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RESEARCH ARTICLE

Carotenoid coloration predicts escape performance in the House Finch (*Haemorhous mexicanus*)

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ABSTRACT

Carotenoid coloration has been repeatedly shown to serve as a sexually selected signal of individual quality. Across different species, individuals showing brighter carotenoid-based signals have been found to have superior foraging abilities, to recover faster from diseases and, in general, to enjoy a better body condition. Experiments with birds have also shown that carotenoid supplementation can enhance flight performance, allowing birds to take off faster from the ground. Healthy, agile individuals should be better prepared to avoid predators, so it could be expected that individuals displaying brighter carotenoid-based coloration would show a higher escape ability from predator attacks. To test this prediction, we measured the escape ability of male House Finches (*Haemorhous mexicanus*) from a human with a net in a large aviary and related the escape ability of each individual to its breast coloration. Males with redder feathers showed a higher individual ability to escape than duller individuals. The superior flight performance of redder birds would be an important asset in escape from predators, as well as when foraging or maintaining a territory. In the specific case of the House Finch, the higher escape ability of redder individuals could be the reason for their higher overwinter survival rate.

Keywords: Haemorhous mexicanus, condition, aerobic capacity, sexual selection, predation, escape ability

La coloración basada en carotenoides determina la capacidad de escape en el *Haemorhous mexicanus*

RESUMEN

Se ha demostrado que las coloraciones basadas en carotenoides funcionan como una señal sexual de calidad individual. En diversas especies, se ha visto que los individuos que muestran una coloración basada en carotenoides más brillante muestran mejores habilidades a la hora de forrajear, se recuperan antes de enfermedades y, en general, disfrutan de una mejor condición física. También se ha podido constatar experimentalmente que una suplementación de carotenoides en la dieta producía mejoras en el vuelo de las aves, al ser capaces éstas de despegar más rápido del suelo. Un individuo más ágil y de mejor salud debería estar potencialmente mejor preparado para escapar de predadores, de modo que podría esperarse que individuos que muestran una coloración basada en carotenoides más brillante deberían ser mejores escapando del ataque de un predador. Para probar esta predicción, medimos la habilidad de escape de machos de *Haemorhous mexicanus*, al ser perseguidos por un humano con una red en un aviario, y relacionamos la capacidad de escape de cada individuo con la coloración del plumaje del pecho. Los machos de plumas más rojas mostraron una mayor capacidad individual de escape. Esta mejor capacidad de vuelo podría no sólo ser una valiosa habilidad contra predadores, sino también podría ofrecer importantes ventajas a la hora de forrajear o mantener un territorio. En el caso específico del *Haemorhous mexicanus*, esta mayor capacidad de escape podría ser la causa de la mayor supervivencia invernal de los individuos de plumas más rojas.

Palabras clave: Haemorhous mexicanus, condición, capacidad aeróbica, selección sexual, depredación, capacidad de escape

INTRODUCTION

Locomotor performance is a key component of survival for many species of animals. Moreover, because courtship behavior, competition for females, or the maintenance of a territory are often determined by locomotor performance, sexual selection can play a role in shaping locomotor evolution (Husak et al. 2006, Husak & Fox 2008). Secondary sexual traits can evolve to signal whole-organism performance abilities, and such traits can function in male–male competition, e.g., the horn of the beetle *Euoniticellus intermediu* (Vanhooydonck et al. 2005) or the dewlap of several *Anolis* lizards (Lailvaux et al. 2005). Prospective females could also benefit from assessing and selecting on ornamental traits that signal, for instance, a higher endurance, a greater aerobic capacity, or a better locomotor performance (Irschick et al. 2008). For example, courtship call rate is related to endurance during exercise in the decorated cricket *Gryllodes sigillatus* (Ketola et al. 2009) and swimming performance is associated with the blue nuptial coloration of male Pecos pupfish *Cyprinodon pecosensis* (Kodric-Brown & Nicoletto 1993), with the size of the sword of male green swordtails *Xiphophorus helleri* (Royle et al. 2006), and with the carotenoid coloration of male guppies *Poecilia reticulata* (Nicoletto 1991).

