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Sexual pigmentation and parental risk-taking in yellow warblers *Setophaga petechia*

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Adult-directed predation risk imposes important behavioral constraints on parents and might thus alter relationships between costly sexual ornaments and parental performance. For instance, under low predation risk, highly ornamented individuals might display better parental performance than others, as predicted by ‘good parent’ models of sexual selection. However, under high risk of predation, highly ornamented individuals might abandon parental effort if conspicuous to predators, or if social partners are more willing to take parental risks when paired with highly ornamented mates. We experimentally elevated perceived adult-directed predation risk near nests to explore how carotenoid- and phaeomelanin-based pigmentation in both sexes relate to parental risk-taking for offspring in the yellow warbler *Setophaga petechia*. Compared to other males, males with more intense carotenoid-based pigmentation maintained higher levels of paternal effort under predation risk at highly concealed nests, but reduced nestling provisioning rate more at exposed nests. Further, when faced with predation risk, females with more phaeomelanin-based pigmentation reduced nestling provisioning rate less than other females, regardless of nest concealment. Females displayed higher parental effort across treatments when paired to males with more colorful carotenoid pigmentation. However, birds did not reduce parental effort under risk less when paired to a highly ornamented mate, suggesting that predation risk did not accentuate differential allocation. Males did not take fewer parental risks than females. Results indicate that nest concealment modifies parental risk-taking by males with colorful carotenoid-based pigmentation, and suggest that female melanin-based pigmentation may indicate boldness and greater a propensity to take parental risks.

Adult-directed predation risk imposes important behavioral constraints on parents, and might thus alter relationships between costly sexual ornaments and parental behaviors in a variety of alternative ways. A deficit of studies renders these alternatives and the behavioral processes involved poorly understood. For instance, under low levels of predation risk, highly ornamented individuals might display better parental performance than others, as predicted by ‘good parent’ models of sexual selection (Hoelzer 1989, Hill 1991, Siefferman and Hill 2003). In contrast, under high predation risk, highly ornamented individuals might abandon parental effort if vulnerable to detection or capture by predators (Martin and Badyaev 1996, Götmark and Olsson 1997, Cabido et al. 2008). Alternatively, highly ornamented individuals might be more willing to maintain parental effort under predation risk if better able to evade predators (Fowler-Finn and Hebets 2011), if ornamentation indicates higher investment towards current reproduction rather than survival (Candolin 1998), or if ornamentation correlates with behavioral characteristics such as boldness and aggressiveness (Roulin 2004, Ducrest et al. 2008, Da Silva et al. 2013). In these latter cases,

ornamentation may signal a willingness to take parental risks to potential mates. A link between boldness, aggressiveness and pigmentation has been particularly proposed for melanin-based pigmentation (Ducrest et al. 2008). For instance, male great tits *Parus major* with large eumelanin-based (black) plumage badges defend nests against predators more vigorously than other males (Quesada and Senar 2007), and female tawny owls *Strix aluco* with darker phaeomelanin-based (a reddish, cysteine-bearing form of melanin) pigmentation are more aggressive towards threats to the nest (Da Silva et al. 2013). However, other types of coloration have also been positively associated with boldness in the face of a predation threat, although in non-parental contexts. For instance, male guppies *Poecilia reticulata* with colorful carotenoid-based coloration are more likely to approach cichlid predators, potentially because these individuals are better able to escape predators (Godin and Dugatkin 1996).

In addition, in biparental species, predation risk might also affect the discrepancy in parental investment between individuals with ‘attractive’ and ‘unattractive’ mates, and between members of a mated pair (Burley 1986, Matessi et al. 2009). The differential allocation hypothesis proposes

that individuals paired to elaborately ornamented mates invest more into parental effort due to high brood value, which might allow their mate to down-regulate effort (Burley 1986, Møller and Thornhill 1998, Harris and Uller 2009, Ratikainen and Kokko 2010). For instance, male rock sparrows *Petronia petronia* paired to females with enhanced sexual pigmentation engaged in higher levels of risky nest defense behavior against a weasel *Mustela nivalis* predator (Matessi et al. 2009). However, males paired to females with enhanced ornaments did not contribute more to lower-risk nestling provisioning behavior (Matessi et al. 2009), suggesting that higher costs of parental care might accentuate differential allocation. On the other hand, other studies have found the opposite pattern. For example, male blue tits *Cyanistes caeruleus* paired to females with reduced ultraviolet reflectance invested less in nestling provisioning, but did not defend nestlings against an aesculapian snake *Zamenis longissimus* at reduced intensity (Mahr et al. 2012).

