Variation in Black Bib of the Eurasian Siskin (*Carduelis spinus*) and Its Role as a Reliable Badge of Dominance

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Rohwer (1975, 1982) proposed that the variation and extent of color patches in the plumage of wintering birds could work as badges of social status. The major advantage of these signals would be that individuals of unequal status competing for limited resources would not need to risk accidental injury or waste energy assessing the relative fighting ability of potential opponents (Rohwer 1982). The status-signalling hypothesis has been tested in several species with variable plumage (reviewed by Whitfield 1987; see also Amat 1986, Watt 1986a, b, Fugle and Rothstein 1987, Møller 1987a, b, 1989, Jackson et al. 1988). These studies have, however, produced contradictory results. For plumage differences to act as true badges of dominance, they should correlate within and not just between sex and age classes. This has been demonstrated in only a few species (Great Tit [*Parus major*], Järvi and Bakken 1984; Yellow Warbler [*Dendroica petechia*], Studd and Robertson 1985; House Sparrow [*Passer domesticus*], Møller 1987a; Whitfield 1987; see however Ritchison 1985, Pöysä 1988, Wilson 1992).

The Eurasian Siskin (*Carduelis spinus*) shows great variability in the extent of blackish plumage in the bib (Newton 1972). This chin patch, as in House Sparrows (Møller 1987a), is present only in males, which are dominant over females. Dominance, however, is unaffected by age (Senar 1985). This lack of a relationship between age and dominance, and the absence of the badge in females simplifies analysis of the significance of the chin patch in status signalling. Other features in the Eurasian Siskin plumage also could be used for dominance signalling. For instance, yellow wing stripes have been found to work as a badge of status in its American counterpart, the Pine Siskin (*Carduelis pinus*; Balph and Balph unpubl. paper); they could have an important role. However, since wings are displayed in only 25% of the agonistic displays used by the Eurasian Siskin (Senar 1990), the chin is always visible, and most of the encounters between unfamiliar birds in wild flocks are between males (i.e. the badged individuals; Senar et al. 1990b), we restricted this analysis to the black bib. We describe variation in the size of the chin patch in male Eurasian Siskins and test (both in captivity and in the field) whether this variation is related to dominance status.

Methods.—Plumage variability and dominance relations in the field were studied in a suburban area of Barcelona (NE Spain) during the 1990–1991 winter.

Birds were trapped at baited feeders using platform traps and clap nets, and were marked with numbered aluminum bands. Trapping was carried out at least twice weekly, but the food was available continually so that Eurasian Siskins used the area heavily. For each male siskin we recorded, whenever possible, age and the maximum length and breadth of the badge. Badge size was measured by tilting the bird's head back in line with the body. Following the procedure of Møller (1987a), we determined the relationship between badge area, length (*L*, mm) and breadth (*B*, mm) from 12 museum skins. Thus, badge area (*A*, mm²) was calculated as:

$$A = 8.38 + 0.448\ LB \qquad (1)$$

($r = 0.83$, $F = 22.042$, $P < 0.001$). Age was determined according to Svensson (1984) and Cooper and Burton (1988). We trapped and measured 638 yearling and 311 adult males.

