Influence of elevation on the sexual dimorphic gap in mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*)

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The influence of elevation on the sexual dimorphic gap in mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*)

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ABSTRACT

This study examined sexual dimorphism and dichromatism in mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) and how it changes over an elevational gradient. Birds living in high elevation habitats are subject to harsh climatic conditions and a shorter breeding season, which affects how many MWCS can inhabit the area, how females select a mate, and how much energy for parental care is required for both males and females to acquire reproductive success. This increased parental effort requirement then has an impact on sexual selection pressures on males and on individual fitness. Mountain white-crowned sparrows were trapped with potter traps and mist nets at low (2962m) and high elevations (3240m) and measurements taken on wing, retrices, tarsus, and culmen length as well as crown stripe width and then compared between three pools of male and female pairs: 1) All birds caught during this study randomly paired from low elevation compared to high elevation, 2) Potentially breeding pairs caught in the same low elevation locations compared to high elevation, and 3) Confirmed nesting pairs compared between low and high elevation sites. Male morphological feature size was also compared across increasing elevation. No significant differences in dimorphism were found for the paired MWCS, but a negative correlation was detected in male crown ratio proportion (R^2 = 0.04, P = 0.08). This trend suggests that sexual dichromatism in MWCS males inversely correlates with elevation based on reduced sexual selection pressures and increased parental care requirements at higher elevations

INTRODUCTION

High-elevation breeding birds must cope with persistently colder temperatures, increased snow cover depth, more extreme fluctuations in weather, more frequent precipitation events, and shorter breeding seasons (Badyaev and Ghalambor 2001, Johnson et al. 2006) to be

reproductively successful. These adverse environmental conditions are commonly associated with various forms of increased parental effort to ensure reproductive success (Badyaev 1997a, Badyaev and Ghalambor 2001, Johnson et al. 2006, Li and Lu 2012). Many high-elevation birds employ monogamy and/or biparental care for young to meet these challenges (Lyon et al. 1987, Badyaev and Ghalambor 2001, Morton 2002, Johnson et al. 2006, Li and Lu 2012). For high-elevation monogamous females, mate choice is important because of the contribution of quality habitat from the male's territory as well as the contribution of male parental care (Lyon et al. 1987, Matysiokova and Remes 2014). A high-quality mate can provide habitat with high intrinsic quality (food availability, preferred nesting vegetation, protection from predators and parasites etc. (Cody 1981, Muller et al. 1997, Badyaev and Ghalambor 2001)) which may provide the female with compensatory resources for increased energy cost at high elevation. In addition to the benefits of quality habitat, male participation in nestling provisioning improves reproductive success in difficult environmental conditions (Lyon 1987, Muller et al. 1997). As observed in a male-removal study with snow buntings (*Plecrophenax nivalis*), a monogamous species that breeds in the high arctic, widows were only able to fledge about 60% of the number of young raised by pairs, and the young had significantly lower mass at fledging (Lyon et al. 1987).

Given the importance of mate choice for monogamous females, dimorphism and /or dichromatism (even if slight) is valued in males because it signifies resource-holding potential (Nicola and De Bernardi 1994, Badyaev 1997b, Laubach et al. 2013). It is well-researched in dichromatic species that greater plumage ornamentation and brightness reflects greater individual fitness and efficiency in territory defense (Nicola and De Bernardi 1994, Saino and Moller 1996). In mostly-monomorphic species, such as the mountain white-crowned sparrow (*Zonotrichia leucophrys oriantha*, hereafter referred to as MWCS), females will typically choose males with greater dimorphism in wing and tarsus length, as well as greater dichromatism from wider white crown stripes (Laubach et al. 2013, Morton 2002). The MWCS exhibits monogamy and biparental care, and higher resource availability from a dominant male's territory will increase fecundity due to decreased parental care effort required by each partner (Badyaev and Ghalambor 2001). The sexual selection pressure from females being choosy for the most fit mate increases male dimorphism and dichromatism, thus creating a sexual dimorphic gap (Nicola and De Bernardi 1994, Badyaev 1997a, Badyaev and Ghalambor 2001).

