BioOne COMPLETE

Plumage brightness, vigilance, escape potential, and predation risk in male and female Eurasian Siskins (Spinus spinus)

Authors: Pascual, Jordi, Senar, Juan Carlos, and Domènech, Jordi

Source: The Auk, 131(1) : 61-72

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-13-220.1

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

The Auk
Ornithological Advances
www.aou.org

Volume 131, 2014, pp. 61–72
DOI: 10.1642/AUK-13-220.1

RESEARCH ARTICLE

Plumage brightness, vigilance, escape potential, and predation risk in male and female Eurasian Siskins (*Spinus spinus*)

Jordi Pascual,* Juan Carlos Senar, and Jordi Domènech

Evolutionary and Behavioral Ecology Research Unit (CSIC), Natural History Museum of Barcelona, Barcelona, Spain
* Corresponding author: jpascualsala@gmail.com

Received November 8, 2013; Accepted November 11, 2013; Published January 15, 2014

ABSTRACT

According to the "sexual selection hypothesis" (SSH), plumage conspicuousness has evolved through mate choice because it signals the quality of the bearer, and this is an honest signal because it involves a predation cost in terms of increased detectability to predators. Alternatively, according to the "unprofitable prey hypothesis" (UPH), conspicuousness is an aposematic signal indicating higher escape potential. We should expect the animals with higher predation risk (either conspicuous or dull, depending on the hypothesis) to have evolved antipredator behaviors to compensate for their higher predation risk (i.e. the "compensation hypothesis"). We tested these hypotheses by studying the vigilance behavior of wintering Eurasian Siskins (*Spinus spinus*) foraging on three feeders with different predation-risk and competition levels. Males were, on average, 50% more brightly colored than females. Males and females had similar wing loading, which allows us to reject male unprofitability related to higher takeoff speed. Males had shorter mean interscan durations (which improves predator detection) than females, especially at the high-predation-risk feeder (which males avoided), but the sexes did not differ in foraging-bout length, percentage of time spent scanning, and mean scan duration. In males, length of yellow tail stripe and brightness were positively correlated with percentage of time spent scanning. Therefore, our results on vigilance behavior and wing loading support the compensation hypothesis and the SSH assumption of a predation cost of conspicuousness, whereas they reject the predictions of the UPH. Compensation vigilance and other antipredator behaviors are expected to have also evolved in the conspicuous sex in other dichromatic species, and we predict that a correlation between plumage conspicuousness and vigilance should be found in future comparative studies.

Keywords: conspicuousness, plumage brightness, predation risk, sexual dichromatism, sexual selection hypothesis, unprofitable prey hypothesis, vigilance

Brillo de plumaje, vigilancia, capacidad de huída, y riesgo de depredación para machos y hembras de lúgano *Spinus spinus*

RESUMEN

De acuerdo con la hipótesis de selección sexual (SSH), la conspicuidad del plumaje ha evolucionado a través de la selección de pareja porque señala la calidad del portador, y es una señal honesta, ya que implica un costo de depredación en términos de una mayor detectabilidad frente a los depredadores. Alternativamente, de acuerdo con la hipótesis de la presa no provechosa (UPH), la conspicuidad es una señal aposemática que indica una mayor capacidad de huída. Deberíamos esperar que los animales sometidos a un mayor riesgo de depredación (aquellos más o menos conspicuos, dependiendo de la hipótesis) hubiesen evolucionado comportamientos anti-depredador para compensar por su mayor riesgo de depredación (hipótesis de la compensación). Pusimos a prueba estas hipótesis mediante un estudio del comportamiento de vigilancia de *Spinus spinus* invernantes mientras se alimentaban en tres comederos de aves con diferentes niveles de riesgo de depredación y de competencia. Los machos de *S. spinus* presentaron una coloración que fue en promedio un 50% más brillante que la de las hembras. Los machos presentaron una carga alar similar a la de las hembras, lo cual nos permite rechazar que los machos no fuesen provechosos por tenor mayor velocidad de despegue. Los machos mostraron una menor duración promedio de los intervalos entre vigilancias (que mejora la detección de los depredadores) que las hembras, especialmente en el comedero de alto riesgo de depredación (evitado por los machos), mientras que los sexos no diferieron en los tiempos de estancia en los comederos, en el porcentaje de tiempo dedicado a vigilancia, y en la duración promedio de las vigilancias. La longitud y el brillo de la banda amarilla de la cola de los machos se correlacionaron positivamente con el porcentaje de tiempo dedicado a la vigilancia. Por lo tanto, nuestros resultados sobre el comportamiento de vigilancia y la carga alar apoyan la hipótesis de la compensación y la suposición de la SSH que la conspicuidad trae un costo de depredación, mientras que rechazan las predicciones de la UPH. Se espera que en otras especies dicromáticas el sexo más conspicuo también haya evolucionado comportamientos de vigilancia u otros comportamientos anti-depredador compensatorios, y

© 2014 American Ornithologists' Union. ISSN 0004-8038, electronic ISSN 1938-4254
Direct all requests to reproduce journal content to the Central Ornithology Publication Office at aoucospubs@gmail.com

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

podemos predecir que se debería encontrar una correlación entre conspicuidad del plumaje y vigilancia en futuros estudios comparativos.

Palabras clave: brillo de plumaje, conspicuidad, dicromatismo sexual, hipótesis de la presa no provechosa, hipótesis de selección sexual, riesgo de depredación, vigilancia

INTRODUCTION

Most bird species are sexually dimorphic, particularly in plumage coloration (Price and Birch 1996, Hill and McGraw 2006). Sexual dichromatism has generally been attributed to an increase in conspicuousness due to mate selection (Andersson 1994; but see Badyaev and Hill 2003). According to the "sexual selection hypothesis" (SSH), the sexually selected traits act as signals that indicate the quality of the bearer (Jones and Ratterman 2009). The honesty of these signals is ensured because they imply fitness costs together with mating benefits (Kotiaho 2001). In birds, plumage conspicuousness is the most widespread sexually selected trait (Butcher and Rohwer 1989, Hill 2006), and its main cost is assumed to be the increase in predation risk (Promislow et al. 1992, Zuk and Kolluru 1998; but see Kotiaho 2001).

Contrary to the SSH assumption of a predation cost of sexually selected conspicuousness, some authors have suggested that this can be an aposematic signal that allows the predators to learn that conspicuous birds are less profitable (Baker and Parker 1979, Endler 1991). The "unprofitable prey hypothesis" (UPH) assumes that conspicuous birds are less edible (Cott 1947, Götmark 1994) or more difficult to catch and, because of this, predicts that they will be avoided as prey and thus have lower predation risk (Baker and Parker 1979). The term "difficult to catch" was originally used in a broad sense to refer to birds with "good vision and escape potential" (Baker and Parker 1979:70). It is clear that a bird with a high takeoff speed (i.e. escape potential; Witter and Cuthill 1993) might benefit from signaling this intrinsic ability to predators.

The UPH was originally tested by Frank Götmark and collaborators, using stuffed Pied Flycatcher (*Ficedula hypoleuca*) mounts that differed in brightness. Birds of prey more often attacked dull females than bright males (Götmark 1992, 1995), but in these experiments the detectability was very similar for both sexes (Slagsvold et al. 1995). Working with the same species, Slagsvold et al. (1995) found a predation cost of conspicuousness during the breeding season, whereas Post and Götmark (2006) concluded that the differential predation risk of the two sexes was mainly related to different parental roles and not to plumage conspicuousness.

