

# Carotenoid-based status signaling by females in the tropical streak-backed oriole

Troy G. Murphy,<sup>a</sup> Diego Hernández-Muciño,<sup>b</sup> Marcela Osorio-Beristain,<sup>c</sup> Robert Montgomerie,<sup>a</sup> and Kevin E. Omland<sup>d</sup>

<sup>a</sup>Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada, <sup>b</sup>Facultad de Ciencias, Universidad Nacional Autónoma de México, D.F. 04510, México, <sup>c</sup>Departamento de Ecología, CEAMISH, Universidad Autónoma del Estado de Morelos, Cuernavaca, Morelos 62209, México, and <sup>d</sup>Department of Biological Sciences, University of Maryland Baltimore County, Baltimore, MD 21250, USA

In many tropical bird species, both males and females maintain elaborate plumage traits. Although there is considerable evidence that many male plumage traits function as status signals that convey information about fighting ability, less is known about status signaling in females. We tested whether the carotenoid-based orange breast coloration of the female streak-backed oriole (*Icterus pustulatus pustulatus*) signals status during territorial interactions. To do this, we simulated territorial intrusions using taxidermic models and compared the roles of the sexes within pairs during territorial defense directed toward different types of simulated intruders. Females were more territorial than their mates during the breeding season, whereas males were more territorial than their mates in the nonbreeding season, contrary to patterns seen in studies of temperate zone birds. The coloration of simulated female intruders also influenced territorial responses: When presented with color-augmented female models, females responded with greater intensity than their mates, whereas the intensity of defense was similar for both sexes when presented with average-colored female models. The greater female response to more colorful intruders suggests that females perceive more ornamented females as greater threats to their territorial tenure or to their pair bond. These results are consistent with the hypothesis that female carotenoid-based coloration signals status in this species. *Key words*: elaborate monomorphism, female ornamentation, female territoriality, sexual selection, social selection, status signal. [*Behav Ecol* 20:1000–1006 (2009)]

Females and males of many species maintain elaborate ornamental traits (Amundsen and Pärn 2006; Clutton-Brock 2009), but it is unclear whether elaborate female traits are generally maintained as sexually selected signals (Johnstone et al. 1996; Amundsen 2000), naturally selected signals (Murphy 2006, 2007), or nonfunctional by-products of selection on male ornaments (Lande 1987). Recent research has produced both strong theoretical support and several convincing empirical examples of selection for ornaments involved in mate choice in both sexes (Jones and Hunter 1993; Hunt et al. 1999; MacDougall and Montgomerie 2003; Torres and Velando 2005; Roulin and Altwegg 2007). Fewer studies, however, have investigated the role of elaborate female traits in status signaling during competition for mates or other resources (Irwin 1994; Kraaijeveld et al. 2004; Heinsohn et al. 2005; Viera et al. 2008).

Status signals allow competitors to assess each other's relative dominance without risking injury or wasting time and energy physically assessing an opponent's fighting abilities (Rohwer 1985; Senar 1990; Moore et al. 2002; Tibbetts and Dale 2004; Chaine and Lyon 2008). Rohwer (1975) proposed that subordinates could use status signals to avoid interactions with individuals that had greater fighting ability, and dominant individuals could avoid escalating during interactions that could clearly be won. Status signals should be favored in species where individuals regularly interact with new rivals, especially in species where challenges over resources or territories are common. Most research into status signaling has focused on birds (for review, see Senar 2006), and status signals are widely

recognized to have evolved in males of many sexually dimorphic avian species (Rohwer 1975; Senar 1999; Pryke et al. 2002; Pryke and Andersson 2003; Tarof et al. 2005); yet, there are few examples of status signals in female birds (Swaddle and Witter 1995). Nonetheless, status signals are expected to evolve in both males and females when both sexes compete for resources or defend territories (West-Eberhard 1983; Amundsen 2000; Lebas 2006; Kraaijeveld et al. 2007), and so it is surprising that little attention has been paid to female signals of fighting ability, even though the idea of social status signaling by both sexes was proposed 3 decades ago (West-Eberhard 1979).

Many tropical bird species are elaborately colored and sexually monomorphic, with males and females having similar plumage traits (Hamilton 1961; Bailey 1978; Peterson 1996; Badyaev and Hill 2003). It has been suggested that status signaling by both sexes may be favored particularly in tropical species because both sexes often invest in territorial defense (both sexes defend territories in for 87% of resident Neotropical passerine birds: Stutchbury and Morton 2001; also see Skutch 1940; Fedy and Stutchbury 2005), and signals of status could reduce investment in the defense of resources associated with the territory (Whittingham et al. 1992; Irwin 1994). Because suitable real estate tends to be fully occupied in the tropics, the benefits of defending territorial ownership and access to limited resources can be accrued by both sexes (Stutchbury and Morton 2001).

In the tropical streak-backed oriole (*Icterus p. pustulatus*), both males and females are ornately colored with carotenoid-based yellow-orange body plumage and vivid crimson-orange feathers on the head and breast. Females are, on average, slightly paler orange than males, but the most colorful females are nearly indistinguishable in body color from males (Jaramillo and Burke 1999). Both sexes participate in defense of a single multiuse territory year-round (see Materials and Methods), and so we hypothesized that female orioles might use their

Address correspondence to T.G. Murphy. E-mail: tgm3@cornell.edu.  
Received 31 October 2008; revised 25 May 2009; accepted 26 May 2009.

orange plumage coloration to communicate fighting ability with competitors over territorial resources and thereby reduce the costs of overt territorial defense.

