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CAROTENOID-BASED MALE PLUMAGE PREDICTS PARENTAL INVESTMENT IN THE AMERICAN REDSTART

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ABSTRACT.—We examined whether male plumage coloration signals parental quality in the American Redstart (*Setophaga ruticilla*), a highly ornamented, migratory warbler. We measured the relationship between both adult male arrival date and phenotype (morphology, melanin- and carotenoid-based plumage), and parental care levels of both parents. Males with brighter flank feathers made more visits to the nest and spent more time at the nest, consistent with the 'good-parent hypothesis'. Female parental care (number of visits) was negatively correlated with intensity of red of her mate's tail feathers and positively associated with her mate's parental effort. These data indicate offspring of brighter males receive more care from both parents. Our results suggest carotenoid-based plumage traits of male American Redstarts may have an important role in intersexual signaling, and add to our understanding of the evolution of multiple ornaments. *Received 10 July 2009. Accepted 20 January 2010.*

Three major models have been developed to explain patterns of association between male ornamentation and parental care. The 'good-parent' hypothesis predicts that when paternal care influences offspring viability directly, males should signal their ability to provide for offspring to prospective mates, and more attractive males should provide more care (Heywood 1989, Hoelzer 1989, Norris 1990, Hill 1999, Siefferman and Hill 2003). Some evidence suggests female parental care does not decrease in response to increased care by their mate, resulting in a net benefit to the offspring of 'good-parent' males (Sanz et al. 2000, Schwagmeyer and Mock 2003, but see Wright and Cuthill 1989, 1990; Markman et al. 1995). Alternatively, the 'differential allocation' hypothesis predicts females mated to more attractive males increase their own level of parental effort to avoid desertion by their mates and to enhance their fitness through production of high-quality offspring (Burley 1986, 1988; Studd and Robertson 1988; Badyaev and Hill 2002). In this model, attractive males restrict their parental investment to allocate more energy towards their own survival, resulting in a negative relationship between male attractiveness and care (Burley 1986, 1988; Møller and Thornhill 1998). A third alternative, the 'trade-off hypothesis', similarly proposes that attractive males provide less care towards their offspring (to be able to seek extra mating opportunities), resulting in a negative relationship between male attractiveness and level of care (Williams 1966, Magrath and Komdeur 2003, Mitchell et al. 2007). Several studies have failed to find a relationship between male plumage and parental care (Rohde et al. 1999, Smiseth et al. 2001, Cooper and Ritchison 2005). Some of these studies, however, involve species with multiple ornaments whose signal function and context are not well understood.

The American Redstart (*Setophaga ruticilla*), a small (7–8 g) neotropical migratory warbler, is particularly suited for studies of male plumage coloration and parental care. American Redstarts are sexually dichromatic and yearling males exhibit delayed plumage maturation, suggesting strong sexual selection on plumage coloration. Adult males are black with bright orange plumage patches on their wings, tail, and sides of the breast (flanks), and a white or black breast, depending on bib size (Sherry and Holmes 1997). The plumage of adult male American Redstarts is highly variable, both in bib size (melanin-based plumage) and orange (carotenoid) coloration (Lemon et al. 1992, Kappes et al. 2009, Reudink et al. 2009b). Recent evidence suggests tail feathers of American Redstarts have an important role in intrasexual signaling during the non-breeding season, where males with brighter tails occupy higher quality winter territories (Reudink et al. 2009a). Additionally, both bib size (Perreault et al. 1997) and flank redness have been linked to a male's ability to secure paternity at his nest during

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the breeding season, and tail brightness to a male's chances of achieving polygyny (Reudink et al. 2009b). In particular, flank feathers may function as a sexual signal in American Redstarts, as males will puff out their breast and flank feathers in a ''fluff display'' during courtship (Sherry and Holmes 1997).

Our objectives were to quantify variation in plumage ornamentation, morphology, and arrival behavior of adult male American Redstarts, and levels of parental care provided by both parents to offspring to identify which features may provide a reliable signal to females of male parental effort in this highly ornamented songbird. We predicted male plumage coloration would correlate with levels of parental care, based on recent evidence suggesting that different plumage regions may be used to signal information in different contexts (Reudink et al. 2009a, b; Kappes et al. 2009); however, we made no *a priori* predictions as to which plumage region(s) might be important.