After the initial tests of the UPH, some authors studied the more general relationship between conspicuousness and predation risk, using comparative approaches based on collections of prey remains at Eurasian Sparrowhawk (*Accipiter nisus*; hereafter "sparrowhawk") nests. They found a generally positive relationship between plumage brightness and vulnerability to predation (Rytkönen et al. 1998, Huhta et al. 2003, Møller and Nielsen 2006). However, the results of these studies may be affected by the different behavior of conspicuous and nonconspicuous species. Huhta et al. (1998) studied predation rates of banded passerines and did not find this relationship.

Finally, some studies in particular species have yielded new insights about the effects of conspicuous patches in either attracting predators or protecting prey from predation. Montgomerie et al. (2001) found that male Rock Ptarmigans (*Lagopus muta*) soiled their plumage to reduce conspicuousness, whereas Palleroni et al. (2005) showed that the white rump played an antipredator role in feral Rock Pigeons (*Columba livia*).

Clearly, the effect of conspicuous plumage coloration on predation risk is not straightforward and is still controversial. If conspicuous birds are subject to higher predation risk, we should expect them to have evolved antipredator behaviors to compensate for such risk, whereas the opposite would be expected if they are unprofitable prey. To date, only Møller et al. (2011) have tested the predictions of this "compensation hypothesis," finding that the conspicuous species and sex modified their antipredator escape behaviors once captured, to compensate for their higher predation risk. Vigilance while foraging is one of the most important behaviors for reducing the probability of capture (Lima and Dill 1990). An interesting and novel approach is to test whether bright males or dull females show compensation vigilance in a dichromatic species, and to do so during the nonbreeding season, when the behavior of the sexes is expected to be very similar.

The aim of the present study was to test the UPH (Baker and Parker 1979) versus the SSH (Darwin 1871) by studying the vigilance and foraging behavior of male and female Eurasian Siskins (*Spinus spinus*; hereafter "siskins") during the wintering season. The siskin is a sexually dichromatic species (Martin and Badyaev 1996, Badyaev 1997), and we measured the plumage color and brightness of both sexes to confirm that males are more conspicuous (i.e. easier to detect, at least in most backgrounds and according to human vision; Eaton 2005, Håstad and Ödeen 2008). We also tested the UPH assumption that conspicuous males are better at escaping from predators and are therefore avoided as prey.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Different vigilance and foraging behaviors are involved in the reduction of predation risk. Short interscan durations allow earlier detection of predators (Hart and Lendrem 1984, Whittingham et al. 2004), and a higher percentage of time spent scanning increases the probability of being vigilant at the time of an attack and, thereby, flushing to cover sooner (Lima 1994). Moreover, the shorter the length of the foraging bout, the lower the probability of encounter with the predator (Newman et al. 1988). Finally, the nearer to protective cover the animals feed, the lower the predation risk (Caraco et al. 1980). Therefore, we predicted that the birds with a higher risk of predation (males according to the SSH, females according to the UPH) would have evolved shorter interscan times, higher percentage of time spent scanning, shorter foraging-bout lengths, and avoidance of feeding sites far from cover.

Given that male siskins are dominant over females (Senar and Domènech 2011), to assess whether the differences found in vigilance variables between sexes were related to the effect of conspicuousness and not to the effect of dominance, we compared the behavior of the sexes at three feeders that differed in predation-risk and competition levels (Pascual and Senar 2013). We considered both the vigilance and foraging variables related to the reduction of predation risk and the variables related to competition (Pascual and Senar 2013), and we tested the interaction between feeder and sex for all of them. Moreover, we studied the relationship between carotenoid-based coloration and vigilance in males, which is related to mate choice and conspicuousness but not to dominance in wintering siskins (Senar et al. 2005).

METHODS

Study Species and Study Site

We selected the siskin, a socially foraging bird (Senar et al. 1992), as our study species because it presents a clear sexual dichromatism (males are 17% brighter than females; Martin and Badyaev 1996, Badyaev 1997) and because it feeds in large groups that are easily attracted to feeders. Wintering siskin populations are formed by resident and transient birds (Senar et al. 1992). Residents stay in the area for several weeks, whereas transients normally stay for a few hours or days. We recorded data only from individually color-ringed birds (i.e. residents) in order to control that both birds within a pair had similar knowledge of the predation risk of the area (Desportes et al. 1991) and to avoid pseudoreplication.

The study was carried out in an area of orchards, small pine woods (*Pinus halepensis*), and gardens in the suburban area of Barcelona, Catalonia, northeastern Spain, from October 1996 to March 1997. An individual sparrowhawk in the study area was hunting the siskins that foraged at feeders, and it plucked the feathers of its prey in a pine wood <20 m from the three feeders. Although we know that prey selection by one individual is not representative, we decided to study it as anecdotic data. We collected prey remains every day in the plucking area and determined the minimum number of individuals by matching wing and tail feathers (following Götmark and Post 1996). We found that the proportion of males in the prey remains was 80% (20 of 25 birds identified). Additionally, we estimated the proportion of males at the population according to the sample of birds trapped at a Yunik platform trap (Senar 1988), and we found that it was 55% (349 of 635 individuals captured). These two percentages differed significantly ($P = 0.014$), and therefore the local sparrowhawk collected more males than expected by chance.

Bird Ringing and Videotaping

Siskins were trapped on a regular weekly basis throughout the wintering season at baited feeders using traps, mist nets, and clap nets and were marked with numbered aluminium rings. Siskins were captured by expert bird ringers under the authorization of the Ornithological Catalan Institute and the Catalan Government. Birds that were repeatedly recaptured (i.e. staying in the area as "residents"; Senar et al. 1992) were additionally given unique color-ring combinations, allowing long-distance identification. From a total of 584 marked birds, 104 were color-ringed. For each individual captured, we noted the day and time of capture, the sex and age (according to plumage coloration cues; Svensson 1992), and the number of the ring and the code of color rings (if resident). We also measured the length (mm) of the yellow wing stripe of 284 males and 68 females, and the length (mm) of the black tail stripe and the total length of the tail of 264 males and 70 females. We calculated the length (mm) of the yellow tail stripe by subtracting the length of the black tail stripe from the total length of the tail.

We placed three feeders in the area at 1 m above the ground. They had a border of 1.5 cm and every day were filled to 0.5 cm with turnip (*Brassica rapa*) seeds, so we can assume the same density of food for all of them. Birds foraging at the feeders were videotaped from a hide with an S-VHS-C movie camera (Panasonic NV-S7E) equipped with 16× digital zoom. In total, 133 flocks were recorded at feeders between 1000 and 1700 hours on 28 days from January 10 to March 11, 1997.