Birds provide good study species for exploring how the sexual ornamentation of focal individuals and social mates relates to levels of parental risk-taking for offspring, since biparental care is prevalent and effects of adult-directed predation risk on parental behaviors are well documented. High rates of visitation to a stationary nest render both avian parents and nest contents conspicuous to predators (Colombelli-Négrel and Kleindorfer 2010). Thus, adult-directed predation risk near nests clearly accentuates the tradeoff between parental effort and adult survival, and indeed reduces parental provisioning rates in a variety of avian species (Ghalambor and Martin 2000, 2001, Peluc et al. 2008, Tilgar et al. 2011). Further, past studies have documented various factors that affect parental responses to predators near avian nests, notably nest concealment (Eggers et al. 2006, Peluc et al. 2008, Lima 2009). Nest concealment may be important to understanding how conspicuously ornamented birds respond to both adult-directed and nest predation risk near nests, since conspicuous individuals may be more likely to maintain parental effort under risk if nests are more concealed.

To assess whether adult-directed predation risk affects the relationship between sexual ornamentation and parental effort, we manipulated perceived adult-directed predation risk near nests, quantified nest concealment, and measured sexual pigmentation in yellow warblers *Setophaga petechia*. The yellow warblers is a biparental passerine with colorful pigmentation and moderate sexual dichromatism. Males express more intense carotenoid-based pigmentation and more phaeomelanin-based breast streaking than females, although considerable variation in pigmentation occurs within each sex (Lowther et al. 1999, Grunst et al. 2014a). The intensity of carotenoid-based pigmentation and the amount of phaeomelanin-based pigmentation are largely uncorrelated in males, and positively correlate in females ($r = 0.41$), but with significant independent variation. Thus, the two pigment types may convey non-equivalent information (Grunst et al. 2014a). We have previously established that carotenoid- and phaeomelanin-based pigmentation are associated with metrics of individual condition in both sexes of the yellow warbler (Grunst et al. 2014a, b), and warblers show assortative social pairing by pigmentation (Grunst and Grunst 2014). Further, a past study found greater extra-

pair paternity among males expressing more melanin-based pigmentation (Yezerinac and Weatherhead 1997), and in our study population males co-expressing high levels of both melanin- and carotenoid-based pigmentation lose less paternity in their social broods (Grunst and Grunst 2014). Thus, as also reported for both carotenoid- and melanin-based pigmentation in other species, sexual pigmentation in the yellow warbler may serve as a sexual signal of individual condition (Hill 1991, Badyaev and Duckworth 2003, Siefferman and Hill 2003, Safran and McGraw 2004, Dunn et al. 2010) or genetic quality (Roulin et al. 2001, Boerner and Krüger 2009), in addition to making individuals conspicuous to predators. As a sexual signal, pigmentation may predict both individual behavioral performance and the parental allocation decisions of the social mate.

We made specific predictions regarding how adult-directed predation risk would alter relationships between sexual pigmentation and the parental behavior of the focal individual and social mate. First, we predicted that predation risk might induce a strong positive relationship between the pigmentation (either carotenoid- or melanin-based) of the social mate and parental effort, by causing individuals with low quality, or 'unattractive' mates to abandon parental effort. Further, we reasoned that highly pigmented birds might have mates more willing to take parental risks (Matessi et al. 2009), and might also be highly conspicuous to predators (Cabido et al. 2008, Journey et al. 2013), particularly if expressing intense carotenoid-based pigmentation, which covers the majority of the body. Thus, compared to less pigmented individuals, we predicted that highly pigmented birds might show lower levels of parental effort under predation risk, but might show higher parental performance under normal, low risk conditions. However, we also predicted that highly pigmented birds might be more likely to maintain parental effort under predation risk at highly concealed nests. In addition, birds with more phaeomelanin-based pigmentation might be more likely to take parental risks, given a genetic correlation between phaeomelanin-based pigmentation, aggression and boldness, as suggested by some previous research (Studd and Robertson 1985a, b, Quesada and Senar 2007, Ducrest et al. 2008). On the other hand, past studies in the yellow warbler found that phaeomelanin-based pigmentation positively correlated with territorial aggression but negatively correlated with paternal effort, including nest defense against a snake (Studd and Robertson 1985a, b). This past research suggests that highly melanic birds might display lower parental motivation and thus take few parental risks. Finally, we predicted that females might take more parental risks than males due to higher certainty of parentage (Yezerinac and Weatherhead 1997), and less intense coloration that would make them less conspicuous to predators (Martin and Badyaev 1996). Therefore, greater inter-sex differences in parental effort might occur under predation risk than under normal conditions.

Methods

Study system and field methods

During the 2010 to 2012 breeding seasons, we studied yellow warblers breeding along riparian corridors at the

Univ. of California's Sierra Nevada Aquatic Research Laboratory (SNARL; 37°36'51"N, 118°49'47"W), and in the adjacent Inyo National Forest. Warblers arrive on the breeding grounds in May, and nesting occurs from mid-May to early July. Pairs re-nest following nest depredation but fledge only one clutch per season. We captured birds in mist nets using conspecific playback during the pre-nesting period, or by placing nets near nests, and marked birds with a United States Geological Survey (USGS) aluminum band and colored leg bands. We located nests through behavioral observation and checked nests every 2–3 d to monitor nest contents. After nests fledged or failed, we scored nest concealment on a scale of 0 to 2. A score of zero indicated that the nest was 100–80% visible (exposed) when viewed from 2 m in front of the substrate plant, 0.5 indicated 80–60% exposure, 1, 60–40% exposure, 1.5, 40–20% exposure, and 2, 20–0% exposure.

