

**Intrasexual Signaling Function of Crown Coloration in
Mountain White-Crowned Sparrows
(*Zonotrichia leucophrys oriantha*)**

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Abstract

There is evidence showing that large differences between age/sex categories in crown morphology of white-crowned sparrows are used to signal status. We investigated the role of more subtle crown characteristics, specifically the proportion of the crown that is white, as a signal used to mediate aggression. The response of resident white-crowned sparrows was measured when decoys with experimentally altered crowns were placed on their territory. We found significant differences between a large and small proportion white decoy treatments when the birds were still nesting early in the season, suggesting proportion white is used as a signal in this system. However, we found no significant results later in the season or when all the trials were analyzed as a whole, suggesting a strong seasonality effect in the responsiveness of the birds.

Introduction

Elaborate morphological displays in animals have long been of interest to behavioral and evolutionary biologists. Such traits suggest that there may be an adaptive value in the signal, as it is maintained despite significant energetic costs. There must also be constraints or costs associated with the display to keep the signal honest (reviewed in Vehrencamp, 2000). There is evidence that parasite infection can affect elaborate displays of plumage in birds (Figueroa et al., 1999; Horak et al., 2004). Thus, indication of parasite resistance may be the basis for selection on some plumage displays, and the constraint keeping them honest, under the “good genes” model of sexual selection (Hamilton and Zuk, 1982; Thompson et al., 1997). Elaborate plumage can also serve intraspecies communication purposes, such as status signaling (Fugle et al., 1984). We hypothesize crown coloration in Mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) may function as a signal mediating social dominance and aggression.

Mountain white-crowned sparrows are migratory passerine birds that winter in Mexico and Texas, and breed at high elevations in the Western United States and Canada, such as the Rocky Mountains of Colorado (Morton, 2002). The birds generally arrive around mid-May, depending on the last year's snowfall, and migrate again in September. They are socially monogamous, although approximately one third of all chicks born are fathered through extra-pair copulations (Morton, 2002). Both males and females are territorial, and males are known to fiercely guard their territory and their mates during the breeding season (Morton, 2002). Males and females both have distinctive black and white striped crowns, which consist of a white stripe running down the middle of the head, flanked by two black stripes known as eyebrows (Figure 1). There is natural variation in the size of the crowns, as well as in the percent of the crown that is white (Johannes Foufopoulos, unpublished data).

Some studies have suggested that the crowns function as social status signals (Fugle et al., 1984). There are clear differences between the crown characteristics of different age/sex categories. Adult males tend to have broader, whiter crowns than adult females, while juveniles have brown and tan crowns. Previous experiments have shown that the type of crown a bird possesses has a large effect on its place in the dominance structure of captive populations of white-crowned sparrows (Fugle et al, 1984). White-crowned sparrows with experimentally increased crowns were able to increase their social status and dominate individuals in their own true age/sex category through the "cheater" strategy of possessing dishonest crown coloration. Presumably, since conflicts rarely escalate into physical violence, the birds use the crown morphology to assess the status and condition of another bird and to predict the outcome of aggressive contest, thus saving both birds energy and possible injury. Fugle and his collaborators also proposed

“status signaling [due to natural variation] within age and sex categories is minimal or non-existent.” (Fugle et al., 1984: 91) In other words, crown characteristics indicated a very general social category, and only the extreme variation between age/sex categories was significant.

We have reason to believe, however, that the crowns may function to provide more specific information that would be beneficial in dominance contests. Data collected in previous summers at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado suggest that certain aspects of crown coloration, specifically the percent of the crown that is white (defined as the stripe width divided by crown width, as measured over the eye), is closely related to *Plasmodium* infection, and that infections of this kind have a significant effect on the survivorship of the birds (Johannes Foufopoulos, unpublished data). This suggests that crown coloration may be an honest signal of the health status of the birds, and that the variation present within age/sex categories may indeed be significant. White-crowned sparrows may therefore use subtle cues about the crown, such as percent of the crown that is white, to aid in decision-making in dominance conflicts and territory disputes. Such cues may indicate the fighting ability of the bird, which could save energy and the risk of injury if conflicts were decided based upon crown coloration characteristics. It may also be true that aggression levels are influenced by crown coloration if the trait is used by females for mate selection. Resident males may be more hostile to an intruder with a plumage signal displaying presumably “good genes” than they would to an intruder with a less impressive ornament, as their mate may be inclined to allow an impressive intruder to father some of her chicks through an extra-pair copulation. These ultimate explanations are not mutually exclusive, and would both

presumably cause the birds to regard birds with a larger percentage of white in their crown to be more of a threat.