Experimental Design

Because we wanted to discriminate between the effects of competition and predation risk on the vigilance behavior of resident male and female siskins, we designed an experiment with three bird tables that differed in their feeding surface (i.e. expected interference competition; Elgar 1987) and distance from protective cover (i.e.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

expected predation risk; Lima 1987). Two feeders with different surfaces were placed below an almond (*Prunus dulcis*) tree at a distance of 1.6 m from a dense, 2.2-m-tall bush (*Rhamnus alaternus*) that covered an area of 10 m^2 and was 4 m from a pine-wood edge. The inner large (IL) feeder was 0.75 × 0.5 m, and the inner small (IS) feeder was 0.08 × 1 m. The third feeder (OS) was placed at 4.7 m from the tree and the bush and at 8.5 m from the pine-wood edge, and was the same size and shape as IS. The feeders were aligned in a northeasterly direction, with the pine woods to the northeast. There was an almond orchard to the southeast, 7 m from all the feeders; a line of *R. alaternus* bushes >5 m from the OS feeder to the southwest; and an area of scrubs 7 m from the feeders to the northwest. Elsewhere (Pascual and Senar 2013), we studied the foraging-bout lengths, departure reasons, aggression rates, and numbers and densities of birds at the three feeders and found that (1) foraging-bout lengths were higher at the IL than at the IS and OS feeders; (2) aggression rates were higher at the IS feeder than at the OS feeder and higher at the OS feeder than at the IL feeder (where almost no aggressive behaviors were observed); (3) the most frequent departures from the IL feeder were individual based (i.e. no apparent reason for leaving the feeder), the most frequent departures from the IS feeder involved aggressive behavior toward the focal birds, and the most frequent departures from the OS feeder were disturbances (i.e. sudden departures of most or all of the feeding birds); (4) the number of birds foraging on the feeder was higher at the IL than at the IS and OS feeders, whereas the density of birds showed the opposite trend; and (5) the IL and IS feeders had many birds around them, perched on the almond tree at <1.2 m, such that the effective group sizes for them were large and similar, whereas the OS feeder did not have birds around it and had much lower effective group size. On the basis of these results, we concluded that IL was a low-predation-risk and low-competition feeder, IS a low-predation-risk and high-competition feeder, and OS a high-predation-risk and intermediate-competition feeder. For more details, see Pascual and Senar (2013).

Birds were videotaped from a permanent wooden hide placed at 2.0 m from OS and at 4.9 m from IL and IS, in the opposite direction from the bush. Therefore, the siskins saw the hide as a feature of the landscape, but if they still perceived it as a possible source of threats, it would further increase the perceived predation risk at OS compared with the risk at IL and IS. During recording at the IL feeder, the other two feeders were emptied of food; during simultaneous recording at the IS and OS feeders (with two video cameras), there was no food at IL. At IS and OS, we recorded only half the feeder (because they were too long), so we shifted the video camera every 2 min from one half to the other.

Data Obtained from Tapes

We selected a subsample of male–female pairs that foraged simultaneously so that we could study the effect of sex while avoiding the confounding effects of flock size and other time-related variables (Elgar 1989). Pairs were selected that were foraging without fighting or moving around for ≥30 s of recordings, the time we analyzed for estimation of the vigilance variables, and therefore this subsample was called "undisturbed." We did so because the vigilance variables, to be comparable between birds, needed to be calculated when they only fed and scanned. We identified 36 pairs of resident males and females in the tapes (16 pairs at the IL feeder, 14 pairs at the IS feeder, and 6 pairs at the OS feeder). No bird was present in more than two pairs at the same feeder, and no pair was repeated. We analyzed the behavior of a bird of a dyad using the frame-by-frame function of the video (25 frames s^{-1}). We then rewound the tape to the start of the focal pair and observed the other member of the dyad. This allowed the same observer to follow both birds. At all feeders, we recorded the percentage of time spent scanning (i.e. with the tip of the beak raised to eye level or higher; Lendrem 1983) and the mean interscan duration as the predation-risk-related variables (see Pascual and Senar 2013), and we recorded the mean scan duration and the pecking rate (as an estimation of food intake rate) as the competition-related variables (see Pascual and Senar 2013).

The selection of birds with ≥30 s of simultaneous feeding almost only feeding and scanning (i.e. with <10% of time devoted to fighting and moving around) could bias the sample toward relatively peaceful birds or periods, and this could affect the comparison between sexes. Therefore, we selected another subsample of birds ("random") with no restrictions on time at feeder, aggression rate, or movements. For each feeder, we registered all the different resident birds we found on the recordings and randomly selected one period for each. We found 27 different resident males and 29 females at the IL feeder, 17 males and 25 females at the IS feeder, and 10 males and 14 females at the OS feeder. For those we analyzed, for the entire time spent on the feeder (or the total time the bird was visible on the recordings), the rate of "aggressions" given and received (i.e. agonistic interactions between individuals wherein the focal bird either attacked or received the attack of a flock mate), the percentage of time spent in aggressions, the hopping rate (number of hops per second, as an estimation of the "moving around" behavior), and the total time spent on the feeder. For one bird on the IL feeder, 11 birds on the IS feeder, and 9 birds on the OS feeder, the times on feeder were incomplete (either because the videotape finished or because we shifted the video camera from one half to the other; see above), and they were treated as censored data (see below).

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

To test whether the differences in vigilance between males and females were similar to the differences between bright and dull males, we used a chromameter (see below) to measure the plumage coloration on the yellow of the tails of 30 resident males captured in the study area. Moreover, we measured the length of the yellow wing stripe and the length of the yellow tail stripe of 22 resident males. Unfortunately, on the videotapes we could find only 12 resident males with the coloration of the tail yellow patch measured and 10 resident males with the lengths of the yellow wing and tail stripes measured. Still, we analyzed the correlation between vigilance and coloration variables with the available males.

To compare the proportion of males between feeders, we analyzed all the video recordings of all the groups of siskins foraging at all the feeders. For the IL feeder, we had 41 different groups in 13 different days, and for the IS and OS feeders, we had 16 groups in 6 different days that were foraging simultaneously at both feeders. We counted, for each foraging group at each feeder, the sex of all the individuals for which we could identify this trait. For the comparison of the proportion of males, we obtained 1,213 individuals at the IL feeder, 318 at the IS feeder, and 346 individuals at the OS feeder.

Plumage Coloration Data

We measured coloration on five points of the plumage for a sample of 52 siskins (23 females and 29 males). Points were chosen that a priori make the bird most visible from the back while it is flying (Figure 1). We did not measure the coloration of the black melanin-based patches. However, 61% of the sexual dichromatism in siskins is related to the carotenoid-based coloration (Badyaev and Hill 2000; compared with the 39% related to melanin-based coloration), and carotenoid-based coloration is also the coloration under stronger sexual selection in birds (Badyaev and Hill 2000) and particularly in the siskin (in which females choose males according to the length of the yellow wing stripe; Senar et al. 2005). In siskins, black patches are related to dominance status (Senar and Camerino 1998) and cover a higher proportion of the overall body plumage in males than in females (Svensson 1992). Therefore, if they contribute to conspicuousness in some backgrounds and because of the contrast between dark and light plumage patches, their effect will be to increase the overall conspicuousness of males compared with females (Stevens et al. 2013).

Coloration was measured using a CR-200 Minolta chromameter with an 8-mm-diameter sensor. The chromameter provides, for each bird, independent values of hue, chroma and lightness, which are the parameters generally used to define a color (Hill 1998). Hue reflects chromatic composition and corresponds to wavelength of light. Chroma, or saturation, is spectral variance and

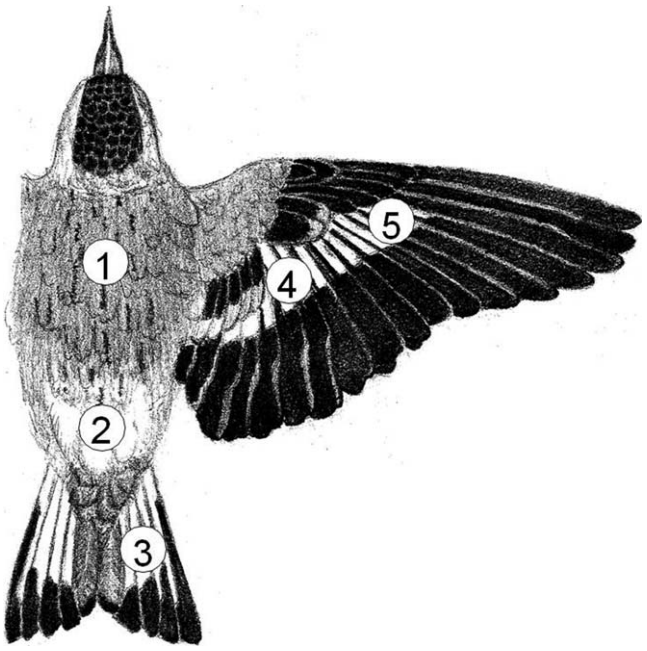


FIGURE 1. Plumage points where we measured the color of male and female Eurasian Siskins, illustrated in an adult male. The circles are equivalent to the area analyzed by the sensor of the chromameter. Labels: 1 = back, 2 = rump, 3 = basal-medium webs of the second to sixth tail feathers, 4 = basal-medium outer webs of the secondaries, and 5 = inner visible third of the outer webs of the primaries.