Measurement of pigmentation

We collected 5 feathers bearing carotenoid pigmentation from non-adjacent breast regions, and stored feathers in closed envelopes until spectrometric analysis. We arranged feathers on a black felt background (with zero reflectance), and then used an USB4000 spectrometer with a xenon light source (range: 200–1100 nm; Ocean Optics, Dunedin, FL, USA) to obtain reflectance spectra between 300–725 nm, across the avian visual range (Montgomerie 2006, Hegyi et al. 2007, Grunst et al. 2014a). We characterized reflectance spectra using colorimetric measurements of total reflectance (brightness), saturation (chroma or spectral purity), and hue (spectral location). Carotenoid pigmentation displays a bimodal reflectance spectrum, with peaks of reflectance for both ultraviolet and yellow (or red) light, and high absorbance of blue–green light. Thus, to characterize reflectance spectra, we calculated carotenoid saturation (chroma), blue saturation, ultraviolet saturation, average reflectance, and lambda 50 (a measurement of hue), as described by Andersson and Prager (2006). We performed a principal component analysis to derive a single factor (PC1) descriptive of variance in reflectance spectra (Montgomerie 2006, Hegyi et al. 2007, Grunst et al. 2014a). Loadings on PC1 were 0.51 for carotenoid saturation, 0.48 for ultraviolet saturation, -0.52 for blue saturation, -0.06 for total reflectance, and 0.47 for lambda 50, with an eigenvalue of 3.61 and 72.5% of total variation explained. Previous studies suggest that increasing the concentration of yellow carotenoids in feathers increases lambda 50 (resulting in a shift towards orange), ultraviolet saturation, and carotenoid saturation, but reduces average reflectance and blue saturation (Andersson and Prager 2006). Thus, PC1 positively correlates with the concentration of carotenoids in feathers. We corrected for a year effect on carotenoid PC1. This correction did not qualitatively alter statistical results.

Further, we used a Stylus 800 Olympus camera to take digital photographs of the front and sides of all birds. For males, we used the threshold colour function in ImageJ to extract the percent coverage of red–brown (phaeomelanin) from photographs (Schneider et al. 2012, see Grunst et al. 2014a for further detail). For most females, melanin coverage was too low to accurately quantify in ImageJ. Thus, we

scored female melanin coverage on a scale of 0 to 2. A score of zero corresponded to no melanin-based streaking, 0.5 to a trace of streaking, 1 to moderate streaking (~ 1 –2% coverage), and 2 to heavy streaking (~ 5 % coverage).

Predator presentation experiment

We experimentally increased perceived adult-directed predation risk at nests by presenting a recording and taxidermic mount of a sharp-shinned hawk *Accipiter striatus*. A decoy and recording of a house finch *Haemorhous mexicanus* served as a negative control. We manually compiled hawk and finch recordings, such that both types of recording consisted of 3 min of vocalization followed by 3 min of silence. We used the same recording for all experiments, but randomly used one of three hawk decoys and one of three finch decoys. We placed decoys ~ 6 –10 m from nests and ~ 2 m off the ground (Ghalambor and Martin 2000, 2001, Peluc et al. 2008), and projected recordings using MP3 players placed in the vegetation next to decoys. We also recorded nests without any decoy present, to assess baseline behavior. We performed recordings (baseline, hawk, finch) in randomly determined order for sequential periods of ~ 1.5 h each with ~ 10 min between recordings, using Canon 800 series camcorders with 124-min tapes. We erected camcorders on tripods concealed ~ 5 m from nests. We initiated recordings between 06:00 and 16:00 Pacific Daylight Time (PDT) due to high recording volume, and controlled for time of recording in statistical analyses. We performed the experiment on day 4–7 of the nestling period. Overall, we performed the experiment at 71 nests of 57 males and 67 females, but performed finch presentations only 45 times, after it became clear that they did not differ from controls (Results). Further, sample sizes for analyses (Results) are reduced in some cases because we did not have pigmentation measurements from all birds. From video-recordings, we determined paternal and maternal provisioning rates. We distinguished the sexes based on plumage differences and colored leg bands.