First, we assessed sex roles during territorial defense to determine how these roles varied with the sex of the intruder and the season. To do this, we simulated territorial intrusions by presenting male and female taxidermic models to territorial pairs (for similar approach, see Mays and Hopper 2004) during both the breeding and nonbreeding seasons.

Second, we tested whether carotenoid-based female coloration signals status during territorial defense by presenting pairs with 2 types of female models: either with plumage color artificially augmented or with average (control) plumage color. We expected that female models with enhanced plumage coloration would have greater effect on female response than on male response because same-sex intruders are more likely to challenge territorial tenure and to take over mates (Levin 1996; Kleiber et al. 2007; Brunton et al. 2008). We therefore predicted that females would invest more in territorial defense than their mates when presented with a color-augmented female model and that there would be less sexual difference in territorial investment when pairs were presented with an average-colored female model. Although status signals are generally expected to reduce the costs of territorial defense, we assumed that the value of a territory was large for current residents and thus predicted that residents would not defer to more colorful (i.e., more threatening) intruders but would instead increase their investment in defense and attempt to expel the intruder.

## MATERIALS AND METHODS

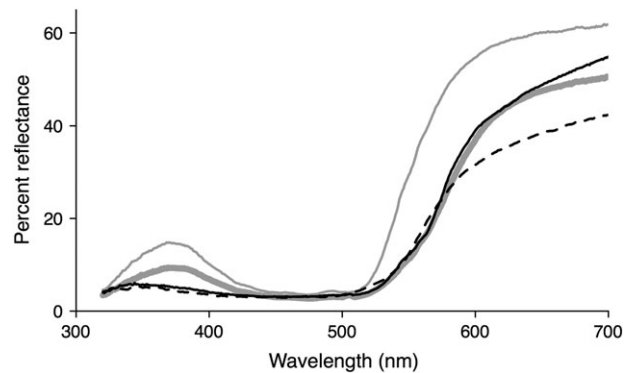
### Study site and species

The study was carried out in southern Morelos, Mexico, adjacent to the Reserve of Biósfera de Sierra de Huautla (18°26'21"N, 99°01'27"W). The habitat at this site is seasonally dry thorn and deciduous tropical forest (Trejo and Dirzo 2000), with an extreme dry season between January and May. Our study plot was along a 0.9-km riparian corridor and included 200 m of adjacent thorn forest on each side of a seasonally ephemeral river. The density of orioles here was high, with 40–50 pairs per km of riparian corridor. In March–May 2006, we captured >200 orioles using mist nets and conspecific playbacks and marked each individual with a unique combination of leg bands. We did not use band colors that resembled plumage colors (i.e., red, yellow, and orange bands). We then conducted model presentation experiments (November–December 2006) in the nonbreeding season, followed by a second round of model presentation experiments (May 2007) during the next breeding season.

Detailed observations at >50 nests at this site revealed that the streak-backed oriole is socially monogamous with biparental care (Murphy TG, unpublished data; see also Jaramillo and Burke 1999). Pairs maintain year-round territories, and both sexes defend this territory throughout the year (see below). Female and male aggression is commonly observed at territorial boundaries and nest sites, and displays and chases often escalate to physical contact and fights that last several minutes.

Oriole nests on our study site were generally placed within large trees in the riparian corridor. Suitable nesting trees were apparently limited, as up to 7 nests were placed in some trees, and territories radiated outward from each nest into adjacent thorn forests. Each breeding season, many individuals of each sex were not paired and did not breed or maintain territories.

We estimated territory boundaries by conducting systematic transects and marking locations of banded birds with a GPS receiver (Garmin 60 cs; accuracy 3–5 m). We surveyed 6 parallel 800-m long transects across the 400 × 900 m study plot by walking at a speed that allowed us to traverse each transect



**Figure 1**

Reflectance spectra for natural and color-augmented breast plumage of female streak-backed orioles: a naturally average-colored female (thin gray line), a naturally colorful female (thick gray line), and a color-augmented female model (black line). A naturally colorful male is also shown (black dashed line).

in about 2 h. Waypoints determined by GPS were later plotted with digital mapping software (MacGPS Pro, James Associates). Territory maps consisted of waypoints compiled from 72 transects (36 in the breeding season from May to June 2006 and 36 in the nonbreeding season from October–November 2006). Our maps indicated that territories were often triangular in shape, as they widened progressively from the nest tree as each territory expanded out from the nest tree into the surrounding forest. We defined the central portion of each pair's territory as the region where most observations occurred away from the nest tree, based on visual evaluation of clusters of GPS waypoints.

Both sexes have colorful orange and yellow plumage. Based on visual inspection of the shape of plumage color spectra (Figure 1, see below for details on color measures), we infer that these colors are produced by carotenoid pigmentation (for similar approach, see Hofmann et al. 2006, 2007). This inference is supported by biochemical analysis of the yellow–orange body plumage of the closely related Baltimore oriole, *Icterus galbula* (Hudon 1991). Male body plumage of the streak-backed oriole is typically more orange, whereas females are more yellow, although the color metrics of the sexes overlap considerably (see below). Because of similarities in male and female body plumage coloration, sex was determined by distinct differences in coloration of adult tail plumage (light brown in females, black in males) or with molecular sexing techniques (blood samples were collected from each individual via the brachial vein, and sexing followed methods in Griffiths et al. [1998], with some modification to primers). Genetic analyses agreed completely with sexing based on tail color ( $n = 80$ ).