determines the pureness of the color. Lightness, or brightness, is the percentage of white and is correlated with physical light intensity (Booth 1990). The higher the values for lightness and chroma of a particular part of the plumage, the higher its brightness. In addition to the brightness of a particular part of the plumage, the extent of this bright patch is also important. Two of the brightest plumage patches are the yellow wing stripe and the yellow of the base of the rectrices (Figure 1). The yellow wing stripe formed by the inner visible third of the outer webs of the primaries and secondaries is wider on males than on females (males: mean [± SE] = 5.36 ± 0.10 mm, $n = 284$; females: mean = 2.06 ± 0.20 mm, $n = 68$; $F = 220.5$, df = 1 and 350, $P < 0.001$), and the same relationship is applicable to the length of the yellow in the base of the second to sixth tail feathers (males: 25.6 ± 0.3 mm, $n = 264$; females: 13.1 ± 0.6 mm, $n = 70$; $F = 308.8$, df = 1 and 332, $P < 0.001$). There is a high correlation between the length of the yellow wing stripe and the length of the yellow tail stripe ($r_s = 0.70$, $P < 0.0001$, $n = 328$).

The chromameter has the advantage of providing numerical values that are easy to interpret, but its limitation is that it is based on the human perception of color and does not take ultraviolet reflectance into account (its spectral range is 400–700 nm; Cuthill et al. 1999a,

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

1999b). However, given that carotenoid colors reflect light primarily in the visible spectrum (Hill 1998), we consider that the differences in conspicuousness detected in our study by the chromameter in the measured points of siskins should not differ in a significant way with the use of a spectrometer (although this statement still needs to be tested).

Wing Loading

We measured the wing loading of 42 pairs of resident male and female siskins trapped together (each pair in a different capture event) at the IL feeder to estimate maneuverability and takeoff speed, assumed to be the most important components of flight performance for small birds escaping from a predator (Witter et al. 1994, Metcalfe and Ure 1995). Males and females of each pair were of the same age. We measured the length of the wing from the elbow to the tip of the longest primary (following Svensson 1992) and the distance of all the primary feathers to the tip of the wing. Then we subtracted these distances from the length of the wing, and the resulting values were added, providing an index of wing area (Evered 1990). We calculated wing loading by dividing body mass by estimated wing area (Norberg and Rayner 1987, Götmark and Unger 1994). We compared the wing loading for male–female pairs captured simultaneously so that the effects of time of day and weather conditions on body mass were the same for both sexes.

Data Analysis and Transformation

Some of the variables of lightness, chroma, and hue for the five measured plumage patches of siskins (Figure 1) did not fit the normality in the distribution of frequencies and, therefore, were transformed by applying logarithmic and power operations. We then performed a principal component analysis (PCA) from the correlation matrix with all these variables, and we computed factor scores for each individual from factor loadings of unrotated principal axes. We used the negative scores on the first axis as the values of brightness for each individual (we changed the sign of the scores because all the variables had negative scores with that axis). The frequency distribution of these scores for males did not fit normality, and therefore we carried out a Mann-Whitney *U*-test to compare the brightness of males and females.

To compare the profitability of male and female siskins, we compared the wing loading, wing area, and body mass of the 42 pairs with the Wilcoxon matched-pairs test (because many of the variables did not fit the normality in the distribution of frequencies).

To compare times on feeder of males and females, because choosing only birds with complete times on feeder (i.e. filmed from arrival to departure) would have biased the data toward birds with short values for this variable (especially at the IS and OS feeders, where every 2 min we moved the video camera), we applied the two-sample test of a survival analysis using STATISTICA version 8.0 (StatSoft, Tulsa, Oklahoma, USA), treating incomplete times on feeder as censored data and taking sex as a grouping variable. We compared the times on feeder of males and females for all the feeders together and for each one independently.

We compared the three variables of aggression (aggression given rate, aggression received rate, and percentage of time spent in aggressions) between sexes for the three feeders together and for every one independently (only IS and OS) by applying the Mann-Whitney *U*-test, because the distribution of these variables was highly skewed to zero or to low values near zero.

We compared the hopping rate of siskins between sexes and analyzed the possible interaction between feeder and sex by applying a factorial analysis of variance (ANOVA). We used a logarithmic transformation of the dependent variable to fit the assumption of normality in the distribution of frequencies. We compared the proportion of males between feeders with the Pearson chi-square test of the function "Tables and Banners" in STATISTICA.

Scan durations, interscan durations, and pecking rates did not fit the assumption of normality in the distribution of frequencies, and we applied logarithmic transformations to normalize their distributions. Because we wanted to compare the values of the vigilance and feeding variables between the two individuals of each pair at each feeder, we computed repeated-measures ANOVAs for each vigilance and foraging variable.

In analyzing the relationship between plumage coloration and vigilance behavior in resident males, we computed Spearman rank-order correlations using STATISTICA and adjusted the level of significance to the number of correlations tested ($P = 0.05 / 10 = 0.005$). We used only percentage of time spent in vigilance and mean interscan duration as the variables most related to the predation risk of siskins (Pascual and Senar 2013). Results are presented as means ± SE.

RESULTS

Differences in Brightness between Sexes

The first principal component of the PCA on lightness, chroma, and hue for the five measured plumage points of siskins accounted for 51% of the total variance (eigenvalue = 7.69). All the variables showed high positive correlations with that axis (except rump hue and lightness of secondaries; Table 1) and could therefore confidently be interpreted as a factor of general brightness of plumage coloration. The comparison between the sexes for this factor showed that males had higher scores than females (i.e. males were brighter than females: males, mean score =

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 1. Mean (± SE) values of lightness, chroma, and hue of plumage-point coloration of males ($n = 29$) and females ($n = 23$) and the M:F ratio (mean value of males/mean value of females) in Eurasian Siskins in northeastern Spain, October 1996–March 1997. Also included are factor score loadings for the first principal component (PC1) from the PCA of lightness, chroma, and hue. Eigenvalue = 7.69; explained variance = 51%. Mean correlations between variables = 0.41 ± 0.03; $n = 105$.