To test these hypotheses, we measured the levels of aggression to an intruding white-crowned sparrow stuffed decoy with manipulated crown characteristics. We hypothesized that the percent white of the crown of an intruding white-crowned sparrow will mediate the level of aggression displayed by the resident male. We predicted that if the whiter crown would be perceived as a bigger threat, that the resident birds should respond more aggressively – specifically sing, alarm call, perch change, attack, and fly over the decoy more, approach to the decoy closer, have a shorter latency to respond, and respond for a longer total time to the decoy with a larger percent white.

Methods

This study was conducted using the population of Mountain white-crowned sparrows breeding near Gothic, Colorado. The study plots were established by Dr. Johannes Foufopoulos, and are located in the East River valley along the road north of the RMBL. The plots include grassland meadows, bare ground, shrubbery, fresh water, and tall conifer trees, which have been found to be necessary components of white-crowned nesting territories (DeWolfe and DeWolfe, 1962). The birds were trapped using Potter traps baited with millet, and are then banded with U.S. Fish and Wildlife Service bands and a unique combination of colored bands. They were measured for various physical characteristics including relevant aspects of crown size and coloration, and bled to collect data on parasite load, immune system condition, and hematocrit levels.

To determine the territory that a male bird defends, territories were mapped by observing locations from which a banded male sang, marking these locations on a map,

and then drawing polygons around the points to identify territory size. We performed trials on 22 males between 16 July and 1 August 2005. Three male mountain white-crowned sparrows found dead on these sites in previous years were stuffed and used as decoys. The proportion white of the crown was easily manipulated by pushing the feathers on the crown using forceps. The crown feathers stay in place when manipulated in this way until the next time they are adjusted. For each decoy, we used two experimental treatments: a large percent white crown (between 40-45% white), and a small percent white crown (between 25-30% white). These percentages were chosen from the extremes of the natural variation in proportion white in crown coloration. The decoys were presented by wiring and clipping them on to an appropriate branch on the territory. To call attention to the decoy, two minutes of white-crowned sparrow song was played at an amplitude of approximately 85 dB through a SONY SRS-77G speaker located within one meter of the decoy, and hidden in vegetation. Four different tracks of white-crowned song examples that have been recorded in previous years at RMBL were used, with a song rate of four songs per minute - a rate used in previous experiment (Gillman et al. in review). Each individual bird received both treatments using the same decoy and song, to control for possible confounding factors related to specific decoys and songs. The only difference between the two treatments an individual bird received was the percent white of the decoy's crown, which allowed us to attribute any differences between trials to this manipulation. Between individuals, the order of the treatments and the song used was randomized.

The resident male's response to the decoy was measured for 7 minutes from the start of the playback. We focused on the following potential responses: latency of response in seconds, total time of response (the time from the first behavior until the last

during the duration of the trial), closest approach to the decoy of the resident male, number of flights over the decoy, number of attacks on the decoy, perch changes, singing rate, and alarm call rate (Astheimer et al., 2000). Observations were spoken into a tape recorder and data were logged using the event-recording software JWatcher (Blumstein et al. 2000).

Responses were not normally distributed, nor were variances homogeneous. Thus, for each response, we tested for differences between treatments using the non-parametric Wilcoxon matched pair signed rank test. We also calculated effect size ranges by dividing the difference in the means of the two treatments by both the standard deviation for the big, and the standard deviation of the small, treatments. One of the 22 individuals was removed from the analysis because the bird did not appear on his territory during the second trial.