METHODS

Field Data and Feather Collection.—We conducted field work at the Queen's University Biological Station in southeastern Ontario, Canada (44° 34′ N, 76° 19′ W), during two consecutive breeding seasons (May–Jul 2006–2007). The 60-ha study site is a mixed deciduous forest, largely dominated by sugar maple (*Acer sacchurum*) and eastern hop-hornbeam (*Ostrya virginiana*). We surveyed transects from 0600 to 1200 hrs EST each day from 1 May to 1 July across the study site to record the arrival date for each individual. We designated arrival date as the number of days after the arrival of the first male each season (i.e., first date of male arrival = 0; male that arrived 5 days later = 5) to standardize arrival date across seasons. We captured adult male redstarts on their respective territories using mist nests and song playback, usually within 7 days of arrival, and females during the nesting phase using mist nets near their nest location. All birds were banded with a Canadian Wildlife Service aluminum band (permit # 10766C) and a unique combination of three color bands (excluding red and orange in males); we recorded unflattened wing chord length (±1.0 mm) as a measure of relative body size. We plucked a single tail feather (third rectrix; R3) and 12–15 orange flank feathers from each male (Quesada and Senar 2006) (CWS collection permit # CA 0154). We classified adult male bib size using a 1–5 scale (1 = small amount of black plumage, 5 = large amount of black plumage with intermediates given half points) following Lemon et al. (1992).

Parental Care Observations.—We monitored American Redstart pairs each season (~40 pairs/season) daily until their nest was found, and observed nests every 1–2 days following completion of nest-building until hatching and recorded the number of young. We confirmed the number of nestlings again on day 5 after hatching and continued to monitor nests until fledging. Fifty nests were observed: 25 in 2006 and 25 in 2007. We erected ground-based video cameras (Canon ZR500) on tripods >5 m from the base of the nest tree on days 5 and 7 after hatching to record parental effort. Cameras were focused on the nest and its immediate (<20 cm) surroundings, and recording occurred between 0600 and 0900 hrs EST. Each recording lasted 120 min and the first 5 min were discarded to allow parents time to recover from human disturbance. The remaining 115 min were used to calculate provisioning rates of males and females, and the time each parent spent at the nest. We recorded and analyzed a total of 148 hrs of video from 38 nests (*n* reduced due to high predation rates). A trained observer recorded the measures of parental care through binoculars at a distance >10 m from the nest using a stopwatch if there were more nests to be watched than cameras available (2006—day 5: $n = 8$, day 7: $n = 5$; 2007—day 5: $n = 2$, day 7: $n = 2$). There was no difference between video camera and trained observer nest watches in either the number of visits to the nest, or total time at the nest (2-sample *t*-test assuming unequal variance, all P values > 0.09). Nests depredated between days 5 and 7 were excluded from analysis (2006: $n = 7$; 2007: $n = 5$).

We recorded both the total (i.e., sum of days 5 and 7) number of visits to the nest and the total nest attendance (in sec) for males and females as measures of parental care. Both variables are effective measures of parental effort in small insectivorous birds that make frequent trips to the nest (Saetre et al. 1995). Total time at the nest for males may include activities such as vigilance and removal of fecal sacs, but does not necessarily represent a direct benefit to rearing of offspring as it would for females (i.e., brooding); trips to the nest may serve as a more accurate representation of care, as males are continually bringing food. We divided both total number of visits per hour and total nest attendance per hour by the number of chicks present in the nest to standardize for brood size and recording time. We compared standardized parental care variables with raw data to ensure that parental effort/hr/chick was representative of total parental effort (linear regressions, all $P < 0.0004$). Six males in our study were polygynous; however, primary and secondary nests were temporally separated, and we included only data from the primary nest (during the period when the male was caring exclusively for the first nest). All individuals were identifiable via color bands, and we were able to ensure that our data set contained no pair duplications across both years.