Plumage point	Variable	Males	Females	M:F ratio	Factor loading (PC1)
Tail	Lightness	58.1 ± 1.2	43.3 ± 0.9	1.34	0.88
	Chroma	29.7 ± 1.7	12.3 ± 1.1	2.41	0.89
	Hue	96.9 ± 0.9	91.5 ± 2.0	1.06	0.57
Back	Lightness	39.9 ± 0.2	39.3 ± 0.3	1.01	0.44
	Chroma	11.1 ± 0.4	7.8 ± 0.3	1.43	0.76
	Hue	92.6 ± 0.6	81.7 ± 1.2	1.13	0.84
Rump	Lightness	54.1 ± 0.9	49.9 ± 0.6	1.08	0.65
	Chroma	32.6 ± 1.3	20.4 ± 0.9	1.60	0.84
	Hue	95.9 ± 0.2	95.8 ± 0.3	1.00	0.03
Primaries	Lightness	41.5 ± 0.8	35.4 ± 0.6	1.17	0.83
	Chroma	11.8 ± 1.1	5.0 ± 0.5	2.37	0.89
	Hue	85.4 ± 2.7	58.1 ± 5.1	1.47	0.88
Secondaries	Lightness	56.5 ± 0.8	56.8 ± 0.5	0.99	0.07
	Chroma	19.7 ± 1.3	15.0 ± 0.9	1.32	0.62
	Hue	95.1 ± 0.5	90.0 ± 1.1	1.06	0.73

0.70; females, mean score = –0.89; $U = 28$, $P < 0.0001$). All females had negative scores for the factor, whereas all the males but three had positive scores. Only these three individuals from the total of 52 could not be correctly sexed according to their factor score. The average male:female ratio for all the different measures on all the plumage points was 1.40, and it was 1.47 when considering only lightness and chroma, which are more related to brightness (Table 1). Males displayed a more saturated plumage color than females (83% more saturated, on average; 141% more for tail and 137% more for primaries) and a slightly higher percentage of white than females (12% more, on average; 34% more for tail and 17% for primaries) (Table 1).

Differences in Profitability between Sexes

Body mass of males was higher than that of females (males, 12.81 ± 0.08 g; females, 12.58 ± 0.08 g; $Z = 2.26$, $P = 0.024$, $n = 42$), but wing area was also higher for males (males, 452 ± 4 mm^2; females, 441 ± 4 mm^2; $Z = 2.56$, $P = 0.010$, $n = 42$), such that they did not differ in wing loading (males, 0.0285 ± 0.0003 g mm^{-2}; females, 0.0287 ± 0.0004 g mm^{-2}; $Z = 0.36$, $P = 0.722$, $n = 42$).

Differences in Predation-risk-related Variables between Sexes

We did not find significant differences between sexes in percentage of time spent scanning ($F = 0.65$, df = 1 and 33, $P = 0.43$; Figure 2A), even at the OS feeder (Tukey's HSD test [OS]: $P = 0.65$). However, we found that males had shorter interscan durations than females ($F = 12.4$, df = 1 and 33, $P = 0.001$; Figure 2D) and that the difference between sexes was significant at the high-predation-risk and intermediate-competition feeder (Tukey's HSD test [OS]: $P = 0.032$) and marginally at the low-competition and low-predation-risk feeder (Tukey's HSD test [IL]: $P = 0.056$) but that sexes did not differ in this variable at the high-competition and low-predation-risk feeder (Tukey's HSD test [IS]: $P = 0.997$) (feeder × sex interaction: $F = 5.17$, df = 2 and 33, $P = 0.011$; Figure 2D). Times on feeder did not differ overall between males and females (test statistic = 0.14, $P = 0.99$) and did not differ among feeders (IL: test statistic = –0.86, $P = 0.39$; IS: test statistic = 0.78, $P = 0.44$; OS: test statistic = –0.27, $P = 0.78$). We found significant differences among the three feeders in the proportion of sexes (Pearson's $\chi^2 = 16.01$, df = 2, $P = 0.0003$). The proportion of males was higher at IS (56%) and IL (53%) than at OS (42%).

Differences in Competition-related Variables between Sexes

Males and females did not differ in either pecking rate ($F = 0.38$, df = 1 and 33, $P = 0.54$; Figure 2B) or mean scan duration ($F = 0.21$, df = 1 and 33, $P = 0.65$; Figure 2C). There were no differences between sexes in the rate of aggressions given and in the percentage of time spent in aggressions ($U = 1672$, $P = 0.33$, and $U = 1569$, $P = 0.14$, respectively). However, females had higher rates of aggressions received than males ($U = 1477$, $P = 0.04$). Males and females did not differ in the hopping rate on the feeders ($F = 1.93$, df = 1 and 110, $P = 0.17$), and there was not a significant interaction between feeder and sex for this variable ($F = 1.08$, df = 2 and 110, $P = 0.34$).

Correlations between Coloration and Vigilance Variables within Males

Percentage of time spent scanning was higher for males with longer yellow tail stripes (Table 2 and Figure 3A),