### Taxidermic models, color measurement, and model manipulation

Six models of each treatment type (male, average-colored female, color-augmented female) were prepared before the experiments began. We collected birds with mist nets, and all birds were collected at least 5 km from the study site to ensure that they would be unfamiliar to the territorial birds being tested. We prepared all models at the same time using standard taxidermic methods, and models were given glass eyes and placed into a life-like perched posture. We randomly assigned each model to a treatment group after taxidermic preparation. After assigning female models to

the average-colored or color-augmented treatment group, we verified that body size (tarsus), mass, and natural coloration (see below) in the 2 groups were not significantly different (Wilcoxon tests,  $P > 0.10$  in each case).

Plumage color was measured on 4 patches (belly, breast, cheek, and crown) on each model. One of us (T.G.M.) measured all colors using an Ocean Optics USB2000+ spectrometer and PX-2 pulsed xenon lamp (Ocean Optics Inc., Dunedin, FL) with the probe perpendicular to the feather surface. Reflectance ( $R$ ) was calculated as the proportion of reflectance compared with a Spectralon white standard (Labsphere Inc., NH) at 1-nm intervals across the avian visual range (320–700 nm). We calculated the mean reflectance of 5 measures for each color patch to compute Hue (wavelength where  $R = [R_{\max} + R_{\min}]/2$ ), mean Brightness (mean  $R$  from 320 to 700 nm), and Saturation (sum of  $R$  from 625 to 700 nm divided by mean Brightness). All color variables were taken from table 3.2 in Montgomerie (2006) and computed using CLR 1.05 software (Montgomerie 2008).

To augment color, we applied a mix of nontoxic Prismacolor felt-tipped art markers (orange pm-16 and yellow pm-123) to the breast, cheek, and crown (for a similar approach to manipulating plumage coloration, see McGraw and Hill 2000; Pryke and Andersson 2003). This augmentation of feather colors significantly shifted the hue toward red (breast mean  $\pm$  standard error [SE]: pretreatment = 549.5 nm  $\pm$  2.2; posttreatment = 558.7 nm  $\pm$  1.2; Wilcoxon paired test,  $z = 10.5$ ,  $P = 0.03$ ,  $N = 6$  models) and increased saturation (breast: pretreatment = 0.55  $\pm$  0.01; posttreatment = 0.59  $\pm$  0.01; Wilcoxon paired test,  $z = 10.0$ ,  $P = 0.03$ ,  $N = 6$ ). There was a slight, but non-significant, reduction in mean brightness of manipulated plumage (breast: pretreatment = 0.23  $\pm$  0.01; posttreatment = 0.21  $\pm$  0.01; Wilcoxon paired test,  $z = 8.5$ ,  $P = 0.09$ ,  $N = 6$ ; Figure 1). This augmentation produced reflectance curves similar to those of the most colorful females in the population (Figure 1). The same body regions of all models were painted in a similar manner to ensure that patch size and postmanipulation color did not vary significantly between models of the same type. Although color-augmented female models were more male-like in body coloration (see Figure 1; male model breast color; mean  $\pm$  SE: Hue = 557.7  $\pm$  2.4, Saturation = 0.59  $\pm$  0.01, Brightness = 0.28  $\pm$  0.01), it is unlikely that territorial owners confused the sex of the model because tail color is highly sexually dichromatic.

We applied a clear Prismacolor marker (pm-121) to the same body regions of average-colored female models as well as to male models. This application did not significantly alter Hue, Brightness, or Saturation (Wilcoxon paired tests:  $P > 0.50$ ,  $N = 6$  in all comparisons). All color manipulations were performed before the first experiment in the nonbreeding season.

### General experimental methods

Each pair was presented with a series of taxidermic models—each model presented on a different day—accompanied by a recording of conspecific chatters and calls. For each presentation, the model was placed on a 1-m tall perch (natural branch), and a speaker was placed below the model. To minimize bias, we used the same perch stick for all experiments. The playback vocalizations were recorded from a bird of the same sex as the model and were played throughout the trial on a loop comprising 20 s of vocalization followed by 60 s of silence. These recordings were taken from a nonneighbor (territories separated by  $>100$  m) and were standardized for both amplitude (energy of spectra) and the number of chatters and calls using Raven Pro 1.3 software (Cornell Lab of Ornithology, Ithaca, NY). Speaker volume was set at the same

level for all experiments, and the amplitude of broadcasts was similar to that of natural vocalizations. To reduce pseudoreplication, models and recordings were randomly selected from a pool of 6 models and 6 recordings of each sex, and each model  $\times$  recording combination was used only once for the whole experiment. We balanced the presentation order of model type for each territory by alternating which type of model was presented first. All trials were conducted between 07:00 and 09:30 local time (GMT  $-6$ ). Neighboring territories were not tested on the same day, and the period between treatments on each territory was 7–10 days. Treatments on each territory were performed at approximately the same time of day ( $\pm 20$  min), and the model and speaker were placed in the same location and oriented in the same direction for each presentation.