Morphology and reproductive behavior have been found to vary along an elevational gradient (Badyaev and Ghalambor 2001, Badyaev 1997a)). Increased biparental care compensates for the female's energy limitations from a higher workload of self-maintenance, incubating eggs, and feeding young in higher elevation conditions (Matysiokova and Remes 2014, Moller and Thornhill 1998). Previous research on cardueline finches has shown that intensity of sexual selection and development of sexual ornamentation decreased with altitude, while more male parental care was observed (Badyaev and Ghalambor 2001). Colder temperatures and more frequent rainfall at higher elevations cause the female to reallocate efforts from self-maintenance (e.g. preening and foraging) to nest attendance to prevent lethal cooling of the eggs and nestlings (Badyaev 1997a). Both parents must also increase feeding effort during the nestling stage because nestlings have higher energy costs for thermoregulation in addition to energy costs for growth at high elevations (Hoset et al. 2004). Many previous studies suggest that sexual dimorphism in passerines is suppressed at higher elevations because the increased requirement of biparental care constrains extrapair fertilizations, thereby lowering the intensity of sexual selection (Owens and Hartley 1998, Badyaev and Ghalambor 2001, Badyaev 1997a, Badyaev 1997b, Moller and Thornhill 1998). However, since extra-pair fertilizations are not prevalent in monogamous species like the MWCS (Verner and Willson 1969, Morton et al. 1972, Morton 2002), this suggestion would not fully explain variation observed in dimorphism or dichromatism.

A lower density of males in high elevation habitats of monogamous species is then what can cause a decrease in sexual selection pressure. Sexual dimorphism as a result will not be as accentuated with the lower variability in mate choices for females. In addition, the harsher conditions force an energy trade-off in males to increase parental care instead of expending as much energy in competition for females, mate-guarding, and territory defense (Matysiokova and Remes 2014), activities which encourage the development of larger morphology (Badyaev 1997a)). This suggests a negative correlation between dimorphism and male parental care (Badyaev 1997a), and a positive correlation between male parental care and altitude (Johnson et al. 2006). Therefore, we predicted that the sexual dimorphic gap will be smaller at high elevations because there will be less dense populations of MWCS and the males will be spending more energy on parental care.

METHODS

Study Site

This study was conducted north of the Rocky Mountain Biological Laboratory in Gunnison County, CO (38.9563802°N, -107.0106015°W) from 01June to 01 August, 2014. Data was collected in six different sites, with four sites along the East River Valley at elevations of 2924m, 2934m, 2950m, and 2989m (Low elevation), one in Schofield Park at 3167m, and one in the North Pole Basin at 3465m (High elevation; Fig1a and b). In this high mountain site, there is a short yet active growing season with mild to hot temperatures, but winter is very long with low temperatures (can reach -40°C) and deep snow which can last for more than 7 months (Inouye et al. 2000). Woody vegetation species present in the study sites were predominantly willow (*Salix* spp.), alder (*Alnus* spp.), cinquefoil (*Potentilla* spp.), and peripheral spruce forest (*Picea* spp.), and herbaceous vegetation within the study sites included primarily *Veratrum* spp., but also *Delphinium* spp., *Castilleja* spp., and *Ipomopsis* spp. etc. The low elevation sites were situated in willow patches along the East River Valley beneath the peaks of the Elk Mountain range. Schofield Park was in a subalpine willow meadow and North Pole Basin was an alpine basin with willow patches throughout.