Color Analysis.—We mounted feathers from each male on black paper (Colorline Ebony #142), and stacked flank feathers as they would naturally lie on the bird (Siefferman and Hill 2003, Quesada and Senar 2006). Mounting feathers on a black background is a standard technique (Siefferman and Hill 2003, Quesada and Senar 2006), and the paper used had low (<5%) reflectance, indicating it would have a minimal impact on our analysis. We omitted samples from further analysis ($n = 5$) in instances where there were too few flank feathers or the orange area on the tail feather was too small to obtain reliable readings. We analyzed male plumage and parental care observations for both males and females from 16 nests in 2006 and 17 nests in 2007.

We gathered reflectance spectra from flank and tail feathers of each male using a PX-2 pulsed xenon light source attached to an Ocean Optics USB2000 spectrometer (Dunedin, FL, USA). We took 25 readings throughout the orange (carotenoid-based) region for both flank and tail feathers following Reudink et al (2009b). We gathered raw reflectance data into 10 nm bins from 320 to 700 nm using CLR1.0.3 (Montgomerie 2008), and averaged across the 25 measurements. We calculated brightness for tail and flank feathers by averaging percent reflectance from 320 to 700 nm (color variable 1: 'brightness'). The carotenoid-based plumage of American Redstarts consists of peaks in both the UV and red/orange regions of the spectrum. We used principal component analysis (PCA) to collapse the spectrum into a smaller set of independent variables that describe the measures of hue and chroma based on shape of the curve while controlling for variation in brightness (Cuthill et al. 1999, Montgomerie 2006, Stein and Uy 2006, Reudink et al. 2009b). We verified this method by calculating hue and chroma using the equations: $\text{hue}=\arctan([R_{415-510} - R_{320-415})/R_{320-700}]/[R_{575-700} - R_{415-575})/R_{320-700}])$, UV chroma $= R_{320-415}/R_{320-700}$, and red chroma $= R_{575-700}/R_{320-700}$.

Flank PC I described 85.5% of the variation in shape of the reflectance curve, and loaded positively on short (UV) wavelengths and negatively on the longer (red/orange) wavelength region of the spectrum. Flank PC I associated negatively with both hue ($r^2 = 0.68$, $n = 32$, $P < 0.001$) and red chroma ($r^2 = 0.99$, $n = 32$, $P < 0.001$), and associated positively with UV chroma ($r^2 = 0.81$, $n = 32$, $P < 0.001$). Tail feather PC I explained 48.4% of the variation, and loaded positively on both the shorter and longer wavelength regions of the spectrum, and negatively on intermediate wavelengths. Tail PC I associated positively with hue ($r^2 = 0.16$, $n = 33$, $P = 0.02$) and red chroma ($r^2 = 0.61$, $n = 33$, $P < 0.001$), but had no association with UV chroma ($r^2 < 0.001$, $n = 33$, $P = 0.94$). The first principal component from both plumage regions was used to describe 'redness' (color variable 2 = 'redness'), where birds with greater 'redness' have more negative flank PC I values, and more positive tail PC I values.

Statistical Analysis.—All statistics were performed using JMP 7.0 (SAS Institute 2007) and R 2.6.1 for Windows (R Development Core Team 2007). We pooled data across both years of study and, in instances where data for the same individual were collected across 2 years ($n = 3$), avoided pseudoreplication by randomly selecting 1 year to exclude. We used paired *t*-tests to compare the parental care variables across both observation days (for both males and females), as well as across gender, and linear regression to examine the relationship between a pair's number of visits to the nest, and total nest attendance. All plumage variables were tested for co-linearity using Pearson's pairwise analysis. We applied backwards stepwise multiple regressions with parental care variables (male visits/hr/chick, female visits/hr/chick, male time at the nest/hr/chick, female time at the nest/hr/chick) as the response variable to calculate the factors that best predicted both male and female parental care. We used measures of male tail brightness, tail redness (PC I), flank brightness, flank redness (PC I), bib score, body size, year, and arrival date as our main effects in each model.