Observations and subsequent data analysis showed a strong seasonality effect on the responsiveness of the birds. For other projects being carried out on our study population of white-crowned sparrows, nest data such as hatching date, fledging date, and failure date is collected on nests every other day. Using these data we determined when 75% of the known nests had either fledged their young or had failed (Figure 2). We split our data using this Julian date (day 199) and then reanalyzed all results.

Less quantitative observations in the field suggested that there was a decline in the responsiveness of the birds specifically after Julian day 203. When we plotted the percent of nests fledged or failed, this date showed a large jump in the percent of nests finished (Figure 2). Since the many more nests finished between days 203 and 204 than between most other days, and since most nests had finished by then, using day 203

appeared to be a more useful cut-off point in the data. We also reanalyzed our data before and after this date.

In all cases, we interpret p -values < 0.05 as significant and $0.05 < p < 0.1$, as moderately significant. We interpret the magnitude of effect sizes following Welkowitz et al. (1982): small $d < 0.4$; moderate $0.41 < d < 0.79$; large $d > 0.8$.

Results

Overall, there was no significant effect of crown size on responsiveness for any of our measures when analyzing our all of our data without a cut-off date (Tables 1 and 2). However, there were non-significant tendencies for the birds to alarm call more to the larger proportioned white decoy ($p = 0.055$) and to respond longer to the whiter decoy ($p = 0.114$). The effect sizes were generally small, and none were large.

When we analyze our data using Julian day 199 – when 75% of the nests had finished – as a cut-off date, there were several significant results (Tables 1 and 2). We found that birds that had their first trial before this date ($N = 8$) showed a significantly higher perch-changing rate ($p = 0.0178$) and approached the decoy significantly closer ($p = 0.0352$) when the whiter decoy treatment was used. There were also moderately significant trends in alarm call rate ($p = 0.0630$) and total time of response ($p = 0.0687$), both showing a higher value towards the whiter decoy. These results are all in the direction expected from our hypothesis that a whiter crown is a bigger threat (Figure 3). In addition, the means for all behaviors measured were in the direction expected, except for flights over the model. Before day 199, most effect sizes were in the moderate to large range, and several effect sizes were very large (up to $d = 2.17$ for perch changes). For individuals that had their first trial after Julian date 199 ($N = 13$) birds did not

respond differently to the two different treatments. The effect size ranges were smaller than before day 199, and the majority of them were in the small range. Only 3 behaviors showed trends in their means in the expected direction.

When we analyzed our data using before and after day 203 – which we feel is a useful cutoff date for detecting seasonality effects – there were several significant results (Tables 1 and 2). We found birds that had their first trial before day 203 approached the model significantly closer ($p = 0.0301$) and alarm called more ($p = 0.0127$) when the whiter decoy treatment was used. There was a moderately significant trend indicating that the birds changed perch more ($p = 0.0595$) during trials with the whiter decoy as well. Before day 203, all behaviors measured showed a trend in their means in the direction expected, and most of the effect size ranges were moderate to large. Birds that had their first trial falling after day 203 showed no significant difference between the treatments for any behavior measured. Only one behavior showed a trend in its mean in the direction expected, and the majority of effect sizes were small.

Discussion

Our results demonstrate that resident male white-crowned sparrows respond differently to models with different crown sizes while still nesting. Response differences were not detected later in the season, nor were they detectable when we examined the entire data set. Thus, there seems to be a strong seasonal effect. Significant differences were all in the predicted direction consistent with the hypothesis that whiter crowns indicate a greater threat, which is in line with evidence that healthier birds have whiter crowns (Johannes Foufopoulos, unpublished data). We can thus conclude that when most

nests are active, the proportion white of the crown of an intruding bird is used as a cue by the defending male to influence the extent of his aggressive response.

A major challenge we faced in doing this study was working with the timing of the breeding season. We were unable to begin performing trials with the decoys until 16 July due to the time that it took to map the territories and stuff the decoys. By this time some nests had already failed or fledged, and many more were close to being finished. Simulation of an intruding male would presumably only be biologically significant to the resident birds if it was very early in the season when territories are being established, or if there was an active nest on their territory. Although we would have liked to perform our trials earlier in the season, we feel that we are justified in analyzing our data before biologically significant cut-off dates. When we analyzed our data in this way, we found that there were several significant results before the cut-off, and none after – both when we used day 199 and day 203 as this date. This suggests that when territoriality would matter most to the birds, our results were significant.