Carotenoid pigments are the basis of many ornamental displays of animals (Olson and Owens 2005). These pigments cannot be synthesized de novo by animals but must be ingested (Brush 1978). Therefore, carotenoid coloration depends on the quantity and/or quality of the food (Goodwin 1986) and on the physiological ability of individuals to process carotenoids (Olson & Owens 1998). Consequently, carotenoid coloration has been considered as a signal of nutritional status, foraging ability, and general condition of the individual (Hill 1999, Hill and McGraw 2006). There is experimental evidence of positive effects of carotenoids in many aspects of animal health (Svensson and Wong 2011). For instance, carotenoids have been related to cognitive function (Mateos-Gonzalez et al. 2011), disease recovery (Hill and Farmer 2005), immunocompetence, and prevention of oxidative damage (Powers and Deruisseau 2004, Simons et al. 2012, but see Hartley and Kennedy 2004). According to a recent hypothesis, the aerobic capacity of an individual could be also related to its carotenoid coloration, given that the metabolism of carotenoid pigments in the production of ornamental coloration is intimately linked to cellular respiration (Hill and Johnson 2012, Johnson and Hill 2013).

These beneficial effects of carotenoids have a joint potential to influence important whole-animal performance abilities such as locomotor performance. In fact, Blount and Matheson (2006) observed that carotenoid supplementation enhanced takeoff performance in Zebra Finches *Taeniopygia guttata*. These results agreed with previous experiments in which Birkhead et al. (1998) observed that Zebra Finches whose carotenoid-based red beaks were redder evaded capture better than those with duller beaks. It could be expected that birds with brighter carotenoid-based plumage would show better escape abilities.

Male House Finches (*Haemorhous mexicanus*) have carotenoid-based plumage that varies from pale yellow to bright red, which they acquire after a complete prebasic molt in the late summer/early fall (Hill 1992). This coloration reflects the nutritional condition of its bearer (Hill et al. 1994), and several experiments have demonstrated that it is used as a primary criterion in female mate choice (Hill 1990, 1991). In this study, we tested the prediction that male House Finches showing redder carotenoid-based breast plumage would show greater evasion abilities. To do so, we simulated aerial predator attacks by pursuing birds in an enclosure with a hand net. We then related the escape ability of each individual to its plumage coloration.

METHODS

During January 10–24, 2011, 16 male House Finches were captured on the campus of Auburn University, Auburn, Alabama, USA, in traps baited with seed. The hue of breast feathers was assessed by visually comparing feather color to plates in Kornerup and Wanscher (1983), which is a repeatable method of determining feather hue (Hill 1998). Feather hue is correlated to carotenoid availability in this and many other species (Hill et al. 1994, Simons et al. 2012). Birds were measured for wing, tail, and tarsus length, given a metal leg band with a unique number, and transported 2 km to an outdoor aviary (3 m wide × 2.5 m high × 3.8 m long). Birds were maintained on a diet of mixed seeds and water. Experiments started in June 2011.

House Finches are highly social birds that form flocks outside the breeding season (Hill 1993). In previous studies (Moreno-Rueda 2003, De Neve et al. 2010), the escape ability of birds was examined by observing the rank order in which birds of a captive flock are captured by a researcher. This method takes into account the flocking behavior that has evolved in many bird species in response to predation pressures, a behavior that can reduce the chances of predation by increasing confusion and dilution effects (Hamilton 1971, Cresswell 1994). However, flock dynamics and accidental interference among birds can mask individual abilities. To determine the escape performance of our experimental birds, we obtained two kinds of measurements: capture rank order from an experimental flock of 16 male House Finches and individual capture time in isolation of these same birds.

Capture rank order was estimated by placing all birds in a common enclosure (3 m wide × 2.5 m high × 3.8 m long). Following the protocol described in De Neve et al. (2010), FMG entered the room with a 30-cm–diameter butterfly net and positioned himself in the middle of the enclosure. Birds immediately reacted to this action as they would in front of a real predator: flying away as far as possible from the threat. As space and perches were limited, some birds would end up being in more exposed spots, at the edges of the flock. In that moment, the experimenter attempted to capture one bird from the flock, aiming for the closest or easiest individual. To capture each bird, FMG tried to position the net over the individual when it was perched. If that individual managed to evade the net, the experimenter would not continue chasing the same individual, and would pursue instead another bird within reach, doing so until a bird was captured. Flight initiation distance (FID), that is the distance at which an animal takes off from a potential predator, is used as a proxy for boldness (Blumstein 2006, Rodríguez-Prieto et al. 2011, Seltmann et al. 2012), so individual differences in fear/boldness could potentially determine the distance at which a bird is perched from the predator in this setup. However, given the length of the enclosure (3.8 m), the experimenter was at all times at a closer distance than usual FIDs for House Finches (e.g., figure 2 in Valcarcel and Fernández-Juricic 2009); this factor created constant movement and escape interferences among birds, which makes very unlikely that boldness could have an effect on which birds were closer to the experimenter at any given time.