RESULTS

Male American Redstarts did not show a difference in mean time (sec ± SD) spent at the nest between days 5 (108.21 ± 112.53) and 7 (77.98 ± 75.66) (paired *t*-test, $t_{32} = 1.65$, $P = 0.11$); however, mean number of visits for males on day 7 (1.92 ± 0.73) after hatching were greater than on day 5 (1.52 ± 0.81) (paired *t*-test, $t_{32} = -2.89$, $P = 0.007$). Females showed no difference in the mean number of visits to the nest between days 5 (1.56 ± 0.59) and 7 (1.72 ± 0.68) (paired *t*-test, $t_{32} = -1.78$, $P = 0.09$), but spent significantly more time at the nest on day 5 (778.04 ± 484.18 sec) than day 7 (616.68 ± 523.90 sec) (paired *t*-test, $t_{32} = 3.54$, $P = 0.001$). Females did not visit the nest more or less frequently than males (paired *t*-test, $t_{32} = 1.27$, $P = 0.21$), but did spend a greater amount of time at the nest (paired *t*-test, $t_{34} = -7.91$, $P < 0.0001$). There was a significant positive relationship between each member of a breeding pair for number of visits ($r^2 = 0.21$, $F_{1,31} = 8.17$, $P = 0.008$) and nest attendance ($r^2 = 0.30$, $F_{1,31} = 13.11$, $P = 0.001$).

Pairwise correlations between all male plumage variables revealed that tail brightness increased with decreasing tail redness (PC I) ($r^2 = 0.12$, $F_{1,31} = 4.30$, $P = 0.05$). No other plumage variables were significantly correlated.

Plumage Color and Provisioning.—Results of a backwards stepwise multiple regression revealed total number of male visits/hr/chick was significantly predicted by the brightness of flank feathers (Table 1). This data set contains one high value for flank brightness (Fig. 1). This point is not due to a technical error in measurement, as readings taken before and after this point were within the normal range, and this point remained high after repeated measurements. This individual was also within the normal range for all other measures. The correlation between male flank brightness and number of visits/hr/chick remained significant when this point was excluded (Fig. 1). Flank brightness was also a significant predictor of total time spent by males at the nest (Table 1). Female visits were significantly predicted by year and mate's tail redness (Table 1), where females in 2007 made more trips to the nest than those in 2006 (two-sample *t*-test assuming unequal variance, $t_{25} = -2.77$, $P = 0.01$). There was a negative relationship between female visits to the nest and male tail redness, where females which made fewer trips to the nest were paired to males with redder tails (Fig. 2). None of the remaining variables related to arrival date, morphology, or plumage predicted male or female levels of parental care.

DISCUSSION

The brightness of flank feathers in adult male American Redstarts predicted their total number of visits to the nest, and total time spent at the nest. Our results are consistent with the 'good-parent' hypothesis and suggest that flank feather brightness may provide a reliable signal of parental effort in adult male American Redstarts. A significant negative correlation was found between number of female visits to the nest and redness of her mate's tail feathers. We found a strong positive correlation between breeding partners for visits to the nest, and nest attendance.

The 'good-parent' hypothesis predicts that attractive males should signal their ability to provide increased levels of parental care, compared to less attractive males (Heywood 1989, Hoelzer 1989). We show brightness of male carotenoid-based flank plumage is associated with levels of male parental care. Plumage brightness has been found to predict mating success in other species, such as Golden-collared Manakins (*Manacus vitellinus*) (Stein and Uy 2006). In addition, it has been linked to stronger immune response to novel antigens (Saks et al. 2003a), suggesting it has an important role in signaling male health status and, potentially, the ability to provide for offspring.

The pairwise correlation analysis among all male plumage variables revealed only one significant association; tail brightness increased with decreasing tail redness. This suggests that in American Redstarts, plumage brightness does not necessarily correspond to greater feather carotenoid content (Saks et al. 2003b, Andersson and Prager 2006). Instead, plumage brightness may be influenced by the underlying structural matrix of feathers (Shawkey and Hill 2005); several studies have linked structural-based colors with condition/individual quality (Doucet 2002, Doucet and Montgomerie 2003) as well as the level of male parental care (Siefferman and Hill 2003). However, the interactions between structural and pigment-based components of feather coloration remain poorly understood and further research is needed to elucidate patterns of plumage brightness.

Recent work by Kappes et al. (2009) with a smaller sample of more southerly breeding

TABLE 1. Multiple regression models examining male and female parental care variables in relation to standardized arrival date, wing length, bib score, flank feather brightness and redness, and tail feather brightness and redness. Initial models are shown for each model. Final models (i.e., models following removal of nonsignificant effects by stepwise backward deletion) are also shown where predictor variables were significant. Sample size increased in the final models where removal of nonsignificant predictor variables added additional individuals to the model that were missing information for these variables.