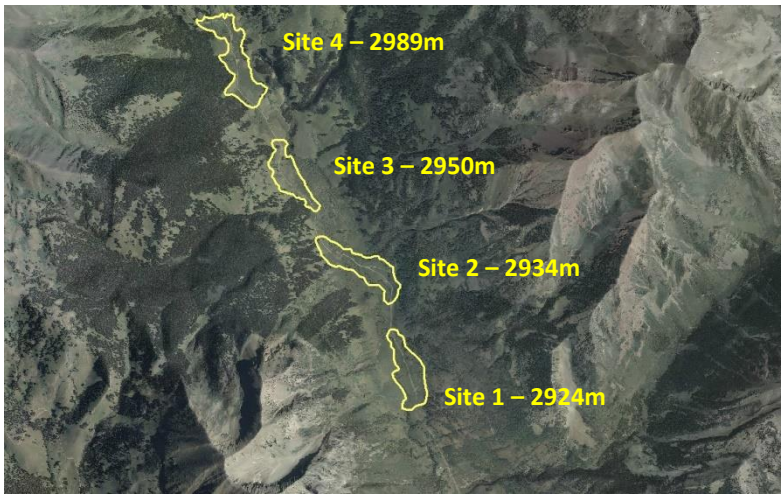

Figure 1a: GIS map of low elevation trap sites (Sites 1-4) and mean elevation of each site.

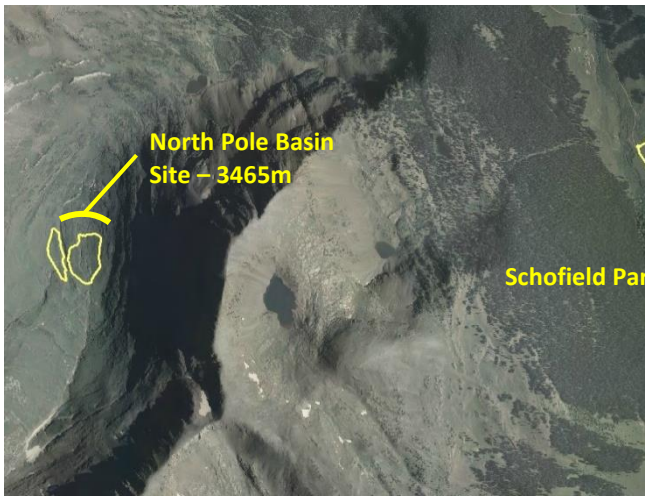

Figure 1b: GIS map of high elevation trap sites (Schofield Park, N Sites 1 and 2) and mean elevation of each site.

Bird trapping and processing

Birds were trapped using wire Potter traps baited with a seed mixture composed mostly of white proso millet, but also wheat, sunflower seed, and milo. Eight to ten traps were situated

in each site in locations selected to avoid multiple captures within a territory. Traps were opened every morning or every other morning (0630-1200h) at 1-3 sites during the study period, checked hourly and each captured bird processed as described below. Half of the trap sites received daily seed supplementation, while the other sites received only enough seed to bait traps on or prior to trapping mornings.

When a MWCS was captured for the first time of the season, we measured the cloacal protuberance, wing chord and rectrices with a wing rule to the nearest millimeter. Sex was determined using the cloacal protuberance measurement (males ≥4 mm, females <4 mm) (Laubach et al. 2013) and the presence of a brood patch in females. We also measured culmen, crown width, and crown-white stripe using calipers to the nearest 0.1mm. Mass was measured using a Pesola© spring scale to the nearest 0.5g. Each MWCS was then banded with a uniquely numbered United States Geological Survey metal leg band (size 1B) and a unique combination of three plastic color bands for identification of individuals from a distance in the field. Males received the service band on the right leg and females on the left, with one colored band above the service band and two colored bands on the opposite leg. Any MWCS that were recaptured had the cloacal protuberance and mass measured, and other species caught were identified and then released. Breeding elevation was determined by the elevation of the trap site where the individual was first caught.

Nest searching and breeding pair identification

Nests were found using the rope-drag method, where a 14m rope with clusters of three aluminum cans attached every 1m was dragged by two observers over the areas of willows in a subset of the trapping sites that included 2 low elevation sites,and 1 high elevation site (Schofield Park). Rope-dragging was conducted in parallel transects over the site, with previously searched transects marked with flagging tape to ensure the entire site was searched effectively. When a bird flushed from the vegetation after the rope drag disturbance, the area was searched for a nest for no more than 10 minutes to avoid disturbing the area (Martin and Geupel 1993). After a nest was found it was discretely (below vegetative canopy to avoid attracting avian predators) flagged at 3m to the north and south, had GPS coordinates recorded and subsequently monitored every 2-3 days until

the nest was no longer active. We identified breeding pairs based on alarm chipping, food holding, or other behavior that indicated they were parents of the nest.