Upon capture, each bird was confined in a transport cage within the enclosure and its band number and capture order were noted. Using this procedure, FMG captured 6 individuals in a row and relocated them in individual enclosures (1.5 m wide × 2.5 m high × 3.8 m long). After a 60-min rest, he performed another capture shift in the common enclosure, capturing 6 more individuals from the main flock, relocating them in individual enclosures. The last 4 birds of the flock were captured in a third capture shift after 90 min, a slightly longer rest to compensate for the fact that they had already been chased twice before. Each capture shift lasted no more than 25 min.

To estimate individual capture time, tests were run in the individual enclosures. FMG entered each individual enclosure, positioned himself in the middle, and proceeded to capture each individual with the same sweep net from the previous test. In the same manner, the experimenter tried to position the net over the bird as soon as it perched. Capture, in every case, took place when the perched bird failed to take off before the sweep net was over it. FMG had already ample experience in the use of a sweep net, so his capture performance was not likely to improve or decrease over the course of the experiment. Despite being less realistic than a setup with a real predator, this method avoided ethical problems and provided more control over the "predator" motivation. The effort needed to capture a bird in a small enclosure is almost negligible, so it was possible to chase the bird without pause, from the start of the attempt until the bird was finally captured. This approach ensured a relatively standardized effort, which helped to control involuntary biases. Total capturing time for each individual was measured using a stopwatch, and ranged from 22 s to 290 s. After each capture, birds were relocated to a common enclosure. No bird was injured as a result of the experiment.

Analysis

We used an information-theoretic approach following Grueber et al. (2011). Two global models, including all measured variables, were defined to generate model sets for each of the two experiments. Both the relationship between capture rank order and color score, and the relationship between individual capture time (log-transformed to meet normality) and color score were fitted in two multiple regressions (*glm* in R, family = *gaussian*). There was no significant correlation between tarsus, wing, and tail lengths (Pearson's product-moment correlation; wing–tail: $P > 05$, $r = 0.17$; wing–tarsus: $P > 0.1$, $r = 0.38$; tail–tarsus: $P > 0.5$, $r = 0.16$), so they were included as covariates in both global models as they might affect takeoff and flight ability. Diagnostic plots were inspected to ensure normality of residuals in both models.

We standardized the input variables of these two global models using the *standardize* function in the *arm* package in R (Gelman et al. 2013). This package includes tools for data analysis using regression and multilevel/hierarchical models. The *standardize* function standardizes regression predictors by centering and dividing by 2 SD.

Then we generated model sets for each analysis, including null models, using the function *dredge* in the *MuMIn* package (Bartoń and Bartoń 2013). From the full model sets we selected "top model sets" using a 95% confidence threshold. Finally, we computed the model-averaged parameters, using the function *model.avg* in *MuMIn* package (Bartoń and Bartoń 2013). All statistical analyses were conducted in R 3.0.0 (R Development Core Team 2013).

RESULTS

Capture rank order and individual capture time in isolation were moderately correlated measures (Pearson's product-moment correlation: $n = 16$, $r = 0.53$, $P = 0.034$; Spearman's rank correlation: $n = 16$, $r_s = 0.49$, $P = 0.055$). An ANCOVA, with experiment (individual capture time or capture order) as grouping factor, color score as dependent variable, and standardized time/order as independent variable, showed that the interaction between experiment and color score was not significant ($P < 0.5$). This result indicates that the standardized slopes of color score on capture rank order ($\beta = 0.357 \pm \mathrm{SE} = 0.32$) and color score on individual capture time ($\beta = 0.674 \pm \mathrm{SE} = 0.286$) did not differ significantly.