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

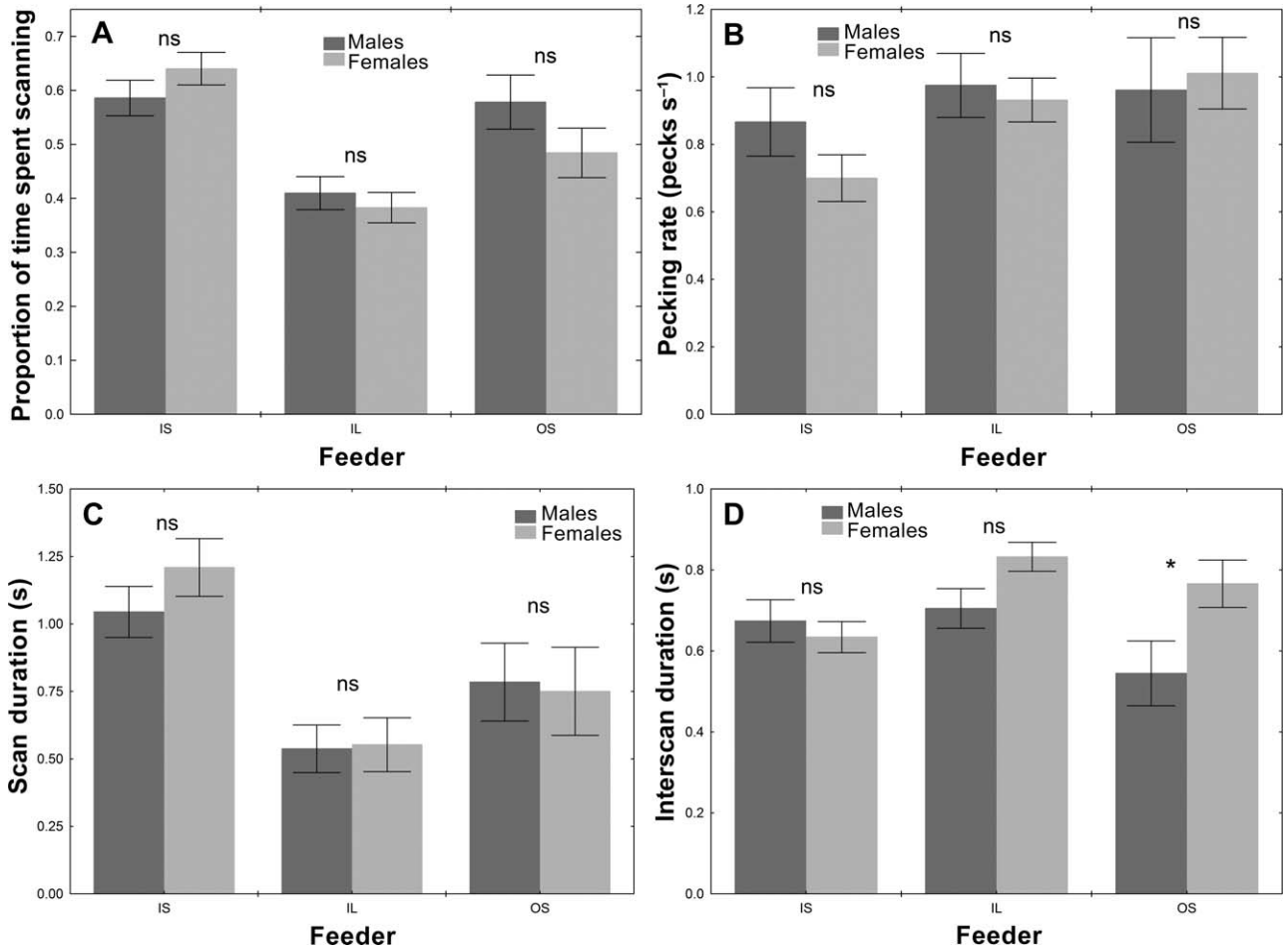


FIGURE 2. Mean (± SE) proportion of time spent scanning (**A**), pecking rate (**B**), scan duration (**C**), and interscan duration (**D**) of paired male and female Eurasian Siskins at three feeders differing in predation risk and competition. IL: $n = 16$; IS: $n = 14$; OS: $n = 6$. Repeated-measures analyses of variance: ns = nonsignificant $P \geq 0.05$; * $P < 0.05$.

lighter tail yellow (Table 2 and Figure 3B), and marginally higher chroma of the tail yellow (Table 2). Mean interscan durations were not significantly correlated with any coloration variable (Table 2). Length of the wing yellow stripe and hue of the tail yellow stripe had nonsignificant correlations with both vigilance variables (Table 2).

DISCUSSION

According to the results of the plumage coloration analysis, and considering only the lightness and chroma of coloration (more related to brightness than hue), we can say that, on average, male siskins were 50% brighter than females. This value was even higher for the traits more

TABLE 2. Spearman rank-order correlations of vigilance and coloration variables measured in resident male Eurasian Siskins in northeastern Spain, October 1996–March 1997. We considered hue, chroma, and lightness of the color of the yellow tail stripe (measured with a chromameter), the length of the yellow wing stripe, and the length of the yellow tail stripe as the variables most related to the detectability of Eurasian Siskins by an avian predator. Significant correlations ($P < 0.005$) are in bold, and tendencies ($P < 0.05$) are in italics.

	Length wing yellow stripe		Length tail yellow stripe		Lightness tail		Chroma tail		Hue tail	
	r_s	P	r_s	P	r_s	P	r_s	P	r_s	P
Percentage of time spent scanning	0.30	0.39	**0.87**	<0.001	**0.81**	0.002	*0.63*	0.03	–0.11	0.72
Mean interscan duration	–0.39	0.27	–0.53	0.12	–0.32	0.31	–0.23	0.48	–0.40	0.20
n	10		10		12		12		12	

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

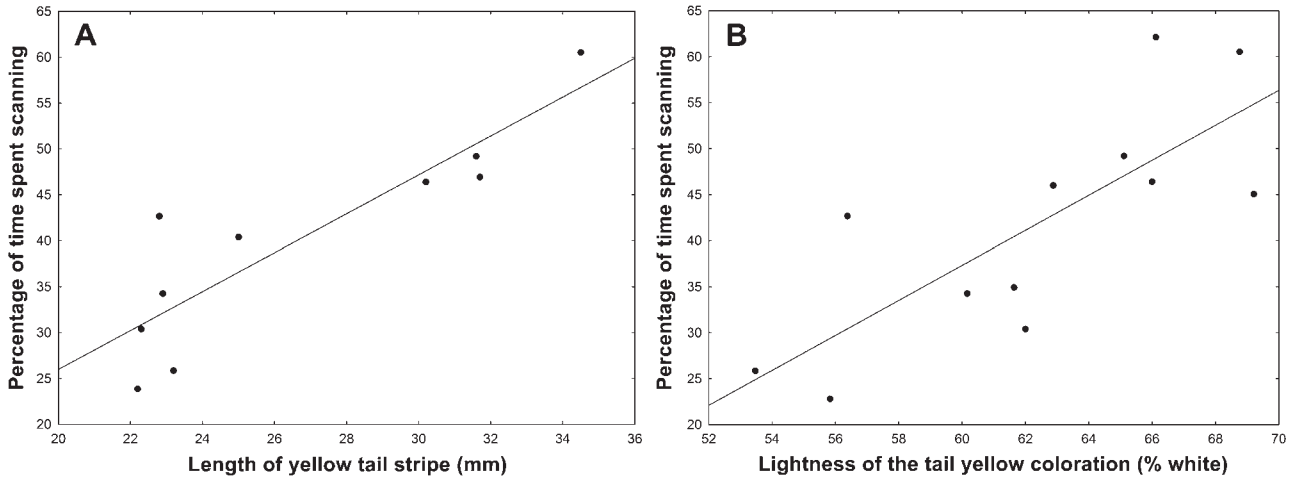


FIGURE 3. (**A**) Correlation between the length of the yellow tail stripe and the percentage of time spent scanning in resident male Eurasian Siskins in northeastern Spain, October 1996–March 1997 ($r_s = 0.87$, $P < 0.001$, $n = 10$). (**B**) Correlation between the lightness of the yellow wing stripe (measured with a chromameter) and the percentage of time spent scanning in resident males ($r_s = 0.81$, $P = 0.002$, $n = 12$).

subject to sexual selection (Senar et al. 2005): 87% for the tail yellow stripe and 77% for the yellow wing stripe of the primaries. These values are higher than that reported for the siskin in previous studies (17%; Martin and Badyaev 1996, Badyaev 1997), probably because we sampled only the yellowish body parts from the back, which we think are the most related to detectability by an avian predator attacking from above. The higher plumage brightness of the yellow spots of males is likely to make them more detectable by predators than the duller females (Zuk and Kolluru 1998).

The escape stage of a bird is mainly related to takeoff speed and maneuverability (Witter et al. 1994, Metcalfe and Ure 1995). Because male and female siskins did not differ in wing loading, the sexes are not expected to differ in their ability to escape from predators, and therefore males are not expected to be less profitable than females. In fact, males are expected to be slightly more profitable than females, given their higher body mass. On the other hand, it is not likely that males were more distasteful than females (Cott 1947, Götmark 1994), because males were the most common prey of the sparrowhawk hunting in our study area (see above).

Males spent roughly the same proportion of time scanning as females, but males used a vigilance strategy with shorter mean interscan durations than females, especially at the feeder with high predation risk (OS). This should allow males to detect predators sooner than females (Hart and Lendrem 1984, Whittingham et al. 2004). We also found that the more brightly colored a male was (i.e. longer yellow tail stripe, with a lighter and more saturated yellow color), the more time it spent in vigilance. On the other hand, males and females did not differ in times on feeder, but the proportion of males was lower on the high-predation-risk feeder (OS) than on the other feeders.

Our results support the SSH (Darwin 1871) and are opposite to the predictions of the UPH (Butcher and Rohwer 1989). Conspicuous siskins adopted a vigilance and foraging strategy that reduced their predation risk compared with duller birds, supporting the view that they were at higher predation risk because they were easier to detect. This is in accordance with most studies' reports of a general relationship between plumage brightness and vulnerability to predation (Rytkönen et al. 1998, Huhta et al. 2003, Møller and Nielsen 2006). Our results also strongly support the "compensation hypothesis" recently formulated by Møller et al. (2011), in that conspicuous birds would have evolved behavioral compensations to reduce their higher vulnerability to predation. They found that the conspicuous species and sex modified their antipredator escape behaviors once captured. Our study is the first to show a compensation related to vigilance behavior, one of the most important behaviors to reduce the probability of capture (e.g., Lima and Dill 1990).