Our findings that there was a seasonality effect on the responsiveness of the birds informs us that care should be taken to insure future studies are performed earlier in the season. The seasonality effect, however, is quite interesting in its own right. There is evidence that white-crowned sparrows modulate their corticosterone levels between winter, breeding, and migration seasons (Astheimer et al., 1994; Romero et al., 1997), but they may also alter their hormone levels on a more subtle scale during the breeding season. It would be very adaptive for the birds to respond more aggressively only when their reproductive success was at stake, and once nests are finished there is much less riding on protection of a territory. It would be interesting to investigate the mechanism behind this phenomenon. We would suspect that hormones, such as testosterone, mediate

the responsiveness and territorial behavior of the birds (reviewed in Balthazart 1983), but would hormone levels be adjusted based on the presence of a nest, or would they be more generally synchronized with the time of the season when most nests are finishing?

Another problem we faced was the way in which white-crowns puff their features when they are presumably agitated (personal observations), which cannot be easily simulated with a decoy. Although our results make us confident that our methods were sound, our results may have been stronger if we would have been able to simulate crown puffing. It is also very likely that the birds move their features in a way that causes a larger percent of their crown to be white when puffing their features than when they are relaxed. This would help make the signal more prominent in aggressive situations while allowing the birds to lessen the risk of predation that an elaborate signal would presumably present. We found it easy to manipulate the amount of white on the crown just by pushing the features from side to side, suggesting that the birds would be able to do the same. They may move their features much in the same way as the red-winged blackbird dynamically alters the appearance of its epaulets. We also observed that the crown features along the border of the white stripe and the eyebrows are often partially white and partially black, further suggesting that the birds may be able to manipulate their crowns in real time depending on behavioral context. An interesting future study would be to paint the crowns of free-living male white-crowns at the beginning of the season, and track the success of the birds with respect crown coloration.

It would also be very interesting to investigate the cost to the defending bird of responding to an intruding male. There was a great deal of variance between our subjects in their level of response to the decoys – some responded a great deal to both treatments and some responded very little to either. We used a within-subject design to get at the

differences between the two treatments, while accounting for idiosyncratic differences. We intend to further analyze our data to see if the level of overall response of the birds is related to their health and condition, which we intend to measure by parasite infection, hematocrit levels, and the crown characteristics of the defending males used in our trials.

Finally, there are many interesting questions about how the crown signal remains honest. There has been work showing that potential cheating between age/sex categories is most likely not controlled by the social-control model of evolutionary stability in white-crowned sparrows (Fugle and Rothstein, 1987). If within-age/sex category variation in proportion white of the crown has evolved to be a cue to mediate aggressive response and to signal status, there must be a mechanism to keep this signal honest and keep subordinates from displaying the dominant signal. Our previous findings that proportion white is related to *Plasmodium* infection (Johannes Foufopoulos, unpublished data) suggest that signal honesty may be parasite-mediated. The nature of the information we presume this signal indicates – health, fighting ability, stamina, strength, etc - suggests that it is most likely a index signal or quality handicap signal (reviewed in Vehrencamp, 2000), and not a conventional signal, as the social-control model assumes. Index and quality handicap signals have physiological and physical constraints or signal production costs, which is consistent with our suspicion that the signal system may be parasite-mediated.

A study in which the crowns of free-living birds are painted could help reveal how this signal evolved. It would be interesting to see if birds with dishonest crowns – that is, crowns that are painted to be whiter than the unmanipulated crown of the bird – are more or less successful than control birds.