There was no significant effect of coloration, tarsus length, wing length, or tail length in the capture order of male House Finches (Table 1). The highest-ranking model could not be distinguished from the null model, given that the difference in corrected Akaike Information Criterion ($\mathrm{AIC_c}$) was less than 2. The model-averaged parameter estimate for all the variables overlapped zero (Table 2), so

TABLE 1. Top models for capture order, resulted from the model average after selection of a 95% confidence model set. Models in the set are arranged from best to worst based on the difference in AIC_c values between the best model and competing models (ΔAIC_c). AIC weights (AIC_w) are the relative likelihoods of a model given the data, and evidence ratios (ER) are the relative likelihood of each model versus the best model.

Models	AIC_c	ΔAIC_c	AIC_w	ER
Tail length	98.75	0	0.31	1
Null model	99.23	0.48	0.24	1.29
Color score	100.95	2.19	0.10	3.1
Tail L + Wing L	101.23	2.48	0.09	3.44
Color score + Tail L	101.82	3.07	0.07	4.43
Wing length	101.91	3.15	0.06	5.17
Tarsus length	102.22	3.46	0.05	6.2
Tail length	102.39	3.64	0.05	6.2
Color score + Tarsus L	103.35	4.60	0.03	10.33

there is little evidence that any of these explanatory variables affected capture order.

However, birds with higher color scores took longer to capture in the individual enclosures than birds with duller colors (Figure 1). The highest-ranking model (Table 3) included only color score. The difference in AIC_c between the best model and the alternative models was larger than 2, indicating that they can be discriminated. The model-averaged parameter estimate for color score did not overlap zero (Table 4), indicating a significant effect of this variable on capture time.

DISCUSSION

As predicted by the hypothesis that red carotenoid coloration is a condition-dependent signal of individual quality (Hill 1990), we observed that male House Finches with redder plumage coloration were harder to capture with a sweep net than birds with duller colors.

In contrast to the significant relationship between individual escape performance and coloration, we found no significant relationship between capture rank and feather color, despite both measures being moderately correlated. We speculate that the lack of relationship between rank order of capture of House Finches and their feather color stems from the interference among flock members that obscures individual ability. When 16 House Finches are being chased in a cage, they frequently crowd onto perches and into corners. The vision and movements of some birds are impaired. When a single bird is chased in a cage following our protocol, in contrast, probably the ability to continue to fly is what determines capture time. Hence, individual capture time is a measure that will better reproduce individual performance, which is in turn reflected by the sexual carotenoid-based signal.

In our trials, all birds were captured when they were perched and failed to take off before the experimenter attempted to put a sweep net over them. Thus, birds that

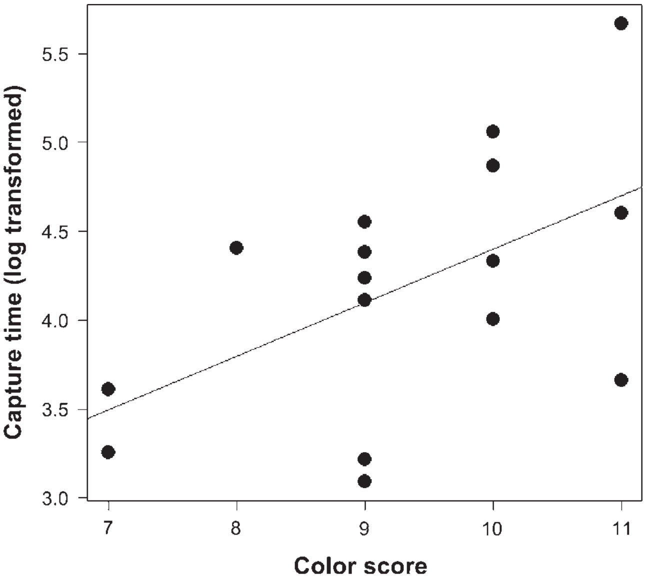

FIGURE 1. Relationship between color score of the different individuals and time required to capture each one (log transformed). The line represents the regression slope.

TABLE 2. Standardized coefficients of model predictors, after model averaging of the top candidate models (95% confidence) (see Table 1). Table includes estimates, relative importance (Σ, sum of Akaike weights of the models in which the predictor was present), unconditional SE, and 95% confidence interval (CI) for estimates. Parameter estimates have a significant effect when the 95% CIs do not include zero.