In addition to these compensatory behaviors, and as suggested by Zuk and Kolluru (1998), we can expect some kind of arms races between predators and prey related to signal exploitation. Accordingly, Håstad et al. (2005) showed that passerines exploited the differences in vision between them and their predators to avoid the exploitation of their visual cues. Both avoidance of exploitation and compensation behaviors may have masked the relationship between conspicuousness and mortality in some species, and they could explain some of the results reporting no such relationship (e.g., Huhta et al. 1998).

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

When attempting to relate the differential conspicuousness of males and females to their differential predation risk, we would like to stress the importance of conducting the studies during the nonbreeding season, thereby avoiding the confounding effect of the differential parental roles that has affected some previous studies (e.g., Slagsvold et al. 1995, Götmark et al. 1997). In fact, the relative importance of sexually selected traits and parental care in the survival probability of males during the breeding season is still a matter of debate (Liker and Székely 2005).

Wintering male and female siskins differ not only in plumage brightness but also in social positions (Senar 1985). In fact, we found that females received more aggressions than males, although the sexes did not differ in percentage of time spent in aggressions, pecking rate, or hopping rate. A difference in dominance can have an important influence on vigilance rates (e.g., Waite 1987a, 1987b). However, we have several reasons to conclude that dominance does not account for our results. (1) Differences between sexes were found in interscan durations, the variable that in a previous study (Pascual and Senar 2013) was found to be modified by siskins when predation risk was increased, and not in scan durations, the variable that was found to be modified when interference competition was increased. (2) Differences between interscan durations of male and female siskins were found in the pooled data and at the high-predation-risk feeder, but not at the high-competition feeder. (3) We found no differences in the proportion of males between the high-competition and low-competition feeders near protective cover, whereas the percentages of males at both were higher than at the high-predation-risk feeder. (4) We found a positive correlation between vigilance and carotenoid-based coloration in males, which in siskins is related to mate choice and not to dominance (Senar et al. 2005).

In summary, male siskins have a brighter plumage than females. If this is a signal of unprofitability, we should expect males to have higher escape potential, to be avoided as prey, and, therefore, to be less vigilant to predators than females. Our data showed exactly the opposite trend: Wintering males had the same escape potential as females and had shorter mean interscan durations than females, especially at the high-predation-risk feeder, which they avoided. We also found a positive correlation between sexually selected carotenoid-based coloration and vigilance in male siskins. Hence, contrary to the UPH (Baker and Parker 1979) and in line with the SSH (Darwin 1871, Promislow et al. 1992), plumage brightness in male siskins appeared to have an added cost of predation risk. According to these results, compensation vigilance and other antipredator behaviors are expected to have evolved in the conspicuous sex in other dichromatic species. Future comparative investigations will have to determine the relationship between plumage conspicuousness and vigilance in birds.

ACKNOWLEDGMENTS

We thank T. Slagsvold, F. Götmark, and anonymous reviewers for critical discussions. We are also grateful to D. Boné, A. Serra, E. Vilamajó, and M. Boix for field assistance, and to N. Mallén and M. Luisa Arroyo for laboratory assistance. This paper is a contribution to projects CGL 2009–10652 and CGL2012-38262 from Ministerio de Ciencia e Innovación and Ministerio de Economía y Competitividad, Spanish Research Council.

LITERATURE CITED

Andersson, M. (1994). Sexual Selection. Princeton University Press, Princeton, NJ, USA.

Badyaev, A. V. (1997). Altitudinal variation in sexual dimorphism: A new pattern and alternative hypotheses. Behavioral Ecology 8:675–690.

Badyaev, A. V., and G. E. Hill (2000). Evolution of sexual dichromatism: Contribution of carotenoid- versus melanin-based coloration. Biological Journal of the Linnean Society 69:153–172.

Badyaev, A. V., and G. E. Hill (2003). Avian sexual dichromatism in relation to phylogeny and ecology. Annual Review of Ecology, Evolution, and Systematics 34:27–49.

Baker, R. R., and G. A. Parker (1979). Evolution of bird colouration. Philosophical Transactions of the Royal Society of London, Series B 287:63–130.

Booth, C. L. (1990). Evolutionary significance of ontogenic colour change in animals. Biological Journal of the Linnean Society 40:125–163.

Butcher, G. S., and S. A. Rohwer (1989). The evolution of conspicuous and distinctive coloration for communication in birds. In Current Ornithology 6 (D. M. Power, Editor). Plenum Press, New York, NY, USA. pp. 51–108.

Caraco, T., S. Martindale, and H. R. Pulliam (1980). Avian time budgets and distance to cover. The Auk 97:872–875.

Cott, H. B. (1947). The edibility of birds: Illustrated by 5 years experiments and observations (1941–1946) on the food preferences of the hornet, cat and man; and considered with special reference to the theories of adaptive coloration. Proceedings of the Zoological Society of London 116:371–524.

Cuthill, I. C., A. T. D. Bennett, J. C. Partridge, and E. J. Maier (1999a). Plumage reflectance and the objective assessment of avian sexual dichromatism. American Naturalist 153:183–200.

Cuthill, I. C., J. C. Partridge, and A. T. D. Bennett (1999b). UV vision and its functions in birds. In Proceedings of the 22nd International Ornithological Congress (N. J. Adams, and R. H. Slotow, Eds.). BirdLife South Africa, Johannesburg. pp. 2743–2758.

Darwin, C. (1871). The Descent of Man and Selection in Relation to Sex. John Murray, London, UK.

Desportes, J. P., A. Gallo, and F. Cézilly (1991). Effect of familiarity with environment on vigilance of Barbary Doves (*Streptopelia risoria*). Behavioural Processes 24:177–183.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Eaton, M. D. (2005). Human vision fails to distinguish widespread sexual dichromatism among sexually ''monochromatic'' birds. Proceedings of the National Academy of Sciences USA 102:10942–10946.

Elgar, M. A. (1987). Food-intake rate and resource availability: Flocking decisions in House Sparrows. Animal Behaviour 35: 1168–1176.

Elgar, M. A. (1989). Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. Biological Reviews of the Cambridge Philosophical Society 64:13–33.

Endler, J. A. (1991). Interactions between predators and prey. In Behavioural Ecology: An Evolutionary Approach (J. R. Krebs and N. B. Davies, Editors). Blackwell Scientific, Oxford, UK. pp. 169–196.

Evered, D. S. (1990). Measures of wing area and wing span from wing formula data. The Auk 107:784–787.

Götmark, F. (1992). Antipredator effect of conspicuous plumage in a male bird. Animal Behaviour 44:51–55.

Götmark, F. (1994). Are bright birds distasteful? A reanalysis of H. B. Cott's data on the edibility of birds. Journal of Avian Biology 25:184–197.

Götmark, F. (1995). Black-and-white plumage in male Pied Flycatchers (*Ficedula hypoleuca*) reduces the risk of predation from sparrowhawks (*Accipiter nisus*) during the breeding season. Behavioral Ecology 6:22–26.

Götmark, F., and P. Post (1996). Prey selection by sparrowhawks, *Accipiter nisus*: Relative predation risk for breeding passerine birds in relation to their size, ecology and behaviour. Philosophical Transactions of the Royal Society of London, Series B 351:1559–1577.

Götmark, F., and U. Unger (1994). Are conspicuous birds unprofitable prey? Field experiments with hawks and stuffed prey species. The Auk 111:251–262.

Götmark, F., P. Post, J. Olsson, and D. Himmelmann (1997). Natural selection and sexual dimorphism: Sex-biased sparrowhawk predation favours crypsis in female chaffinches. Oikos 80:540–548.