Figures and Graphs

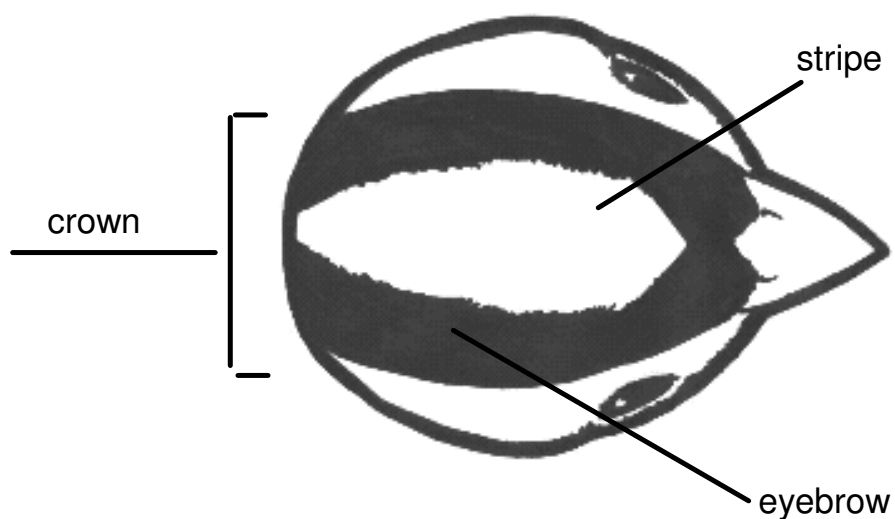


Figure 1. Crown Morphology of the white-crowned sparrow.

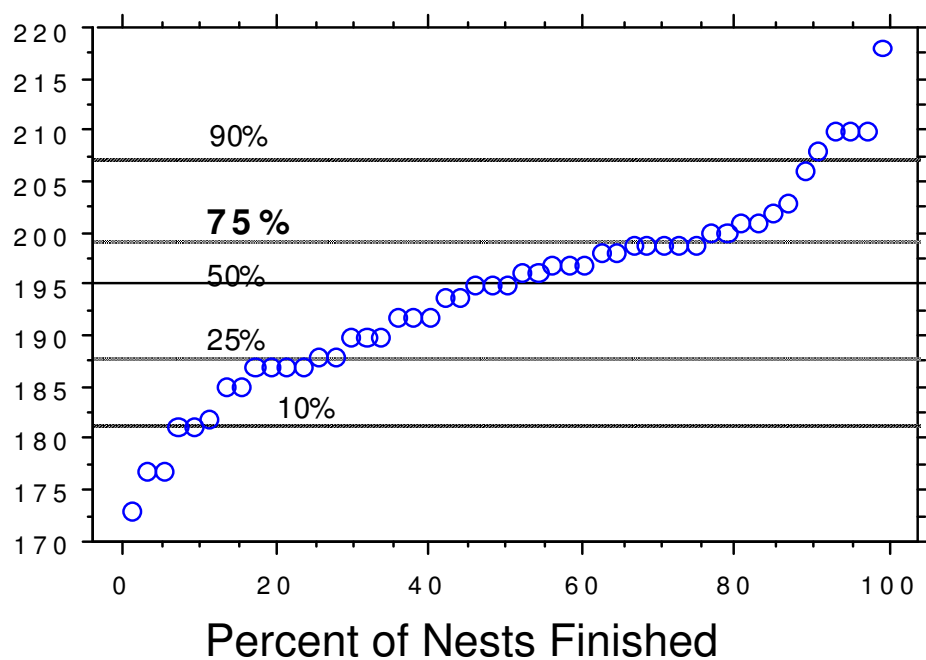


Figure 2. Percent of nests finished (defined as either fledged or failed) by Julian date. Lines are drawn at 10, 25, 50, 75, and 90 percent.

Table 1. p-values and effect sizes (d) for alarm calls, total response time, closest approach, and perch changes for all trials, and for before and after each cut-off date.