Predictors	$\sum$	Estimate	SE	2.5%	97.5%
Tail length	0.51	−4.256	2.325	−9.255	0.742
Color score	0.2	2.599	2.637	−3.028	8.227
Wing length	0.15	1.958	2.430	−3.263	7.178
Tarsus length	0.13	−0.970	2.782	−6.883	4.944

TABLE 3. Top models for individual capture time, resulting from the model average after selection of a 95% confidence model set. Models in the set are arranged from best to worst based on the difference in AIC_c values between the best model and competing models (ΔAIC_c). AIC weights (AIC_w) are the relative likelihoods of a model given the data, and evidence ratios (ER) are the relative likelihood of each model versus the best model.

Models	AIC_c	ΔAIC_c	AIC_w	ER
Color score	35.9	0	0.44	1
Null model	38.2	2.23	0.14	3.14
Color score + Tarsus L	38.7	2.72	0.11	4
Color score + Tail L	39.1	3.21	0.09	4.89
Color score + Wing L	39.4	3.44	0.08	5.5
Tail length	39.9	3.99	0.06	7.33
Tarsus length	41.1	5.14	0.03	14.67
Wing length	41.2	5.26	0.03	14.67
Color score + Tail L + Tarsus L	42.9	6.97	0.01	44

TABLE 4. Standardized coefficients of model predictors, after model averaging of the top candidate models (95% confidence) (see Table 3). Table includes estimates, relative importance (Σ, sum of Akaike weights of the models in which the predictor was present), unconditional SE, and 95% confidence interval (CI) for estimates. Parameter estimates have a significant effect when the 95% CIs do not include zero (highlighted in bold).

Predictors	$\sum$	Estimate	SE	2.5%	97.5%
Color score	0.73	0.776	0.343	**0.039**	**1.513**
Tarsus length	0.16	−0.227	0.426	−1.131	0.677
Tail length	0.16	−0.266	0.367	−1.052	0.519
Wing length	0.11	−0.074	0.366	−0.858	0.711

managed to take off faster and perched for shorter periods were probably better able to evade capture, which could indicate that these birds had a greater aerobic capacity than males with less-red plumage. A recent hypothesis proposes that carotenoid coloration links to performance because the metabolism of carotenoid pigments in the production of ornamental coloration is intimately linked to cellular respiration (Hill and Johnson 2012, Johnson and Hill 2013). Our results could suggest that the potential greater aerobic capacity of redder birds is derived from a more efficient cellular respiration (Hill and Johnson 2012, Johnson and Hill 2013).

Carotenoid coloration has also been hypothesized to reflect other aspects of condition beside cellular respiration including energy stores, reduced oxidative stress, and enhanced immunocompetence (Svensson and Wong 2011, Simons et al. 2012). Any one of these aspects of condition could explain the relationship between carotenoid coloration and capture evasion. Carotenoids could also have a direct effect on flight performance. Blount and Matheson (2006) reported that birds that had been supplemented with carotenoids improved their takeoff capability, a skill that seemed to be of importance in our experiments. Even though our birds were maintained with the same diet, individual variation in absorption or allocation of pigments could result in some individuals having access to more circulating carotenoids. These individuals could then take advantage of the potential beneficial effects of carotenoids, such as reduced oxidative muscle damage, enhanced motor performance or cognition processes, and improved immune defense (Blount and Matheson 2006, Svensson and Wong 2011, Simons et al. 2012).

In addition to simply allowing them to avoid being captured and killed, the greater escape ability of redder male House Finches could confer on them important fitness advantages when defending their nest against predators (Reyer et al. 1998). Better flight ability could also enable more efficient foraging, which could in turn result in better parental care. This advantage would grant direct benefits to female House Finches choosing redder males (Hill 1990).

Female House Finches are dominant over males (Thompson 1960) and more aggressive toward drabber males (Belthoff and Gowaty 1996). This higher aggression could be a reason for drabber males to change social groups more frequently than the more stable redder males (Oh and Badyaev 2010). The stability of redder males in social groups could be driven by a social female preference for males with higher foraging and antipredator abilities. Ultimately, the lower female aggression toward redder males, and their more efficient foraging and better antipredator abilities, could jointly explain the higher overwinter survival rate of redder House Finches (Hill 1991, Belthoff and Gowaty 1996).

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