Statistical analysis

We analyzed the dimorphic and/or dichromatic differences between elevational treatments using one-way ANOVA models and linear regressions in JMP® 11 statistical software. Visual comparisons are displayed using 95% confidence intervals to represent significance using an alpha of 0.05. Analyses were conducted for three different categories of male-female combinations: 1) breeding pairs (males and females confirmed as parents of a nest by observing them tending a nest and/or alarm-calling when nestlings were being banded), 2) all potentially breeding MWCS pairs (males and females caught in the same trap, randomly paired), and 3) all birds caught in the 2014 field season (randomly paired). For comparisons of dimorphism, the mean elevation of all trap sites at the low elevation sites and high elevation sites was used (2962m and 3240m, respectively). The amount of dimorphism between pairs was notated as proportional difference in morphological feature size (wing, tail, tarsus, and culmen length, or crown ratio). Crown ratio (CR) refers to the proportion of the total crown stripe width by the total crown width. Proportional size difference was calculated by the equation: 1 – (Female size/Male size), a value representing the amount that females differed from the males, standardized for each feature.

The change in morphological feature size of males at different elevations was analyzed by making bar graphs including 95% confidence interval error bars that compared morphological feature sizes of low elevation males to high elevation males. This was also done for female size differences at low and high elevation. A linear regression analysis was made of all male CR values plotted against the elevation of the trap site where each male was caught.

RESULTS

Forty-eight total females and 84 total males were caught in the field season during this study and had data on morphological feature size and breeding elevation (taken from trap site). Six breeding pairs were confirmed from nest observations (2 high elevation, 4 low elevation), and 25 potentially breeding pairs were randomly paired with individuals of the other sex that were caught in the same trap (8 high elevation, 17 low elevation).

Confirmed breeding pairs

Proportional size difference between male and female wing, tail, tarsus, culmen, and CR of low elevation pairs were compared with the pairs from the high elevation site (Figure 2). One high elevation male lacked a culmen measurement, meaning there was only one sample of high elevation dimorphism to compare to the low elevation pairs, thus culmen dimorphism was excluded from this comparison. A one-way ANOVA showed no significant difference in dimorphism in pairs from low to high elevations (wing ($P = 0.48$), tail ($P = 0.94$), tarsus ($P = 0.81$), and CR ($P = 0.39$)).

Potential breeding pairs

Twenty-three trap sites (7 high elevation, 11 low elevation) had both male and female MWCS morphological feature size data, which were randomly paired into 25 total potentially breeding pairs (8 high elevation, 17 low elevation) (Figure 3). If any trap sites had unequal numbers of males to females, we took the mean of the extra male size measurements to pair with a female, and vice versa for extra females to males. The one-way ANOVA showed no significant difference from low to high elevations for wing ($P = 0.87$), rectrices ($P = 0.81$), tarsus ($P = 0.46$), culmen ($P = 0.14$), and CR ($P = 0.32$).

All possible pairs

Thirty-eight pairs were randomly matched from the low elevation sites and 14 from the high elevation sites (Figure 4). The one-way ANOVA showed no significant difference in wing ($P = 0.87$), tail ($P = 0.62$), tarsus ($P = 0.35$), culmen ($P = 0.89$) and CR ($P = 0.51$) dimorphism between pairs at low and high elevations.