	Predictor variables	β	F	P
Male visits/hr/chick (initial model, $n = 31$, $r^2 = 0.46$)	Year	0.13	0.09	0.77
	Standardized arrival	0.01	0.26	0.62
	Wing	0.06	0.51	0.48
	Bib score	0.06	0.15	0.70
	Flank brightness	0.12	3.91	0.06
	Flank redness (PC I)	0.03	0.92	0.35
	Tail brightness	−0.03	0.12	0.74
	Tail redness (PC I)	−0.04	1.37	0.25
Male visits/hr/chick (final model, $n = 32$, $r^2 = 0.37$)	Flank brightness	0.11	15.004	**0.0006**
Male visits/hr/chick (initial model, $n = 31$, $r^2 = 0.19$)	Year	22.45	0.18	0.68
	Standardized arrival	1.34	0.20	0.66
	Wing	1.50	0.03	0.88
	Bib score	−6.74	0.14	0.71
	Flank brightness	4.81	0.52	0.48
	Flank redness (PC I)	3.40	0.84	0.37
	Tail brightness	1.31	0.02	0.89
	Tail redness (PC I)	−2.19	0.24	0.63
Male visits/hr/chick (final model, $n = 32$, $r^2 = 0.1$)	Flank brightness	6.39	4.34	**0.05**
Female visits/hr/chick (initial model, $n = 31$, $r^2 = 0.42$)	Year	0.69	4.15	0.05
	Standardized arrival	−0.02	0.69	0.42
	Wing	0.02	0.10	0.76
	Bib score	0.06	0.30	0.59
	Flank brightness	−0.02	0.17	0.69
	Flank redness (PC I)	0.004	0.03	0.87
	Tail brightness	0.03	0.19	0.67
	Tail redness (PC I)	−0.05	3.24	0.09
Female visits/hr/chick (final model, $n = 32$, $r^2 = 0.33$)	Year	0.49	9.30	**0.005**
	Tail redness (PC I)	−0.05	8.16	**0.008**
Female visits/hr/chick (initial model, $n = 31$, $r^2 = 0.14$)	Year	357.2	1.14	0.30
	Standardized arrival	−9.75	0.27	0.61
	Wing	43.61	0.49	0.49
	Bib score	64.12	0.31	0.58
	Flank brightness	−28.60	0.46	0.50
	Flank redness (PC I)	27.75	1.39	0.25
	Tail brightness	61.82	1.11	0.30
	Tail redness (PC I)	−5.15	0.03	0.86
Female visits/hr/chick (final model, $n = 33$)	No significant predictors			

American Redstarts, found males with brighter flanks provisioned less than duller males, and those with less red flanks sired more total young. Flank brightness and tail brightness in our study, in agreement with Kappes et al. (2009), were not related suggesting the two plumage regions may be used as signals in different contexts. Flank redness (PC I) is related to genetic paternity (indicating that it may act as a measure of genetic quality) (Reudink et al. 2009b), and our results suggest that flank brightness may also act as an intersexual signal of parental care.

Recent evidence suggests American Redstart tail feather coloration acts as an intrasexual signal. Specifically, tail brightness is related to both territory quality in wintering areas (Reudink et al.

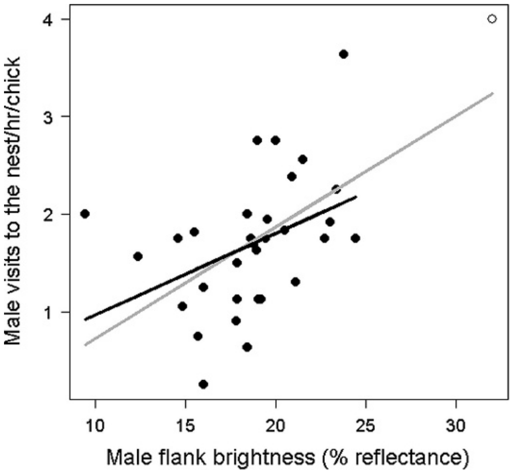

FIG. 1. Linear regression of male visits to the nest (standardized/hr/chick) on flank feather brightness. Gray regression line (r^2 = 0.34, $F_{1,30}$ = 15.29, P = 0.0005) includes high value (open circle). Black regression line (r^2 = 0.16, $F_{1,29}$ = 5.66, P = 0.02) excludes this individual.