	Alarm calls		Total response time		Closest approach to decoy		Perch changes	
	p-value	d	p-value	d	p-value	d	p-value	d
All trials (N=21)	.0552	.35-.69	.1138	.37-.41	.1588	.32-.48	.3600	.16-.17
Before 75% finished (N=8)	.0630	.56-1.4	.0687	.91-1.3	.0352	.54-3.3	.0178	.70-2.2
After 75% finished (N=13)	.3863	.19-.20	.6002	.0002	.7798	.05-.06	.6563	.06
Before day 203 (N=14)	.0127	.51-1.3	.1094	.69-1.1	.0301	.60-1.5	.0595	.51-1.3
After day 203 (N=7)	.7532	.13-.15	.8658	.23-.28	.3105	.44-1.3	.2489	.46-.17

Table 2. p-values and effect sizes (d) for songs, latency to respond, and flights over the decoy for all trials, and for before and after each cut-off date.

	Songs		Latency to respond		Flights over decoy	
	p-value	d	p-value	p-value	d	p-value
All trials (N=21)	.6747	.003-.004	.4979	.6747	.003-.004	.4979
Before 75% finished (N=8)	.8539	.12-.27	.1614	.8539	.12-.27	.1614
After 75% finished (N=13)	.4405	.09-.10	.6002	.4405	.09-.10	.6002
Before day 203 (N=14)	.7667	.04-.08	.3305	.7667	.04-.08	.3305
After day 203 (N=7)	.7150	.07	.7353	.7150	.07	.7353

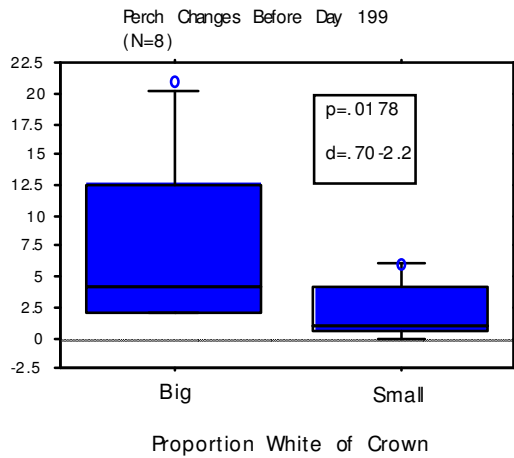
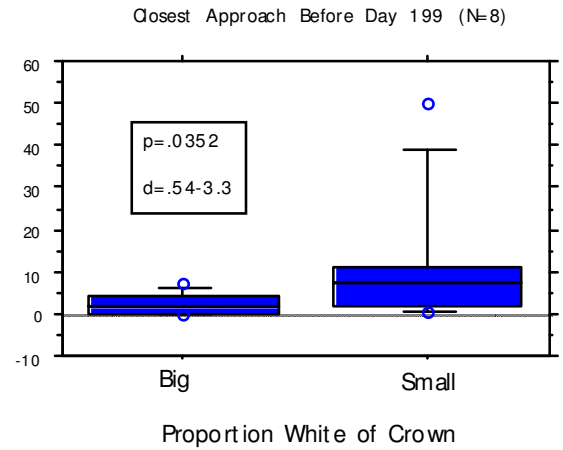
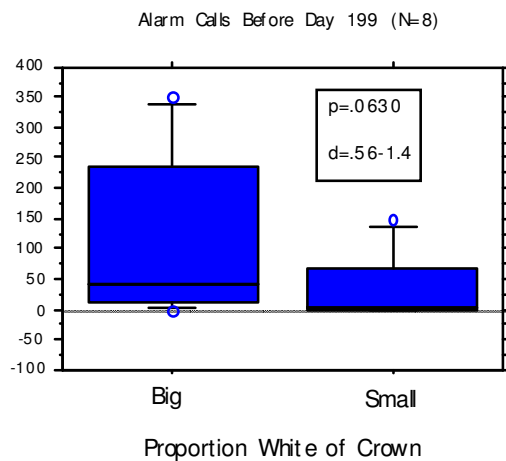
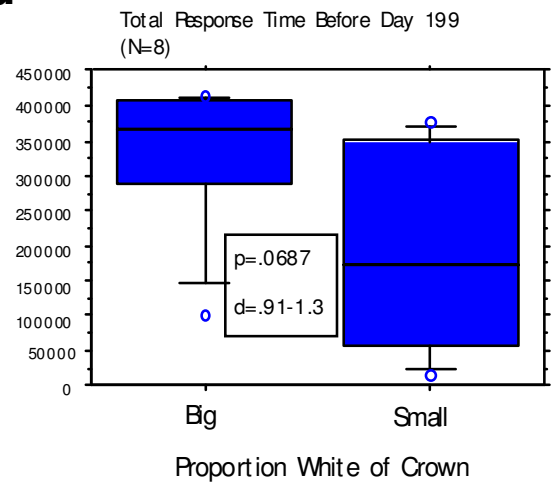
a**b****c****d**