Using telescopes and binoculars from a hide approximately 30 m from the model, 2 observers monitored the responses of the male and female—each observer focusing on one member of the pair and collecting continuous data for that individual. Landmarks were established before trials began to indicate 30 and 5 m radii around each model, and the hide was placed in a location that allowed the 30-m radius around the model to be observed with relative ease. After the model was placed in the territory and the conspecific vocalizations started, we recorded and collected behavioral data onto a voice recorder for 20 min. We defined duration of territorial response as the time spent within 30 m of the model, and we defined intensity of territorial response as a combination of 3 variables: 1) number of agonistic chatter vocalizations, 2) time spent less than 5 m from the model, and 3) closest approach to the model. We used principal component analysis to create a score of response intensity. The first principal component (PC1) explained 60% of the variation in the responses we measured and had high positive loadings for chatters and time spent  $<5$  m from the model (eigenvectors = 0.65, 0.81, respectively) and a high negative loading for closest approach to model (eigenvector =  $-0.85$ ). Thus, higher PC1 scores indicated a more aggressive bird that spent more time  $<5$  m from the model, chattered more, and approached closer to the model.

When a bird failed to respond during a trial, it was assigned a value of 31 m for closest approach and zero for all other measures. Our previous work on this species has shown that female streak-backed orioles sing up to 6 times as many solo songs per unit time as males (Price et al. 2008). However, female song is not clearly tied to territorial defense, and the context and function of female song remains obscure in this species (but see Brunton et al. 2008; Illes and Yunes-Jimenez 2009). In this study, we did not include song as a measure of the intensity of territorial response because the extreme female bias in song rate would have overwhelmed all other measures of sex-role differences in territorial response.

### Nonbreeding season experiment

From 18 November to 4 December 2006, during the nonbreeding season, we measured the territorial response of 20 pairs to simulated intruders. Each pair was presented with a male and a female taxidermic model with average-colored plumage.

### Breeding season experiment

From 3 to 23 May 2007, during the following breeding season but before the initiation of clutches, we measured territorial responses of pairs to simulated intruders on the same 20 territories. We followed the same protocol we used for the nonbreeding season experiment, except that each pair was also presented with a female taxidermic model whose plumage color had been artificially augmented. Thus, in the breeding

season, each pair was presented with 3 models: a male model, an average-colored female model, and a color-augmented female model.

Because we found that territory shape and size typically did not vary much between seasons, we presented models in the same locations that were used in the nonbreeding season experiment. Between the nonbreeding season and breeding season experiments, one or both territory owners remained the same on 15 of the 20 territories. There was thus a complete change in ownership on 5 territories, but the territorial boundaries for these new pairs were similar to those of the pairs they replaced.

**Analyses**

We tested whether there were sex-role differences in territorial response within each pair. Males and females responded simultaneously to the simulated intruders, so this approach allowed us to investigate relative responses of the male and female territorial owners to the same (simulated) territorial intruder. By comparing male and female responses to each model, we obviate the need to control for the many variables that might influence responses to models that are independent of the relative responses of pair members (e.g., stage of season, weather, time of day, presence of predators, distractions, etc.).

To analyze the within-pair differences (i.e., sex bias) in response duration and intensity to each type of model, we used repeated-measures analyses of variance (ANOVAs). We used this paired analysis separately for each model type (male, average-colored female, and color-augmented female) to test whether females were more responsive than their mates when they encountered each type of simulated intruder. To test whether the within-pair differences were significant in response to different models (i.e., was sexual bias in response greater to one type of model compared with another type of model), we included an interaction term (model type × sex) in the repeated-measures ANOVAs.

The male and female of 3 pairs completely failed to respond to the simulated intrusions in each season and so were not included in any analyses. To validate the use of parametric statistics, we used Shapiro–Wilk *W* test to analyze whether residuals from repeated-measures ANOVAs were normally distributed. Due to a deviation from normality, PC1 response intensity scores were log<sub>10</sub> transformed.

**RESULTS**

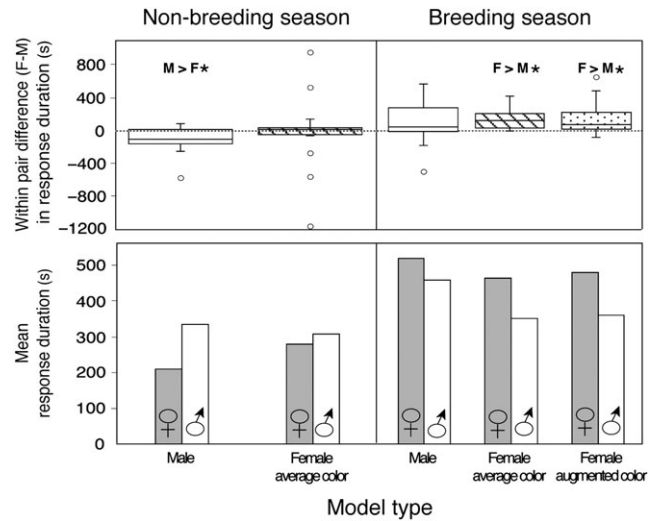
**Responses to male versus average-colored female models: nonbreeding season**

When territorial responses to both male and average-colored female models were combined, there was no significant within-pair difference between the sexes in the duration of their responses (repeated-measures ANOVA,  $F_{1,33} = 1.8$ ,  $P = 0.19$ ), but response intensity (PC1) was significantly higher for males than for their mates ( $F_{1,33} = 8.8$ ,  $P = 0.006$ ).