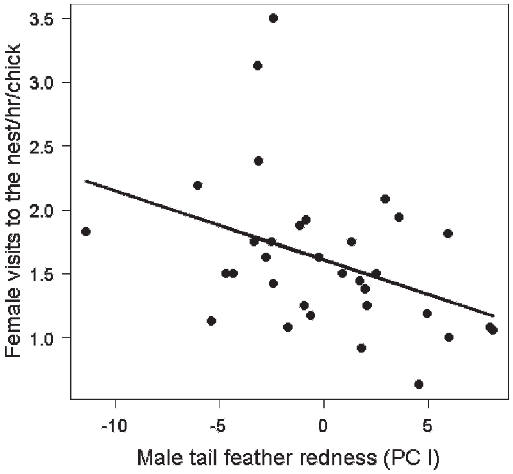

FIG. 2. Linear regression of female visits to the nest (standardized/hr/chick) on tail feather redness (PC I) (r^2 = 0.15, $F_{1,31}$ = 5.60, P = 0.02). X-axis values are from low to high, where individuals with more negative score (e.g., −10) have tails with lower redness than those with higher values.

2009a) and polyterritorial polygyny in breeding areas (Reudink et al. 2009b). We found no relationship between tail brightness and either male or female parental care; however, female visits to the nest were negatively correlated with the redness of male tail feathers. Plumage redness is often associated with greater carotenoid deposition into the feather structure; high quality birds would be assumed to have redder feathers (Saks et al. 2003b). However, the redness of American Redstart tail feathers has been found to significantly decrease across subsequent breeding seasons (Reudink et al. 2009b). One suggestion is that female American Redstarts alter their level of parental care based on the perceived age of their mates with females providing more care when paired with older males, although we do not currently have the data to address this possibility.

Neither male bib size nor arrival date was correlated with any measure of parental care by males or females. Consistent with previous studies (Perreault et al. 1997, Reudink et al. 2009b, but see Lemon et al. 1992), bib size does not appear to have a prominent signaling role; however, arrival date has previously been shown to be an important predictor of reproductive success (Norris et al. 2004, Reudink et al. 2009c). Reudink et al. (2009c) demonstrated that early arriving males were more likely to achieve polygyny than those which arrived at a later date. However, when males occupy multiple territories and provide care for multiple nests, there may be a limit to the amount of care one male can provide, as evidenced by male American Redstarts providing relatively less care at their second nest, than at their primary nest (Secunda and Sherry 1991; RRG, unpubl. data).

The strong relationship between both female and male visits to the nest, and nest attendance suggests that offspring of more ornamented males are receiving the benefit of more care by both parents. Our results also suggest the potential for assortative mating, where females that provide more care pair with males which do the same. These data conform to models which suggest that equality of investment in species with biparental care is an evolutionarily stable strategy (offspring receive a benefit from both parents providing high amounts of care, reviewed in Wright and Cuthill 1989). Unfortunately, our data do not allow us to differentiate the effects of individual feeding effort from those of territory quality, as both male and female feeding rates could be affected by availability of food on their territory. It is also possible that male coloration is not indicative of parental care, but rather the association arises from brighter males obtaining higher quality territories and provisioning chicks more often with less effort. Male American Redstarts able to secure high quality territories during the overwintering season arrive earlier in breeding areas and show higher levels of realized reproductive success (Reudink et al. 2009c). One possibility is that socially dominant males arriving earlier from high quality winter territories also obtain higher quality territories during the breeding season, in which case we should observe a relationship between arrival and provisioning. We did not observe a relationship between male arrival date and parental care, but direct measurements of territory quality are needed to discern how variations in individual and territory quality influence provisioning.

The brightness of male American Redstart flank feathers may have an important role in intersexual signaling but further research is needed to clarify female mate choice in this system. Experimental approaches that measure female response to changes in male ornamentation would be most useful. Research on the ornamental qualities of female plumage to examine if females with brighter carotenoid-based plumage provide more for their offspring and pair with brighter males would also be informative.