Figure 3. Box plots of (a) perch changes, (b) closest approach to the decoy, (c) alarm calls, and (d) total response time for the big and small proportion white decoy treatments before day Julian day 199.

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Literature Cited

- Astheimer, L. B., W. A. Buttemer, J. C. Wingfield. 1994. Gender and Seasonal Differences in the Adrenocortical Response to ACTH Challenge in an Arctic Passerine, *Zonotrichia leucophrys gambelii*. *General and Comparative Endocrinology*. 94: 33-43
- Astheimer, L. B., W. A. Buttemer, J. C. Wingfield. 2000. Corticosterone Treatment Has No Effect on Reproductive Hormones or Aggressive Behavior in Free-living Male Tree Sparrows, *Spizella arborea*. *Hormones and Behavior*. 37: 31-39.
- Balthazart, J. 1983. Hormonal Correlates of Behavior. *Journal of Avian Biology*. 7: 221-365
- Blumstein, D. T., Evans, C. S. & Daniel, J. C. 2000 JWatcher 0.9. An introductory user's guide. <http://www.jwatcher.ucla.edu>.
- DeWolfe, B. B., and R. H. DeWolfe. 1962. Mountain White-Crowned Sparrows in California. *Condor*. 64: 378-389.
- Figuerola, J., E. Munoz, R. Gutierrez, and D. Ferrer. 1999. Blood Parasites, leucocytes and Plumage Brightness in the Cirl Bunting, *Emberiza cirlus*. *Functional Ecology*. 13: 594-601.
- Fugle, G. N., S. I. Rothstein, C. W. Osenberg. 1984. Signals of Status in Wintering White-Crowned Sparrows, *Zonotrichia leucophrys gambelii*. *Anim. Behav.* 32: 86-93.
- Fugle, G. N., and S. I. Rothstein. 1987. Experiments on the Control of Deceptive Signals of Status in White-Crowned Sparrows. *The Auk*. 104: 188-197
- Gillman, S., D.T. Blumstein, and J. Foufopoulos. In 2nd review. The effect of

haemosporidians on white-crowned sparrow singing behaviour. *Anim. Behav.*

Hamilton, W.D., and M. Zuk. 1982. Heritable True Fitness and Bright Birds: A Role for Parasites? *Science*. 218: 384-387.

Horak, P., L. Saks, U. Karu, I. Ots, P. Surai, and K. McGraw. 2004. How Coccidian Parasites Affect Health and Appearance of Greenfinches. *Journal of Animal Ecology*. 73: 935-947

Morton, M. 2002. *The Mountain White-Crowned Sparrow: Migration and Reproduction at High Altitude*. Allen Press: Lawrence, Kansas.

Romero, L.M., M. Ramenofsky, and J.C. Wingfield. 1997. Season and Migration Alters the Corticosterone Response to Capture and Handling in an Arctic Migrant, the White-Crowned Sparrow (*Zonotrichia leucophrys gambelii*). *Comparative Biochemistry and Physiology*. 166C: 171-177

Thompson, C.W., N. Hillgarth, M. Leu, and H.E. McClure. 1997. The American Naturalist. 149: 270-294.

Vehrencamp, S. 2000. Handicap, Index, and Conventional Signal Elements of Bird Song. In Animal Signals: Signaling and Signal Design in Animal Communication. Ed. By Y. Espmark, T. Amundsen, and G. Rosenqvist. pp277-300. Tapir Academic Press: Trondheim, Norway.

Welkowitz, J., Ewen, R. B., & Cohen, J. 1982. Introductory Statistics for the Behavioral Sciences. Harcourt Brace Jovanovich, Publishers: San Diego, CA.