Statistical analysis

We performed linear mixed effect models (LMMs) in R 2.15.2 (packages lme4 and lmerTest) (Bates et al. 2012, Kuznetsova et al. 2013), with nest, male, and female identity as random effects. We sequentially removed non-significant predictors ($\alpha = 0.05$) from models and obtained final p-values using type III F-tests with Satterthwaite approximations for degrees of freedom. First, we constructed separate LMMs to predict paternal and maternal provisioning rate from treatment (baseline, finch, hawk), treatment order (hawk presented first or subsequently), pigmentation of the focal bird, brood size, nestling age, nest concealment, and time of day. We included three-way interactions between pigmentation variables, nest concealment, and treatment, to assess whether pigmentation and nest concealment combine to predict the response to predation risk near nests. We also included a two-way interaction between treatment and treatment order, since treatment order might affect behavior primarily in the baseline recording (due to carryover effects from the predator presentation). Second,

we used separate models, constructed in the same way, to assess whether the social mate's sexual pigmentation interacted with treatment to predict the focal individual's provisioning effort. Finally, to assess the relationship between sex and parental risk-taking, we constructed an LMM to predict parental provisioning rate from the interaction between sex, treatment, and nest concealment, with the same covariates included as above (but not sexual pigmentation). We square-root transformed provisioning rates to normalize model residuals, and centered continuous predictor variables to facilitate the interpretation of main effects when including interactions in the model (Schielzeth 2010).

Results

Pigmentation of the focal individual and parental risk-taking

Birds did not provision nestlings at different rates during the negative control (finch) treatment compared to at baseline (LMM: males: $t_{145} = 0.12$, $p = 0.89$, females: $t_{145} = -0.17$, $p = 0.26$), so we collapsed baseline and negative control into a single category.

Males strongly reduced paternal provisioning rate under adult-directed predation risk and reduced provisioning rate less under risk at highly concealed nests (Table 1, Fig. 1). Further, the effect of nest concealment on the response to the predator was stronger for males with more colorful carotenoid-based pigmentation than for males with less intense carotenoid pigmentation (significant treatment \times carotenoid PC1 \times nest concealment interaction, Table 1). Indeed, the treatment \times nest concealment interaction was highly significant when restricting the dataset to the most intensely pigmented half of males (males with pigmentation above the median value; $F_{1,58} = 7.28$, $\beta = 0.54 \pm 0.20$, $p = 0.009$), but was non-significant when restricting the dataset to the least intensely pigmented half of males ($F_{1,58} = 2.35$, $\beta = 0.42 \pm 0.25$, $p = 0.09$). Thus, compared to less pigmented males, males with more intense carotenoid-based pigmentation were more likely to maintain paternal provisioning rates under predation risk at highly concealed nests, but displayed large reductions in provisioning rate under risk at highly exposed nests (Fig. 2). Male melanin

pigmentation was not associated with paternal responses to predation risk near nests (LMM: treatment \times melanin, $F_{1,110} = 0.23$, $\beta = -0.06 \pm 0.13$, $p = 0.62$), regardless of nest concealment (treatment \times melanin \times nest concealment, $F_{1,110} = 0.28$, $\beta = 0.08 \pm 0.12$, $p = 0.50$). Further, nestling age ($F_{1,131} = 2.53$, $\beta = 0.12 \pm 0.07$, $p = 0.11$) and brood size ($F_{1,78} = 0.23$, $\beta = 0.03 \pm 0.06$, $p = 0.62$) were not significantly related to paternal provisioning rate (Supplementary material Appendix 1, Table A1, initial full model), but the final model retained effects of treatment order and time of day (Table 1).

Like males, females reduced provisioning rate under adult-directed predation risk (Table 2, Fig. 1), and reduced provisioning less under risk at more concealed nests (Table 2). Further, females expressing more melanin-based pigmentation reduced provisioning rates under predation risk less than other females (Table 2, Fig. 3), and this effect was independent of nest concealment (LMM: treatment \times melanin score \times nest concealment; $F_{1,67} = 1.22$, $\beta = -0.16 \pm 0.14$, $p = 0.27$). Female carotenoid-based pigmentation was not related to maternal responses to predation risk near nests (treatment \times carotenoid PC1; $F_{1,65} = 2.47$, $\beta = -0.24 \pm 0.16$, $p = 0.12$), irrespective of nest concealment (treatment \times carotenoid PC1 \times nest concealment, $F_{1,64} = 0.27$, $\beta = -0.07 \pm 0.15$, $p = 0.59$). Nestling age ($F_{1,98} = 2.33$, $\beta = 0.13 \pm 0.08$, $p = 0.13$), treatment order ($F_{1,110} < 0.001$, $\beta = 0.19 \pm 0.19$, $p = 0.98$), and time of day ($F_{1,98} = 2.05$, $\beta = -0.06 \pm 0.04$, $p = 0.15$) were also unrelated to maternal provisioning behavior (Supplementary material Appendix 1, Table A2, initial full model), but the final model retained a positive effect of brood size on maternal provisioning rate (Table 2).

Pigmentation of the social mate and parental risk-taking

When faced with adult-directed predation risk, warblers with more intensely pigmented social mates did not reduce parental effort less than birds with less pigmented mates. Males did not maintain higher provisioning effort under risk when paired to females with more intense carotenoid pigmentation (LMM: treatment \times female carotenoid PC1; $F_{1,63} = 0.04$, $\beta = -0.03 \pm 0.17$, $p = 0.83$), or more melanin pigmentation (treatment \times female melanin score;

Table 1. LMM predicting paternal provisioning rate from male carotenoid-based pigmentation, predation risk treatment, and nest concealment.