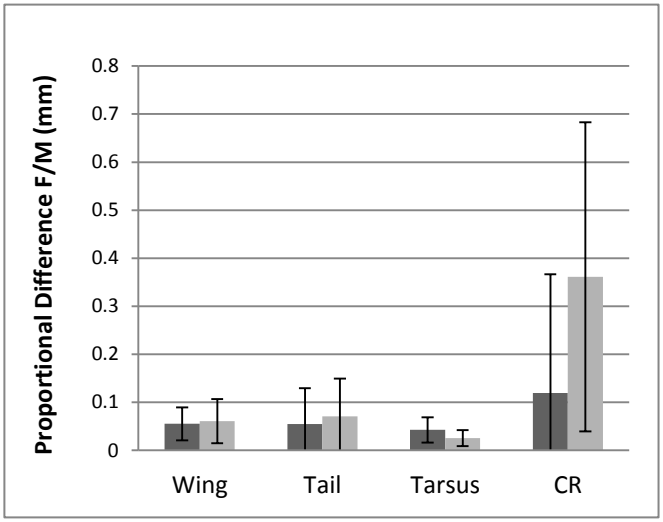

Figure 2: Proportional size difference of features within confirmed breeding pairs compared between low and high elevations. Dark grey indicates low elevation pairs (2978m) and light grey indicates high elevation pairs (3173m). The 95% confidence intervals indicate that dimorphism in all features was not significant between pairs breeding at low and high elevations.

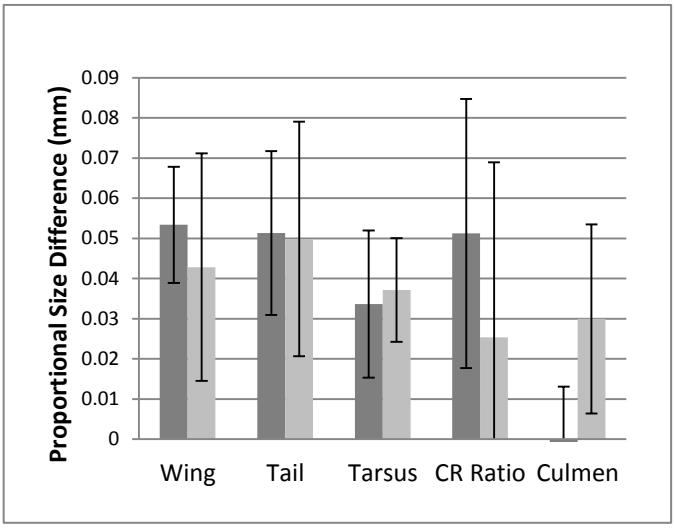

Figure 3: Dimorphism differences in potentially breeding pairs trapped at same locations compared between low and high elevations. Dark grey indicates low elevation pairs (2978m) and light grey indicates high elevation pairs (3173m). The 95% confidence intervals suggest that there is no significant change in dimorphism from low to high elevation.

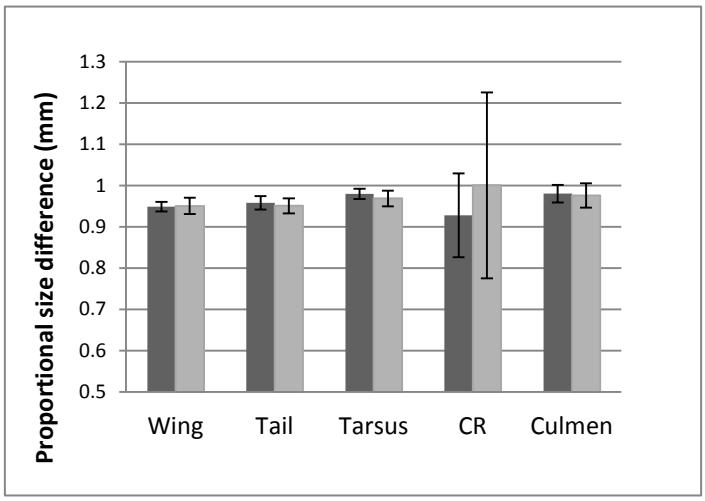

Figure 4: Dimorphism differences between pairs from the same elevation, comparing all MWCS pairs from low elevation sites to high elevation sites. Dark grey indicates low elevation pairs (2978m) and light grey indicates high elevation pairs (3173m). The 95% confidence confidence intervals do not indicate any significant changes in dimorphism at low and high elevation.

Size differences between all males and females at low versus high elevation

The means of morphological feature sizes of all male and female birds at low elevation were compared with those of males and females at high elevation to observe if the amount of dimorphism was changing with increasing elevation (Figure 5). The dichromatism of male and

female CR is not significantly different at high elevation, as female CR increases with elevation and male CR decreases.