When territorial responses to each type of model were analyzed separately, males responded significantly longer ( $F_{1,16} = 9.4$ ,  $P = 0.007$ ) and with greater intensity (PC1) ( $F_{1,16} = 6.6$ ,  $P = 0.02$ ) than did their mates when they were presented with male models, but there was not a significant within-pair difference in these responses to average-colored female models (duration:  $F_{1,16} = 0.07$ ,  $P = 0.79$ ; intensity:  $F_{1,16} = 2.9$ ,  $P = 0.11$ ; Figures 2 and 3).

**Responses to male versus average-colored female models: breeding season**

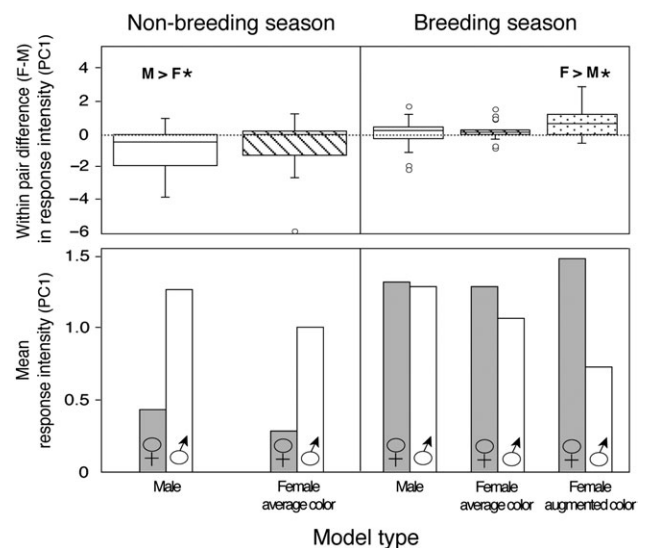
When territorial responses to both types of models were combined, response duration by females was significantly



**Figure 2** Within-pair sex differences in duration of response to simulated territorial intrusion by taxidermic models of different types (male models, female models with average-colored plumage, and female models with color-augmented plumage) in the nonbreeding (left) and breeding seasons (right). The differences between male and female responses within pairs (top, Tukey box plots) and the mean response of each sex to each model type (bottom) are shown. Asterisks denote significant sex-role differences in responses within pairs.

longer than that of their mates (repeated-measures ANOVA,  $F_{1,33} = 7.1$ ,  $P = 0.01$ ), in contrast to the nonbreeding season when males responded for longer than their mates. Response intensity (PC1), however, did not differ significantly between sexes within pairs ( $F_{1,33} = 1.2$ ,  $P = 0.28$ ).

When territorial responses to each type of model were analyzed separately, there was not a significant within-pair difference in response duration or intensity (PC1) when the pair was presented with male models (duration:  $F_{1,16} = 1.1$ ,



**Figure 3** Within-pair sex differences in intensity of response (PC1) to simulated territorial intrusion by taxidermic models of different types (for details, see Figure 2). Intensity (PC1) scores were converted to positive values by adding 1 to all scores (PC1 + 1.0). Asterisks denote significant sex-role differences in responses within pairs.

$P = 0.31$ ; intensity:  $F_{1,16} = 0.2$ ,  $P = 0.67$ ). However, when pairs were presented with average-colored female models, the duration of female response was significantly longer than that of their mate ( $F_{1,16} = 16.6$ ,  $P = 0.0009$ ), but there was not a significant sex difference in response intensity (PC1) within pairs ( $F_{1,16} = 1.8$ ,  $P = 0.21$ ; Figures 2 and 3).

### Responses to color-augmented versus average-colored female models

When territorial responses to each type of model were analyzed separately, the duration of female response was significantly longer than that of their mate when they were presented with both color-augmented ( $F_{1,16} = 6.3$ ,  $P = 0.02$ ) and average-colored female models (see above; Figure 2). However, response intensity (PC1) of the 2 sexes was significantly different depending on the color of the female model: Females responded with significantly greater intensity (PC1) than their mates to color-augmented female models ( $F_{1,16} = 14.0$ ,  $P = 0.002$ ); yet, there was not a significant female bias in response intensity when a pair was presented with an average-colored female model (see above; Figure 3). The magnitude of female bias in response intensity (i.e., difference between PC1 of pair members) differed significantly in response to the 2 model types (model type  $\times$  sex interaction:  $F_{1,32} = 4.42$ ,  $P = 0.04$ ).

### DISCUSSION

Results from the model presentation experiments indicate that the plumage color of a female intruder influences the relative investment by each sex in territorial defense and that females respond with greater intensity (PC1) than their mate when the intruding female is more colorful. These results suggest that females perceive a greater risk of losing either territory tenure or their mate when faced with a female intruder that signals relatively high fighting ability. This finding suggests that carotenoid-based plumage color of female plumage is a signal of status in this species.