	Estimate ($\beta \pm SE$)	<i>F</i>	DF (Denom.)	<i>p</i> ($> F$)
Intercept ^a	2.10 \pm 0.33	–	–	< 0.001
Treatment ^b	–1.11 \pm 0.12	85.49	117.86	< 0.001
Carotenoid PC1	0.11 \pm 0.11	1.14	75.87	0.28
Nest concealment	0.001 \pm 0.10	2.96	95.29	0.08
Treatment order ^c	–0.35 \pm 0.15	5.04	167.86	0.02
Time	0.07 \pm 0.03	5.74	156.75	0.01
Treatment \times carotenoid PC1	–0.01 \pm 0.11	0.01	117.14	0.91
Treatment \times nest concealment	0.33 \pm 0.11	7.94	117.10	0.005
Carotenoid PC1 \times nest concealment	–0.12 \pm 0.10	0.11	155.24	0.73
Treatment \times carotenoid PC1 \times concealment	0.32 \pm 0.12	6.20	117.94	0.01

n = 176 observations, 66 nests, 65 females, 56 males.

^a*p* value from initial LMM output, not an *F* test.

^bPredation risk treatment contrasted to baseline.

^cPredation treatment first contrasted to baseline first.

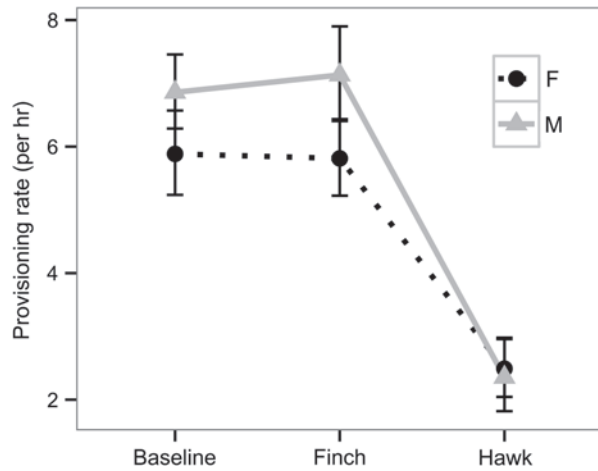


Figure 1. Adult-directed predation risk reduced nestling provisioning rates in both sexes. Means are back transformed and include only replicates for which finch (negative control) presentations were performed ($n = 45$). Error bars represent 95% confidence intervals.

$F_{1,65} = 2.00$, $\beta = 0.25 \pm 0.18$, $p = 0.16$), and female pigmentation did not correlate with paternal provisioning rate across treatments (non-significant main effects; $p > 0.30$; Supplementary material Appendix 1, Table A3, full model). Similarly, male carotenoid pigmentation (treatment \times male carotenoid PC1; $F_{1,105} = 1.23$, $\beta = 0.14 \pm 0.12$, $p = 0.26$) and melanin pigmentation (treatment \times male melanin coverage; $F_{1,104} = 0.08$, $\beta = -0.03 \pm 0.13$, $p = 0.77$) were unrelated to maternal responses to predation risk (Supplementary material Appendix 1, Table A4, full model). However, across treatments, females provisioned nestlings at higher rates when paired to males with more intense carotenoid pigmentation (LMM: $F_{1,51} = 4.13$, $\beta = 0.19 \pm 0.09$, $p = 0.04$).

Sex and parental risk-taking

Finally, sex was not related to how warblers reduced provisioning effort in response to predation risk (LMM:

Table 2. LMM predicting maternal provisioning rate from female melanin-based pigmentation, predation risk treatment, and paternal provisioning rate.

	Estimate ($\beta \pm SE$)	F	DF (Denom.)	$p(>F)$
Intercept ^a	2.24 ± 0.25	–	–	< 0.001
Treatment ^b	-0.88 ± 0.13	45.41	72.02	< 0.001
Melanin score	-0.08 ± 0.13	2.44	38.55	0.12
Nest concealment	-0.04 ± 0.12	0.37	40.30	0.54
Brood size	0.22 ± 0.08	7.54	35.17	0.009
Treatment \times melanin score	0.32 ± 0.13	13.05	72.51	< 0.001
Treatment \times concealment	0.47 ± 0.13	5.44	72.59	0.02

$n = 120$ observations, 45 nests, 42 females, 40 males.

^a p value from initial LMM output, not an F test.

^bCoefficient estimate for predation risk treatment contrasted to baseline.

sex \times treatment; $F_{1,295} = 1.03$, $\beta = -0.19 \pm 0.19$, $p = 0.30$), irrespective of nest concealment (sex \times treatment \times nest concealment; $F_{1,295} = 0.02$, $\beta = 0.03 \pm 0.19$, $p = 0.87$). Further, males and females did not display different levels of provisioning effort across treatments, as indicated by a non-significant main effect of sex ($F_{1,295} = 0.37$, $\beta = 0.03 \pm 0.11$, $p = 0.54$, Fig. 1; Supplementary material Appendix 1, Table A5, full model).