Further statistical modeling through a linear regression was done to analyze the change in male CR with increasing elevation (Figure 5). The line fit to the data points of male CR plotted against trap location elevation had a slight negative correlation and an $R^2 = 0.04$, indicating that there is a very slight trend of decreasing CR with elevation.

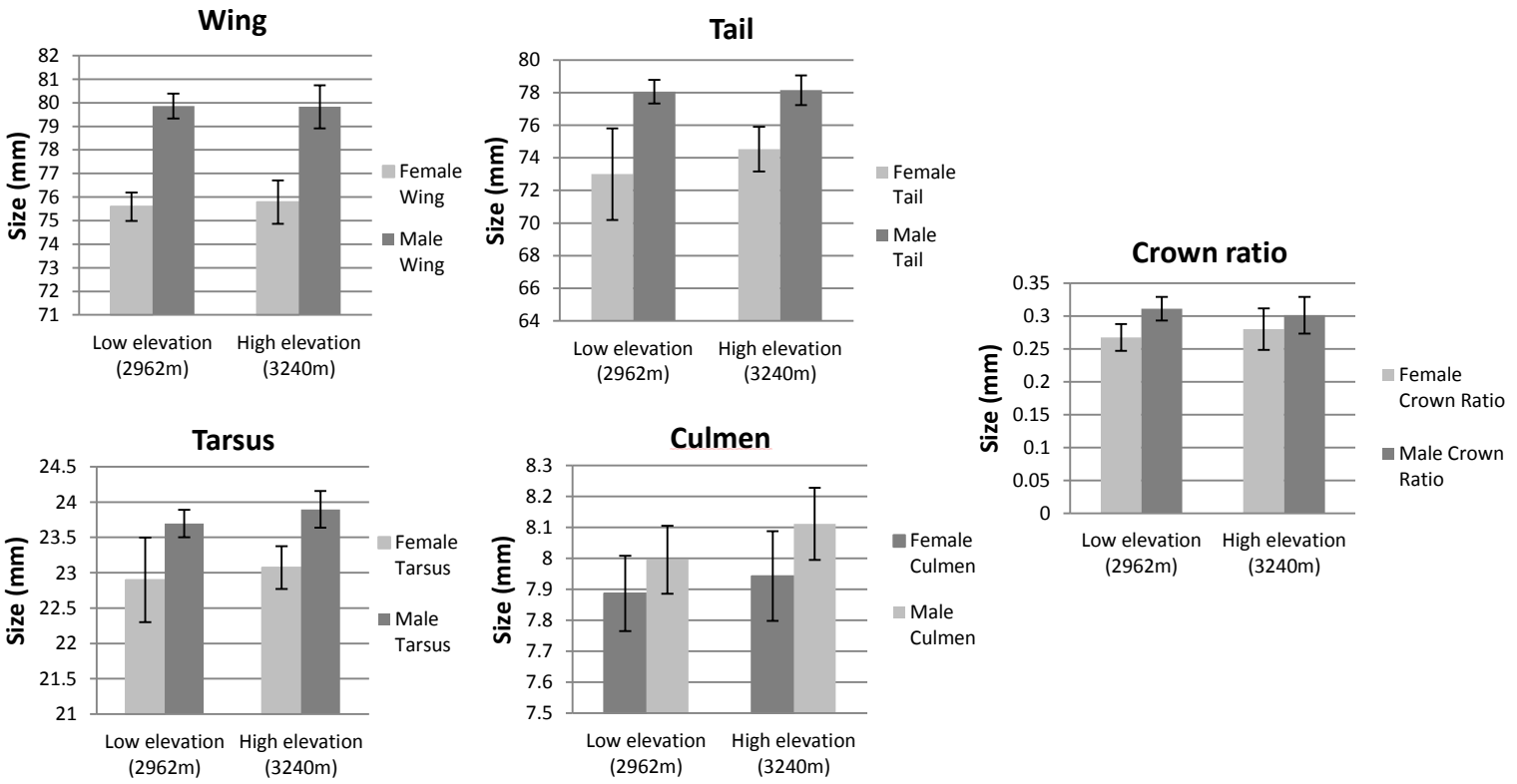

Figure 5: Comparisons of all female versus male mean feature sizes at low elevation to all female versus male mean feature sizes at high elevation. The 95% confidence intervals indicate that there is significant sexual dimorphism in all features at both elevations except for male CR at high elevation. At high elevation, male and female CR dimorphism is not significantly different.