Few other studies have provided data consistent with the prediction that elaborate female traits signal status (for review, see Amundsen and Pärn 2006). For example, Stiles and Wolf (1970) showed an interspecific relationship between female aggression and elaborate female plumage among tropical hummingbirds (see also Wolf 1969; Bleiweiss 1985), and Whittingham et al. (1992) found that females of a tropical subspecies of red-winged blackbirds (*Agelaius phoeniceus*) that maintain year-round territories are elaborately plumed, whereas nonterritorial temperate subspecies have drab females (see also Irwin 1994). In addition to these comparative studies, intraspecific analyses have indicated a relationship between female plumage color and status (Swaddle and Witter 1995; Heinsohn et al. 2005; Viera et al. 2008), and dominance (Järvi and Bakken 1984; Watt 1986; Johnson 1988; Jones 1990). To the best of our knowledge, our study represents the first experimental evidence that variation within the natural range of carotenoid-based coloration functions to mediate contests among females.

In contrast to the increased territorial response of females to color-augmented female models, male response decreased. Why would males decrease the intensity of their response to a more colorful female intruder? One possibility is that reduced male aggressiveness toward a female intruder increases the probability that the more colorful female will successfully usurp his mate. Thus, a male may passively encourage female–female competitive interactions—acting as a willing participant in an “assisted divorce” (sensu Ens et al.

1993)—as the usurping female might be more effective than the current mate in cooperative territorial defense. Under this scenario, males should be expected to reduce investment in territory defense when the intruder is more dominant than the current mate. Another possibility is that males might not be influenced directly by the intruder’s plumage color but rather by the intensity of his mate’s response. Thus, when a female invests heavily in territorial defense, the male is able to reduce both his energy expenditure and risks by letting the female do the majority of the work. Regardless of the reasons underlying reduced male aggression, male behavior only enhanced the female bias in response to color-augmented female models. Future work should test whether male behavior is directly affected by the coloration of female intruders.

Our results indicate a switch from male-biased territoriality in the nonbreeding season to female-biased territoriality during the breeding season, and this pattern was especially pronounced in response to same-sex models. We can only speculate on the cause of this pattern, but it is possible that the territory is more valuable to females than males during the breeding season because females alone build the large pendulum nest, and this structure often requires 20–30 days to complete. This valuable resource—coupled with intense competition for nest sites, driven by the lack of suitable nesting trees and a large population of unpaired birds—could make the benefits of territory defense greater for females than for males during the breeding season. Few studies have shown female bias in territoriality in socially monogamous birds (for examples of greater female response to intrasexual intruders, see Levin 1996; Logue and Gammon 2004), so there is much to be learned from studying sex roles in territory defense in the tropics, especially when resources vary between seasons.

Females of tropical species often compete over resources that can be defended by territoriality, including food, access to water, safety from predators, roosting sites, and mates (Stutchbury and Morton 2001). However, the large investment by female streak-backed orioles in territory defense throughout the year suggests that territoriality functions to defend resources rather than mates. Further research on this system should test whether plumage coloration mediates only female–female competition or whether it also plays a role in female–male interactions. Such information will help clarify whether coloration is used to mediate conflict over mates (during within-sex interactions) or if plumage color is more likely to resolve resource-based conflict (during both within- and between-sex interactions).

Our research on the streak-backed oriole provides evidence that female plumage color affects the behavior of territorial residents in response to intruders, and represents the first manipulative study to support the role of female plumage in signaling status in a tropical bird species. These results may help to explain the often-noted geographic pattern in sexual dimorphism: That females of tropical species tend to have elaborate traits (elaborate monomorphic), whereas females of temperate zone species tend to be drab (dimorphic, with males more elaborately ornamented; for reviews, see Badyaev and Hill 2003; Omland and Hofmann 2006). Our results suggest that status signaling may be common in tropical birds because both sexes generally participate in year-round territorial defense, and both sexes are likely to benefit from defending real estate that is in limited supply. To better assess the breadth of this hypothesis in explaining geographic patterns of sexual dimorphism, future research on tropical birds should use manipulative approaches, both in the field and aviary, to assess the effect of coloration on same and opposite sex competitive interactions.

## FUNDING

National Science Foundation (NSF) International Research Fellowship Program (IRFP) and the Americas Program (0700953 to T.M.); NSF CAREER (DEB-0347083 to K.O.); Natural Sciences and Engineering Research Council Discovery Grant (to R.M.); and PROMEP-UAEM (to M.O.B.).

We are especially grateful to Roxana Torres for insightful feedback throughout the study, for support while in Mexico, and for comments on the manuscript. We thank Laila Yunes-Jimenez, Emily Cramer, Jenelle Dowling, Lynna Kiere, Andrea Lindo, Valerie Steen, Rachel Sturge, David Yuan, Jennyfer Femat-Rodriguez, and Cristina Acasuso for assistance in the field. We are grateful to Jeff Peters for help in modifying primers used for molecular sexing. Adolfo Navarro provided invaluable support for our research.