Discussion

Our study demonstrates that sexual pigmentation in both males and females may be associated with changes in parental provisioning rates in response to adult-directed predation risk near nests. Further, for males, our results suggest that nest concealment modifies the relationship between conspicuous carotenoid-based pigmentation and maintenance of parental effort under predation risk. Past researchers have suggested a genetic correlation between melanin-based pigmentation, stress resistance, and the boldness of parents

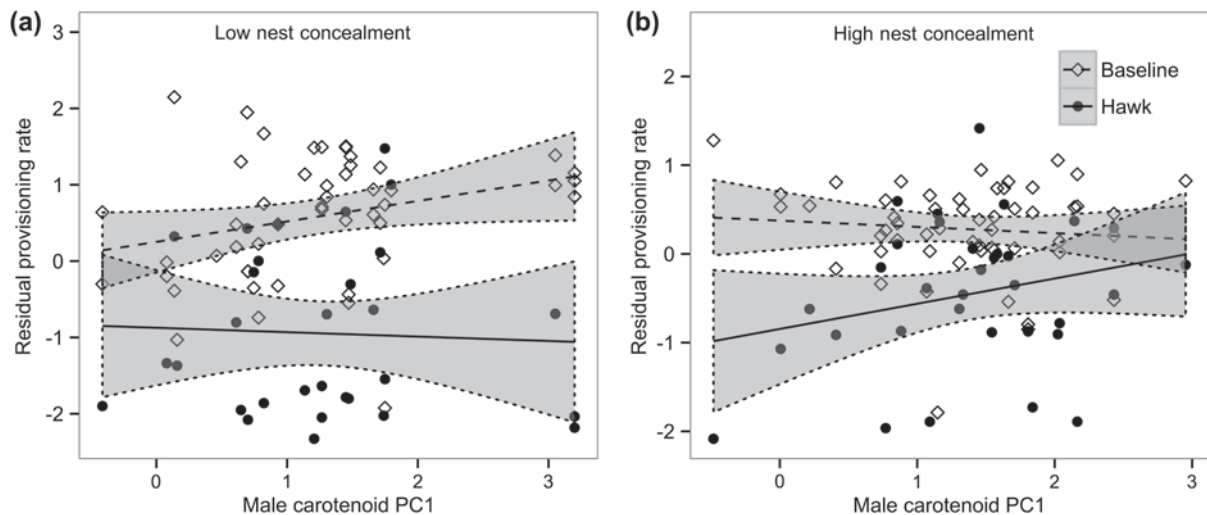


Figure 2. Relationship between male carotenoid-based pigmentation and paternal provisioning rate (feeding trips h^{-1} , square-root transformed) under predation risk versus baseline conditions at nests with low concealment (a), versus high concealment (b). Residual provision rate (y-axis) controls for treatment order, time of day, and variation in nest concealment within the low and high concealment categories. Shaded regions within dotted lines represent 95% confidence intervals.

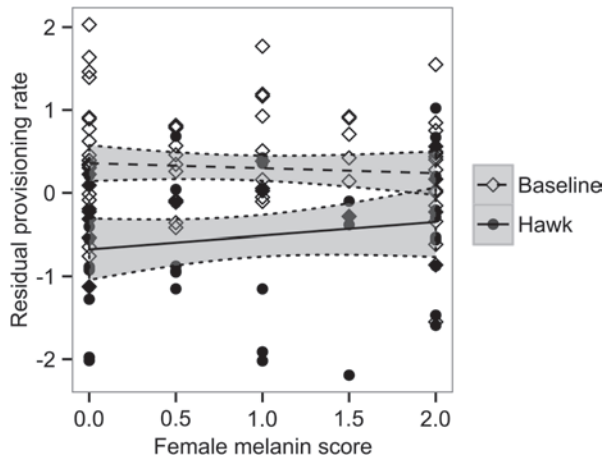


Figure 3. Relationship between female melanin score and maternal provisioning rate under predation risk versus baseline conditions. Residual provisioning rate (Square root h^{-1}) controls for brood size and variation in nest concealment within the low and high nest concealment categories. Shaded regions within dotted lines represent 95% confidence intervals.

when defending nests against predators (Quesada and Senar 2007, Ducrest et al. 2008, Boerner and Krüger 2009, van den Brink et al. 2012). Further, in non-parental contexts, researchers have found that individuals with more intense carotenoid-based pigmentation are bolder under predation risk (Godin and Dugatkin 1996), perhaps because they better evade predation (Cabido et al. 2008). However, conspicuous coloration might also increase the risk of detection by predators, and thus induce stronger responses to predation threats, especially where vegetative cover is limited. Indeed, a recent study documented that species with more conspicuous coloration (origin of coloration was not considered) respond more intensely to the vocal calls of a raptor predator (the broad-winged hawk *Buteo platypterus*, Journey et al. 2013). However, few studies document a relationship between sexual pigmentation and changes in parental provisioning behavior under adult-directed predation risk within a species, or indicate that an interaction between nest concealment and sexual pigmentation is associated with parental responses to adult-directed predation risk.