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LITERATURE CITED

ANDERSSON, S. AND M. PRAGER. 2006. Quantifying colors. Pages 41–89 *in* Bird coloration. Volume 1, Mechanics and measurements (G. E. Hill and K. J. McGraw, Editors). Harvard University Press, Cambridge, Massachusetts, USA.

BADYAEV, A. V. AND G. E. HILL. 2002. Paternal care as a conditional strategy: distinct reproductive tactics associated with elaboration of plumage ornamentation in the House Finch. Behavioral Ecology 13:591–597.

BURLEY, N. 1986. Sexual selection for aesthetic traits in species with biparental care. American Naturalist 127: 415–445.

BURLEY, N. 1988. The differential allocation hypothesis: an experimental test. American Naturalist 132: 611–628.

COOPER, S. W. AND G. RITCHISON. 2005. Nestling provisioning by male and female Yellow-breasted Chats: no relationships between morphology and parental care. Journal of Field Ornithology 76: 298–302.

CUTHILL, I. C., A. T. D. BENNETT, J. C. PARTRIDGE, AND E. J. MAIER. 1999. Plumage reflectance and the objective assessment of avian sexual dichromatism. American Naturalist 153: 183–200.

DOUCET, S. M. 2002. Structural plumage coloration, male body size, and condition in the Blue-black Grassquit. Condor 104: 30–38.

DOUCET, S. M. AND R. MONTGOMERIE. 2003. Multiple sexual ornaments in Satin Bowerbirds: ultraviolet plumage and bowers signal different aspects of male quality. Behavioral Ecology 14: 503–509.

HEYWOOD, J. S. 1989. Sexual selection by the handicap mechanism. Evolution 43: 1387–1397.

HILL, G. E. 1999. Mate choice, male quality, and carotenoid-based plumage coloration. Proceedings of the International Ornithological Congress 22: 1654–1668.

HOELZER, G. A. 1989. The good parent process of sexual selection. Animal Behaviour 38: 1067–1078.

KAPPES, P. J., B. J. M. STUTCHBURY, AND B. E. WOOLFENDEN. 2009. The relationship between carotenoid-based coloration and pairing, within- and extra-pair mating success in the American Redstart. Condor 111: 684–693.

LEMON, R. E., D. M. WEARY, AND K. J. NORRIS. 1992. Male morphology and behavior correlate with reproductive success in the American Redstart (*Setophaga ruticilla*). Behavioral Ecology and Sociobiology 29:399–403.

MAGRATH, M. J. L. AND J. KOMDEUR. 2003. Is male care compromised by additional mating opportunity? Trends in Ecology and Evolution 18: 424–430.

MARKMAN, S., Y. YOM-TOV, AND J. WRIGHT. 1995. Male parental care in the Orange-tufted Sunbird: behavioural adjustments in provisioning and nest guarding effort. Animal Behaviour 50: 655–669.

MITCHELL, D. P., P. O. DUNN, L. A. WHITTINGHAM, AND C. R. FREEMAN-GALLANT. 2007. Attractive males provide less parental care in two populations of the Common Yellowthroat. Animal Behaviour 73:165–170.

MØLLER, A. P. AND R. THORNHILL. 1998. Male parental care, differential parental investment by females and sexual selection. Animal Behaviour 55: 1507–1515.

MONTGOMERIE, R. 2006. Analyzing colors. Pages 90–147 *in* Bird coloration. Volume 1, Mechanisms and measurements (G. E. Hill and K. J. McGraw, Editors). Harvard University Press, Cambridge, Massachusetts, USA.

MONTGOMERIE, R. 2008. CLR, Version 1.03. Queen's University, Kingston, Ontario, Canada. (available at http://post.queensu.ca/~mont/color/).

NORRIS, D. R., P. P. MARRA, T. K. KYSER, T. W. SHERRY, AND L. M. RATCLIFFE. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society of London, Series B 271: 59–64.

NORRIS, K. J. 1990. Female choice and the quality of parental care in the Great Tit *Parus major*. Behavioral Ecology and Sociobiology 27: 275–281.

PERREAULT, S., R. E. LEMON, AND U. KUHNLEIN. 1997. Patterns and correlates of extrapair paternity in American Redstarts (*Setophaga ruticilla*). Behavioral Ecology 8: 612–621.