## REFERENCES

- Amundsen T. 2000. Why are female birds ornamented? *Trends Ecol Evol.* 15:149–155.
- Amundsen T, Pärn H. 2006. Female coloration in birds: a review of functional and non-functional hypotheses. In: Hill GE, McGraw KJ, editors. *Bird coloration. Vol. 2: function and evolution.* Cambridge (MA): Harvard University Press. p. 280–345.
- Badyaev A, Hill G. 2003. Avian sexual dichromatism in relation to phylogeny and ecology. *Annu Rev Ecol Evol Syst.* 34:27–49.
- Bailey S. 1978. Latitudinal gradients in colors and patterns of passerine birds. *Condor.* 80:372–381.
- Bleiweiss R. 1985. Iridescent polychromatism in a female hummingbird: is it related to feeding strategies? *Auk.* 102:701–713.
- Brunton DH, Evans B, Cope T, Ji W. 2008. A test of the dear enemy hypothesis in female New Zealand bellbirds (*Anthornis melanura*): female neighbors as threats. *Behav Ecol.* 19:791–798.
- Chaine AS, Lyon BE. 2008. Intra-sexual selection on multiple plumage ornaments in the lark bunting. *Anim Behav.* 76:657–667.
- Clutton-Brock T. 2009. Sexual selection in females. *Anim Behav.* 77:3–11.
- Ens BJ, Safriel UN, Harris MP. 1993. Divorce in the long-lived and monogamous oystercatcher, *Haematopus ostralegus*: incompatibility or choosing the better option. *Anim Behav.* 45:1199–1217.
- Fedy B, Stutchbury BJM. 2005. Territory defence in tropical birds: are females as aggressive as males? *Behav Ecol Sociobiol.* 58:414–422.
- Griffiths R, Double MC, Orr K, Dawson RJG. 1998. A DNA test to sex most birds. *Mol Ecol.* 7:1071–1075.
- Hamilton TH. 1961. On the functions and causes of sexual dimorphism in breeding plumage characters of North American species of warblers and orioles. *Am Nat.* 95:121–123.
- Heinsohn R, Legge S, Endler J. 2005. Extreme reversed sexual dichromatism in a bird without sex role reversal. *Science.* 309:617–619.
- Hofmann CM, Cronin TW, Omland K. 2006. Using spectral data to reconstruct evolutionary changes in coloration: carotenoid color evolution in new world orioles. *Evolution.* 60:1680–1691.
- Hofmann CM, McGraw KJ, Cronin TW, Omland KE. 2007. Melanin coloration in New World orioles I: carotenoid masking and pigment dichromatism in the orchard oriole complex. *J Avian Biol.* 38:163–171.
- Hudon J. 1991. Unusual carotenoid use by the western tanager (*Piranga ludoviciana*) and its evolutionary implications. *Can J Zool.* 69:2311–2320.
- Hunt S, Cuthill IC, Bennett ATD, Griffiths R. 1999. Preferences for ultraviolet partners in the blue tit. *Anim Behav.* 58:809–815.
- Illes AE, Yunes-Jimenez L. 2009. A female songbird out-sings male conspecifics during simulated territorial intrusions. *Proc R Soc Lond B Biol Sci.* 276:981–986.
- Irwin RE. 1994. The evolution of plumage dichromatism in the new world blackbirds: social selection on female brightness. *Am Nat.* 144:890–907.
- Jaramillo A, Burke P. 1999. *New World Blackbirds.* Princeton (NJ): Princeton University Press.
- Järvi T, Bakken M. 1984. The function of the variation in the breast stripe of the great tit (*Parus major*). *Anim Behav.* 32:590–596.
- Johnson K. 1988. Sexual selection in pinyon jays 2: male choice and female-female competition. *Anim Behav.* 36:1048–1053.
- Johnstone RA, Reynolds JD, Deutsch JC. 1996. Mutual mate choice and sex differences in choosiness. *Evolution.* 50:1382–1391.
- Jones IL. 1990. Plumage variability functions for status signaling in least auklets. *Anim Behav.* 39:967–975.
- Jones IL, Hunter FM. 1993. Mutual sexual selection in a monogamous seabird. *Nature.* 362:238–239.
- Kleiber D, Kyle K, Rockwell SM, Dickinson JL. 2007. Sexual competition explains patterns of individual investment in territorial aggression in western bluebird winter groups. *Anim Behav.* 73:763–770.
- Kraaijeveld K, Gregurke J, Hall C, Komdeur J, Mulder RA. 2004. Mutual ornamentation, sexual selection, and social dominance in the black swan. *Behav Ecol.* 15:380–389.
- Kraaijeveld K, Kraaijeveld-Smit F, Komdeur J. 2007. The evolution of mutual ornamentation. *Anim Behav.* 74:657–677.
- Lande R. 1987. Genetic correlations between the sexes in the evolution of sexual dimorphism and mating preferences. In: Bradbury JW, Andersson MB, editors. *Sexual selection: testing the alternatives.* New York: Wiley. p. 83–94.
- Lebas N. 2006. Female finery is not for males. *Trends Ecol Evol.* 21:170–173.
- Levin R. 1996. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*: 2. Playback experiments. *Anim Behav.* 52:1107–1117.
- Logue DM, Gammon DE. 2004. Duet song and sex roles during territory defence in a tropical bird, the black-bellied wren, *Thryothorus fasciatoventris*. *Anim Behav.* 68:721–731.
- MacDougall AK, Montgomerie R. 2003. Assortative mating by carotenoid-based plumage colour: a quality indicator in American goldfinches, *Carduelis tristis*. *Naturwissenschaften.* 90:464–467.
- Mays H, Hopper K. 2004. Differential responses of yellow-breasted chats, *Icteria virens*, to male and female conspecific model presentations. *Anim Behav.* 67:21–26.
- McGraw KJ, Hill GE. 2000. Carotenoid-based ornamentation and status signaling in the house finch. *Behav Ecol.* 11:520–527.
- Montgomerie R. 2006. Analyzing colors. In: Hill GE, McGraw KJ, editors. *Bird coloration. Vol. 1: mechanisms and measurements.* Cambridge (MA): Harvard University Press. p. 90–147.
- Montgomerie R. 2008. CLR, version 1.05. Kingston (ON): Queen's University. [Internet] Available from: available at <http://post.queensu.ca/~mont/color/>.
- Moore A, Haynes K, Preziosi R, Moore P. 2002. The evolution of interacting phenotypes: genetics and evolution of social dominance. *Am Nat.* 160:S186–S197.
- Murphy TG. 2006. Predator-elicited visual signal: why the turquoise-browed motmot wag-displays its raked tail. *Behav Ecol.* 17:547–553.
- Murphy TG. 2007. Raked tail of the male and female turquoise-browed motmot: male but not female tail length correlates with pairing success, performance, and reproductive success. *Behav Ecol Sociobiol.* 61:911–918.
- Omland K, Hofmann C. 2006. Adding color to the past: ancestral state reconstruction of bird coloration. In: Hill G, McGraw KJ, editors. *Bird coloration. Vol. 2: function and evolution.* Cambridge (MA): Harvard University Press. p. 417–454.
- Peterson A. 1996. Geographic variation in sexual dichromatism in birds. *Bull Br Ornithol Club.* 116:156–172.
- Price J, Yunes-Jimenez L, Osorio-Beristain M, Omland K, Murphy TG. 2008. Sex-role reversal in song? Females sing more frequently than males in the streak-backed oriole. *Condor.* 110:387–392.
- Pryke S, Andersson S. 2003. Carotenoid-based status signalling in red-shouldered widowbirds (*Euplectes axillaris*): epaulet size and redness affect captive and territorial competition. *Behav Ecol Sociobiol.* 53:393–401.
- Pryke S, Andersson S, Lawes M, Piper S. 2002. Carotenoid status signaling in captive and wild red-collared widowbirds: independent effects of badge size and color. *Behav Ecol.* 13:622–631.
- Rohwer S. 1975. The social significance of avian winter plumage variability. *Evolution.* 29:593–610.
- Rohwer S. 1985. Dyed birds achieve higher social-status than controls in Harris' sparrows. *Anim Behav.* 33:1325–1331.
- Roulin A, Altwegg R. 2007. Breeding rate is associated with pheomelanism in male and with eumelanism in female barn owls. *Behav Ecol.* 18:563–570.
- Senar JC. 1990. Agonistic communication in social species—what is communicated. *Behaviour.* 112:270–283.