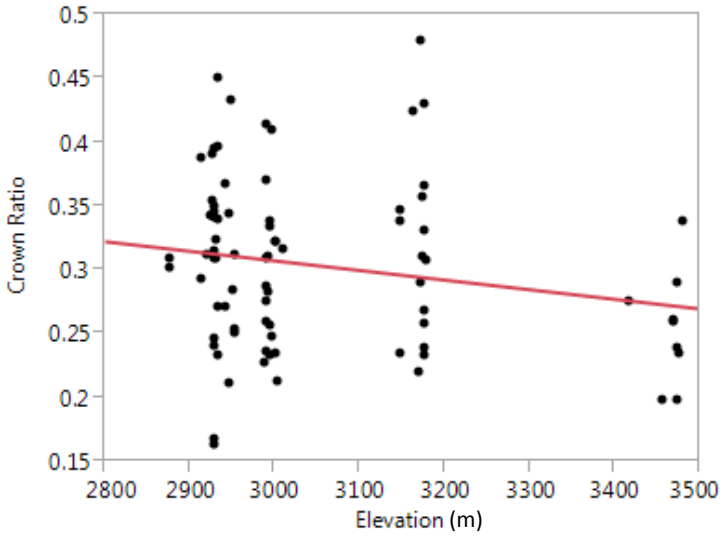

Figure 6: Linear regression of male crown ratio plotted against elevation of trap location. The R^2 value for the line is 0.04, showing that there is not a strong relationships between male CR and increasing elevation, but there is a slight negative trend in MWCS male CR with increasing elevation.

DISCUSSION

We predicted that the sexual dimorphic gap in MWCS pairs inversely correlates with elevation based on reduced sexual selection pressures at higher elevations. When sexual dimorphism in MWCS was analyzed for changes from low to high elevation, it was found that only the dichromatic feature of crown-stripe ratio was influenced in males, and not in pairwise comparisons of dimorphism (Figure 5). In all pairwise comparisons, elevation was not associated with wing, tail, tarsus, or culmen dimorphism (Figures 2-4). Dimorphism was first observed by comparing the size differences between confirmed nesting pairs, because this would account for the effects of female sexual selection pressure on male feature size, but we had an inadequate sample size of 6 pairs total, 4 low elevation pairs and 2 high elevation pairs. There was no significant change in the dimorphic gap between nesting pairs at low and high elevations ($p \geq 0.39$ for all features). This lack of significance was also observed in pairwise comparisons of potentially breeding birds and all total birds at low and high elevations, even though sample size was increased ($p \geq 14$ for all features). When the means of total low elevation male and female dimorphism were compared, however, we then observed a trend that male CR decreases with increasing elevation (Figures 5-6).

The reduction in male dichromatism supports our prediction that male morphological differences will decrease with increasing elevation due to reduced sexual selection pressure in less dense populations of MWCS and more parental care effort required of males at higher elevation conditions. Since CR is a previously reported badge of male dominance (Laubach et al. 2013), it is understandable that this feature would be most affected by reduced sexual selection pressure. In the 1997 Badyaev study on cardueline finches at high elevations, a similar result of unaffected dimorphism but reduced dichromatism with increasing elevation was found. The considerable energy and time expenditures of increased male parental care at high elevations may decrease time and energy available for molt and development of sexual traits (Bent and Austin 1968, A. Badyaev 1997).

Much future work could be done to improve this study, including a largely increased sample size for confirmed nesting pairs. We also assumed that high elevations indicated lower habitat quality according to previous literature (Cody 1981, Muller et al. 1997, Badyaev and Ghalambor 2001, Johnson, et al. 2006), but we did not survey our specific trap sites for ideal MWCS habitat quality. This could be quantified by surveying some habitat features such as willow size for preferred nesting, insect abundance for high efficiency nestling provision, or snowmelt date as an influence on vegetation and insect abundance later in the season.

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