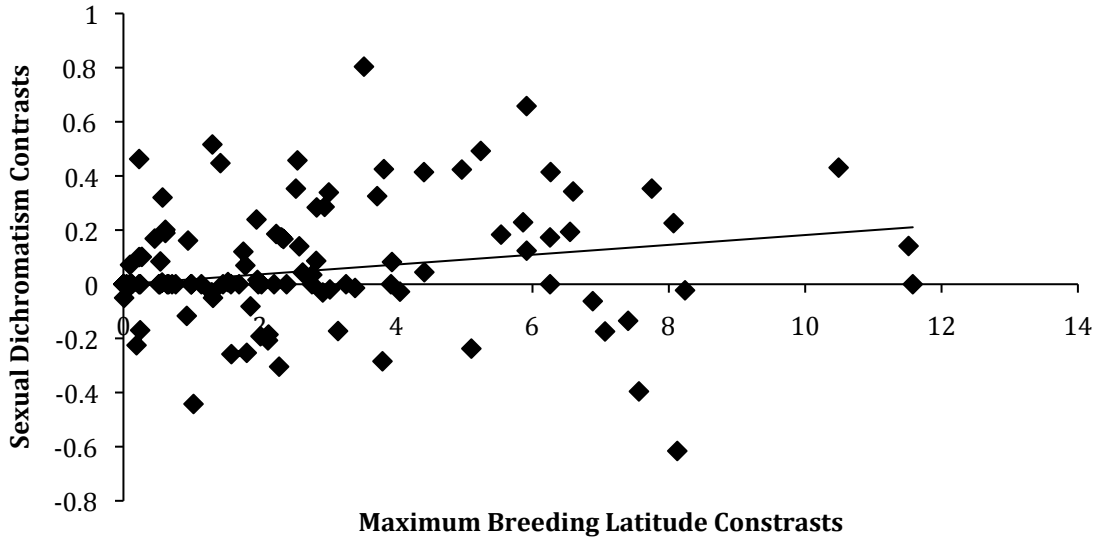


Figure 11. Independent contrasts of maximum breeding latitude and independent contrasts of sexual dichromatism for wood warblers ($n = 107$). The trend line is based on a standard linear regression analysis using positivized independent contrasts and forced through the origin ($P < 0.001$) (following Garland et al. 1992).