- Senar JC. 1999. Plumage colouration as a signal of social status. *Proc Internat Ornithol Congr.* 22:1669–1686.
- Senar JC. 2006. Color displays as intrasexual signals in birds. In: Hill G, McGraw KJ, editors. *Bird coloration. Vol. 2: function and evolution.* Cambridge (MA): Harvard University Press. p. 87–136.
- Skutch AF. 1940. Some aspects of Central American bird-life. *Science Monthly.* 51409500–418511.
- Stiles F, Wolf L. 1970. Hummingbird territoriality at a tropical flowering tree. *Auk.* 87:467–491.
- Stutchbury BJM, Morton ES. 2001. *Behavioral ecology of tropical birds.* San Diego (CA): Academic Press.
- Swaddle JP, Witter MS. 1995. Chest plumage, dominance and fluctuating asymmetry in female starlings. *Proc R Soc Lond B Biol Sci.* 260:219–223.
- Tarof S, Dunn P, Whittingham L. 2005. Dual functions of a melanin-based ornament in the common yellowthroat. *Proc R Soc Lond B Biol Sci.* 272:1121–1127.
- Tibbetts E, Dale J. 2004. A socially enforced signal of quality in a paper wasp. *Nature.* 432:218–222.
- Torres R, Velando A. 2005. Male preference for female foot colour in the socially monogamous blue-footed booby, *Sula nebouxi*. *Anim Behav.* 69:59–65.
- Trejo I, Dirzo R. 2000. Deforestation of seasonally dry tropical forest: a national and local analysis in Mexico. *Biol Conserv.* 94:133–142.
- Viera VM, Nolan PM, Côté SD, Jouventin P, Groscolas R. 2008. Is territory defence related to plumage ornaments in the king penguin *Aptenodytes patagonicus*? *Ethology.* 114:146–153.
- Watt D. 1986. Relationship of plumage variability, size and sex to social dominance in Harris' sparrows. *Anim Behav.* 34:16–27.
- West-Eberhard MJ. 1979. Sexual selection, social competition, and evolution. *Proc Am Philos Soc.* 123:222–234.
- West-Eberhard MJ. 1983. Sexual selection, social competition, and speciation. *Q Rev Biol.* 55:155–183.
- Whittingham LA, Kirkconnell A, Ratcliffe LM. 1992. Differences in song and sexual dimorphism between Cuban and North American red-winged blackbirds. *Auk.* 4:928–933.
- Wolf L. 1969. Female territoriality in a tropical hummingbird. *Auk.* 86:490–504.