First, our results suggest that males with colorful carotenoid-based pigmentation respond to adult-directed predation risk near nests in a fashion that depends on nest concealment. Compared to less intensely pigmented males, males with more intense carotenoid-based pigmentation displayed greater maintenance of nestling provisioning rates under predation risk at concealed nests, but showed greater reductions in paternal effort under risk at highly exposed nests (Fig. 2). These results suggest that males with intense carotenoid pigmentation are ‘good parents’ under predation risk at concealed nests, but not exposed nests. We predicted that highly pigmented males might display large reductions in nestling provisioning rate under predation risk because these birds (especially males) might be more conspicuous to predators (Martin and Badyaev 1996), and this appeared to occur at highly exposed nests. However, we also predicted that highly pigmented males might be more likely to maintain provisioning effort at concealed nests, in accordance with results. In our population, carotenoid pigmentation

increases longitudinally with male age (Grunst et al. 2014a, b), and is greater in first year breeding males that are in better condition as nestlings and at pre-breeding molt (Grunst et al. 2014a). Thus, carotenoid-based pigmentation may be related to quality and age-related differences in both the ability to evade predation, and experience with assessing predation threats (Cabido et al. 2008, Fowler-Finn and Hebets 2011). Therefore, at concealed nests, males with intense carotenoid pigmentation may maintain higher provisioning effort under predation risk than less pigmented males due to a better capacity to evade predation combined with more experience with assessing how predation risk varies with vegetation cover. In contrast, at highly exposed nests, males with intense carotenoid pigmentation may show large reductions in paternal effort under predation risk because the risk of detection and depredation is too high. Nest concealment and predation risk in combination may thus affect the paternal benefits that females obtain from conspicuously pigmented males.

Notably, carotenoid-based pigmentation in yellow warblers appears more conspicuous than melanin-based pigmentation, which is restricted to narrow streaks on the breast. Thus, one might expect carotenoid rather than melanin pigmentation to be associated with the relationship between nest concealment and paternal responses to predation risk near nests, in accordance with our results. However, we did not actually quantify how carotenoid-based pigmentation affects the conspicuousness of birds, which would require quantifying the contrast between background coloration and birds differing in carotenoid-based pigmentation (Delhey et al. 2010). Thus, our results could reflect differences in the capacity of males to assess how nest concealment affects the predation threat, independent of differences in conspicuousness between individuals. Future research to clarify this point would be interesting.

In contrast to males, in females melanin-based pigmentation was related to responses to predation risk, but this relationship was independent of nest concealment. Results support the hypothesis that melanin-based pigmentation may indicate a willingness to take parental risks (Quesada and Senar 2007, Da Silva et al. 2013), since females with more melanin pigmentation reduced maternal provisioning rate under risk less than other females. Past research has linked melanin-based pigmentation with greater boldness and risk-taking, and researchers have suggested a genetic correlation between the two (Quesada and Senar 2007, Ducrest et al. 2008, Mafli et al. 2011, Da Silva et al. 2013). Indeed, a cross fostering experiment in barn owl *Tyto alba* nestlings showed that antipredatory behavior and melanin-based pigmentation are correlated and heritable (van den Brink et al. 2012). Thus, although the work in barn owls involved a eumelanin-based (black) trait, pheomelanin-based pigmentation in female yellow warblers may also reflect genetic differences in antipredator strategy and risk responsiveness. However, it is unclear why male melanin-based pigmentation did not also correlate with paternal responses to the predation threat, given a genetic association between melanin pigmentation and risk-taking behavior.

Alternatively, females with more melanin-based pigmentation might reduce provisioning under predation risk less than other females because melanin-based pigmentation

is related to individual quality, a better capacity to evade predation, and greater parental motivation. Indeed, in our population, females with more pheomelanin pigmentation are in better condition at pre-breeding molt and are less likely to be first year breeders (Grunst et al. 2014a), and pheomelanin pigmentation has also been associated with metrics of individual quality in species such as barn swallows *Hirundo rustica* (Safran and McGraw 2004, Galván and Møller 2013, but see Saino et al. 2013) and barn owls *Tyto alba* (Roulin et al. 2008). Further, past studies in eastern bluebirds *Sialia sialia* and barn owls have associated pheomelanin-based pigmentation with greater parental effort (Roulin et al. 2001, Siefferman and Hill 2003), although past research in male yellow warblers found a contrary result (Studd and Robertson 1985a, b, but see Lozano and Lemon 1996).