Hart, A., and D. W. Lendrem (1984). Vigilance and scanning patterns in birds. Animal Behaviour 32:1216–1224.

Håstad, O., and A. Ödeen (2008). Different ranking of avian colors predicted by modeling of retinal function in humans and birds. American Naturalist 171:831–838.

Håstad, O., J. Victorsson, and A. Ödeen (2005). Differences in color vision make passerines less conspicuous in the eyes of their predators. Proceedings of the National Academy of Sciences USA 102:6391–6394.

Hill, G. E. (1998). An easy, inexpensive means to quantify plumage coloration. Journal of Field Ornithology 69:353–363.

Hill, G. E. (2006). Female mate choice for ornamental coloration. In Bird Coloration, vol. 2: Function and Evolution (G. E. Hill and K. J. McGraw, Eds.). Harvard University Press, Cambridge, MA, USA. pp. 137–200.

Hill, G. E., and K. J. McGraw (Editors) (2006). Bird Coloration, vol. 2: Function and Evolution. Harvard University Press, Cambridge, MA, USA.

Huhta, E., H. Hakkarainen, and P. Lundvall (1998). Bright colours and predation risk in passerines. Ornis Fennica 75:89–93.

Huhta, E., S. Rytkönen, and T. Solonen (2003). Plumage brightness of prey increases predation risk: An among-species comparison. Ecology 84:1793–1799.

Jones, A. G., and N. L. Ratterman (2009). Mate choice and sexual selection: What have we learned since Darwin? Proceedings of the National Academy of Sciences USA 106:10001–10008.

Kotiaho, J. S. (2001). Costs of sexual traits: A mismatch between theoretical considerations and empirical evidence. Biological Reviews 76:365–376.

Lendrem, D. W. (1983). Predation risk and vigilance in the Blue Tit (*Parus caeruleus*). Behavioral Ecology and Sociobiology 14: 9–13.

Liker, A., and T. Székely (2005). Mortality costs of sexual selection and parental care in natural populations of birds. Evolution 59:890–897.

Lima, S. L. (1987). Distance to cover, visual obstructions, and vigilance in House Sparrows. Behaviour 102:231–238.

Lima, S. L. (1994). On the personal benefits of anti-predatory vigilance. Animal Behaviour 48:734–736.

Lima, S. L., and L. M. Dill (1990). Behavioral decisions made under the risk of predation: A review and prospectus. Canadian Journal of Zoology 68:619–640.

Martin, T. E., and A. V. Badyaev (1996). Sexual dichromatism in birds: Importance of nest predation and nest location for females versus males. Evolution 50:2454–2460.

Metcalfe, N. B., and S. E. Ure (1995). Diurnal variation in flight performance and hence potential predation risk in small birds. Proceedings of the Royal Society of London, Series B 261:395–400.

Møller, A. P., and J. T. Nielsen (2006). Prey vulnerability in relation to sexual coloration of prey. Behavioral Ecology and Sociobiology 60:227–233.

Møller, A. P., S. S. Christiansen, and T. A. Mousseau (2011). Sexual signals, risk of predation and escape behavior. Behavioral Ecology 22:800–807.

Montgomerie, R., B. Lyon, and K. Holder (2001). Dirty ptarmigan: Behavioral modification of conspicuous male plumage. Behavioral Ecology 12:429–438.

Newman, J. A., G. M. Recer, S. M. Zwicker, and T. Caraco (1988). Effects of predation hazard on foraging ''constraints'': Patch-use strategies in grey squirrels. Oikos 53:93–97.

Norberg, U. M., and J. M. V. Rayner (1987). Ecological morphology and flight in bats (Mammalia; Chiroptera): Wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London, Series B 316:335–427.

Palleroni, A., C. T. Miller, M. Hauser, and P. Marler (2005). Prey plumage adaptation against falcon attack. Nature 434:973–974.

Pascual, J., and J. C. Senar (2013). Differential effects of predation risk and competition over vigilance variables and feeding success in Eurasian Siskins (*Carduelis spinus*). Behaviour 150: 1665–1687.

Post, P., and F. Götmark (2006). Predation by sparrowhawks *Accipiter nisus* on male and female Pied Flycatchers *Ficedula hypoleuca* in relation to their breeding behaviour and foraging. Journal of Avian Biology 37:158–168.

Price, T., and G. L. Birch (1996). Repeated evolution of sexual color dimorphism in passerine birds. The Auk 113:842–848.

Promislow, D. E. L., R. Montgomerie, and T. E. Martin (1992). Mortality costs of sexual dimorphism in birds. Proceedings of the Royal Society of London, Series B 250:143–150.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Rytkönen, S., P. Kuokkanen, M. Hukkanen, and K. Huhtala (1998). Prey selection by sparrowhawks *Accipiter nisus* and characteristics of vulnerable prey. Ornis Fennica 75:77–87.

Senar, J. C. (1985). Interactional rules in captive Siskins (*Carduelis spinus*). Miscel·lània Zoològica 9:347–360.

Senar, J. C. (1988). Trapping finches with the Yunick platform trap: The residency bias. Journal of Field Ornithology 59:381–384.

Senar, J. C., P. J. K. Burton, and N. B. Metcalfe (1992). Variation in the nomadic tendency of a wintering finch *Carduelis spinus* and its relationship with body condition. Ornis Scandinavica 23:63–72.

Senar, J. C., and M. Camerino (1998). Status signalling and the ability to recognize dominants: An experiment with Siskins (*Carduelis spinus*). Proceedings of the Royal Society of London, Series B 265:1515–1520.

Senar, J. C., and J. Domènech (2011). Sex-specific aggression and sex ratio in wintering finch flocks: Serins and siskins differ. Acta Ethologica 14:7–11.

Senar, J. C., J. Domènech, and M. Camerino (2005). Female Siskins choose mates by the size of the yellow wing stripe. Behavioral Ecology and Sociobiology 57:465–469.

Slagsvold, T., S. Dale, and A. Kruszewicz (1995). Predation favors cryptic coloration in breeding male Pied Flycatchers. Animal Behaviour 50:1109–1121.

Stevens, M., K. L. A. Marshall, J. Troscianko, S. Finlay, D. Burnand, and S. L. Chadwick (2013). Revealed by conspicuousness: Distractive markings reduce camouflage. Behavioral Ecology 24:213–222.

Svensson, L. (1992). Identification Guide to European Passerines, 4th ed. Published by the author, Stockholm, Sweden.

Waite, T. A. (1987a). Dominance-specific vigilance in the Tufted Titmouse: Effects of social context. The Condor 89:932–935.

Waite, T. A. (1987b). Vigilance in the White-breasted Nuthatch: Effects of dominance and sociality. The Auk 104:429–434.

Whittingham, M. J., S. J. Butler, J. L. Quinn, and W. Cresswell (2004). The effect of limited visibility on vigilance behaviour and speed of predator detection: Implications for the conservation of granivorous passerines. Oikos 106:377–385.

Witter, M. S., and I. C. Cuthill (1993). The ecological costs of avian fat storage. Philosophical Transactions of the Royal Society of London, Series B 340:73–92.

Witter, M. S., I. C. Cuthill, and R. H. C. Bonser (1994). Experimental investigations of mass-dependent predation risk in the European Starling, *Sturnus vulgaris*. Animal Behaviour 48:201–222.

Zuk, M., and G. R. Kolluru (1998). Exploitation of sexual signals by predators and parasitoids. Quarterly Review of Biology 73:415–438.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use