QUESADA, J. AND J. C. SENAR. 2006. Comparing plumage color measurements obtained directly from live birds and from collected feathers: the case of the Great Tit *Parus major*. Journal of Avian Biology 37: 609–616.

R DEVELOPMENT CORE TEAM. 2007. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

REUDINK, M. W., P. P. MARRA, P. T. BOAG, AND L. M. RATCLIFE. 2009b. Plumage colouration predicts paternity and polygyny in the American Redstart. Animal Behaviour 77: 495–501.

REUDINK, M. W., C. E. STUDDS, T. K. KYSER, P. P. MARRA, AND L. M. RATCLIFFE. 2009a. Plumage brightness predicts non-breeding season territory quality in a long-distance migratory songbird. Journal of Avian Biology 40:34–41.

REUDINK, M. W., P. P. MARRA, T. K. KYSER, P. T. BOAG, K. M. LANGIN, AND L. M. RATCLIFFE. 2009c. Non-breeding season events influence polygyny and extra-pair paternity in a long-distance migratory bird. Proceedings of the Royal Society of London, Series B 276:1619–1626.

ROHDE, P. A., A. JOHNSEN, AND J. T. LIFJELD. 1999. Parental care and sexual selection in the Bluethroat, *Luscina s. svecica*: a field-experimental test of the differential allocation hypothesis. Ethology 105: 651–663.

SAETRE, G. P., T. FOSSNES, AND T. SLAGSVOLD. 1995. Food provisioning in the Pied Flycatcher: do females gain direct benefits from choosing bright-colored males? Journal of Animal Ecology 64: 21–30.

SAKS, L., O. INDREK, AND P. HÕRAK. 2003a. Carotenoid-based plumage coloration of male Greenfinches reflects health and immunocompetence. Oecologia 134: 301–307.

SAKS, L., K. MCGRAW, AND P. HÕRAK. 2003b. How feather colour reflects its carotenoid content. Functional Ecology 17: 555–561.

SANZ, J. J., S. KRANENBARG, AND J. M. TINBERGEN. 2000. Differential response by males and females to manipulation of partner contribution in the Great Tit (*Parus major*). Journal of Animal Ecology 69: 74–84.

SAS INSTITUTE. 2007. JMP® Version 7.0.2. Duxbury, Pacific Grove, California, USA.

SCHWAGMEYER, P. L. AND D. W. MOCK. 2003. How consistently are good parents good parents? Repeatability of parental care in the House Sparrow, *Passer domesticus*. Ethology 109: 303–313.

SECUNDA, R. C. AND T. W. SHERRY. 1991. Polyterritorial polygyny in the American Redstart. Wilson Bulletin 103:190–203.

SHAWKEY, M. D. AND G. E. HILL. 2005. Carotenoids need structural colours to shine. Biology Letters 1: 121–125.

SHERRY, T. W. AND R. T. HOLMES. 1997. American Redstart (*Setophaga ruticilla*). The birds of North America. Number 277

SIEFFERMAN, L. AND G. E. HILL. 2003. Structural and melanin coloration indicate parental effort and reproductive success in male Eastern Bluebirds. Behavioral Ecology 14: 855–861.

SMISETH, P. T., J. ÖRNBORG, S. ANDERSSON, AND T. AMUNDSEN. 2001. Is male plumage reflectance correlated with paternal care in Bluethroats? Behavioral Ecology 12: 164–170.

STEIN, A. C. AND J. A. C. UY. 2006. Plumage brightness predicts male mating success in the lekking Golden-collared Manakin (*Manacus vitellinus*). Behavioral Ecology 17: 41–47.

STUDD, M. V. AND R. J. ROBERTSON. 1988. Differential allocation of reproductive effort to territorial establishment and maintenance by male Yellow Warblers (*Dendroica petechia*). Behavioral Ecology and Sociobiology 23: 199–210.

WILLIAMS, G. C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, New Jersey, USA.

WRIGHT, J. AND I. CUTHILL. 1989. Manipulation of sex differences in parental care. Behavioral Ecology and Sociobiology 25: 171–181.

WRIGHT, J. AND I. CUTHILL. 1990. Manipulation of sex differences in parental care: the effect of brood size. Animal Behaviour 40: 462–471.