Our results were contrary to the prediction that predation risk might accentuate differential allocation (Matessi et al. 2009), since neither males nor females showed greater maintenance of parental effort under predation risk when paired to highly pigmented mates. Increasing parental risk-taking when paired to a highly ornamented mate could be adaptive if ornamentation positively correlates with offspring genetic or phenotypic quality (Burley 1986), or if individuals risk abandonment by 'attractive' partners by not taking parental risk (Matessi et al. 2009). However, our results suggest that differential allocation is not particularly strong under increased risk to the adult (Mahr et al. 2012), which might indeed be expected if acute risks to survival lower variance in parental effort. On the other hand, we found some support for the idea that birds adjust levels of parental effort to the ornamentation of their mates, as predicted by the differential allocation hypothesis (Burley 1986, Ratikainen and Kokko 2010). Specifically, females paired to males with more intense carotenoid-based pigmentation provisioned nestlings at higher rates across treatments. However, as a caveat, this result might also reflect superior territory or mate quality among males with more intense carotenoid pigmentation (Sheldon 2000), particularly since warblers assortatively pair by both carotenoid- and melanin-based pigmentation in our study population (Grunst and Grunst 2014).

Our results also did not suggest differential parental risk-taking by males and females (Michl et al. 2000). Males and females did not take different levels of parental risk even at highly exposed nests, and also did not provide different levels of parental care at baseline. We predicted that males might provide less parental care than females under predation risk. First, under a predation threat, males might take less parental risk than females because more colorful sexual pigmentation makes them more conspicuous and vulnerable to predation (Zuk and Kulluru 1998, Stuart-Fox et al. 2003, Journey et al. 2013, but see Bókony et al. 2008). It is unclear why greater conspicuousness of males did not lead to lower provisioning rates under predation risk in comparison to females, especially at highly exposed nests. However, this result might arise due to variance in coloration within the sexes (Grunst et al. 2014a), because males risk losing social mates by not demonstrating comparable willingness to take parental risks (Matessi et al. 2009), or if males are overall less risk sensitive than females (Breitwisch and Hudak 1989, Ensminger and Westneat 2012). Further, males might

also respond more to predators near nests than females if males pursue a reproductive strategy focused on multiple mating rather than parental care (Kokko 1998, Magrath and Komdeur 2003), and have low certainty of parentage (Yezerinac et al. 1996, Yezerinac and Weatherhead 1997). The high rate of extra-pair paternity in our study population renders this later hypothesis particularly feasible (30.7% of nestlings are extra-pair offspring, Grunst and Grunst 2014). However, previous studies have also found that male yellow warblers do not provide less parental care than females, despite high rates of extra-pair paternity, potentially due to relatively low between-season survival rates (Yezerinac et al. 1996, Lozano and Lemon 1996). We hypothesized that higher costs of parental care under predation risk could induce parental differences between the sexes. However, equal parental effort under baseline conditions suggests that the two sexes have equivalent investments in the social brood. Males and females might thus weight costs to survival against parental care in a similar fashion under predation risk.

Finally, our study involved parental risk-taking under an adult-directed predation risk, whereas others have also considered responses to nest predation risk (Ghalambor and Martin 2000, Peluc et al. 2008). Given nest predation risk, parents reduce provisioning rate at exposed nests more than at concealed nests, but to prevent nest detection (Ghalambor and Martin 2000), rather than depredation of the adult. Thus, the interaction between male carotenoid-based pigmentation, nest concealment, and nest visitation rate might have been similar if we had presented a predator that only targets nests, instead of the sharp-shinned hawk. On the other hand, the relationship between melanin-based pigmentation and maternal provisioning rate under adult-directed predation risk might arise because highly melanic females are less sensitive to highly stressful situations (Almasi et al. 2008, Ducrest et al. 2008). Thus, this relationship might not be present under a nest predation threat, which does not pose a direct threat to the adult and might thus be less stressful.

In summary, our results suggest that both carotenoid- and melanin-based pigmentation may be associated with parental responses to adult-directed predation risk near nests. The relationship between male carotenoid-based pigmentation and paternal provisioning under predation risk depended on nest concealment, with highly pigmented males maintaining higher levels of nestling provisioning under predation risk only at highly concealed nests. Thus, our results suggest that nest concealment and predation risk interact to determine the paternal benefits that females receive from males with intense carotenoid-based pigmentation. In contrast, females with more melanin-based pigmentation showed greater maintenance of provisioning effort under predation risk irrespective of nest concealment, suggesting that female melanin-based pigmentation is associated with a willingness to take parental risks. Finally, neither males nor females maintained higher parental effort under predation risk when paired to a highly pigmented mate, despite an overall positive association between maternal provisioning rate and male carotenoid pigmentation. Therefore, in this species, differential allocation does not appear to be accentuated by predation risk, but the sexual pigmentation of focal individuals is associated with parental risk-taking.

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Supplementary material (Appendix JAV-00496 at <www.avianbiology.org/readers/appendix>). Appendix 1.