Field observations on agonistic interactions between large- and small-badged male birds were conducted from a blind located a few meters from a bird feeder. Data were collected on 11 and 12 March 1991, and we only recorded interactions in which one of the birds clearly had a larger badge than his opponent. An individual was considered to have won an encounter if its opponent gave a submissive posture or withdrew (Senar et al. 1990a). In order to avoid bias in deciding which interactions to focus on at any one time, we designed a long bird table (8 × 100 cm) that constrained the birds into forming a "linear" flock; observations always commenced at the right-hand end by noting all interactions occurring within the focal field of the binoculars (four to five birds at a time) and, once a maximum of three interactions (maximum two per individual) had taken place within each set of birds, observations switched to the next group of siskins to the left. Usually, there were about 30 to 40 siskins feeding on the feeder at any one time, and there were often more than 50 additional birds waiting in a tree 1 m from the feeder, with birds continuously flying from one place to another. Banding operations showed that there was a high turnover in the population, both from week to week (Senar et al. 1992), and within a given hour, with birds arriving and leaving the feeding patch continuously. Therefore, although the animals were not individually color banded and the possibility of pseudoreplication always remains, we think it is unlikely that individual
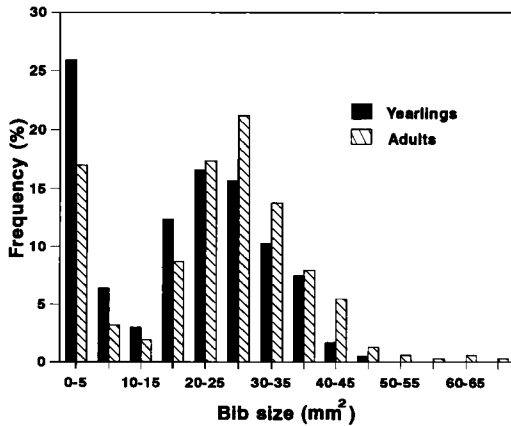
Fig. 1. Frequency distribution of male Eurasian Siskin bib-size classes in relation to age ($n = 638$ yearling and 311 adult males).
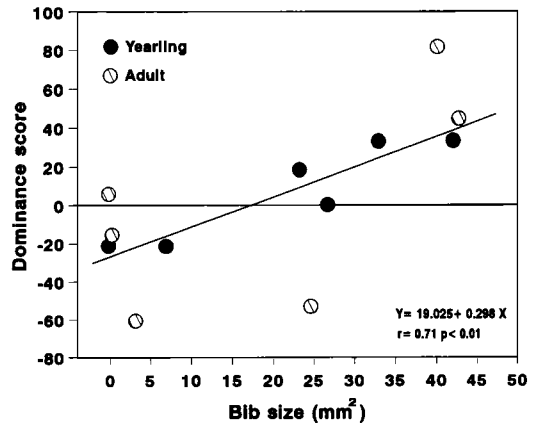

Fig. 2. Relationship in captive Eurasian Siskins between bib size and dominance score.

birds contributed more than one or two data points to the analyses.

The laboratory flock was composed of six adult and six yearling males. These were selected so that individuals exhibiting the full range of badge sizes were represented in both age classes. For each captive individual we measured (on capture) badge size, wing length, third primary length, and mass. Birds were color banded for individual identification and housed in an outdoor aviary (100 × 100 × 60 cm; for details of feeding schedule, see Senar et al. 1990a). All observations were made within 20 days of initial capture (i.e. less than the time needed by siskins to become familiar with one another; see Senar et al. 1990a). The experiment, therefore, was designed so that interactions were recorded in a non-established group (see Watt 1986a). We recorded 1,806 contests over resources (food, water or perches) in 11.5 h of observation. In any interaction we recorded the behavior used by the actor (the initiating bird) and the response by the reactor. The behaviors used by siskins in aggressive encounters are described in Senar (1990) and Senar et al. (1990a). The resulting data were used to construct a matrix relating each of the 12 individuals with the number of times that they either used or received the different behavior patterns. Correspondence analysis (CA; Heijden et al. 1990) based on this matrix produced a dominance score for each individual (see Senar et al. 1990a), which was used in subsequent analyses relating dominance to the morphological variables.

Results.—Badge size in male siskins ranged between 0.0 and 66.4 mm², with a mean of 20.04 ± SE of 0.43 mm² ($n = 949$). Adults had on average larger badges than yearlings (adult $\bar{x} = 23.43 \pm 0.76$ mm², $n = 311$; yearling $\bar{x} = 18.39 \pm 0.50$ mm², $n = 638$; Mann-Whitney test, $U = 78,449.5$, $P < 0.001$). This was due to the fact that, although both age classes

had a similar range of badge sizes, there were more adults than expected with large badges (Fig. 1).

We recorded 39 agonistic interactions in which both contestants were males and one of the individuals clearly had a larger badge than the other. Larger-badged birds won 77% of these interactions, significantly more than expected by chance (binomial test, two-tailed $Z = 0.0014$), and so were appreciably dominant over smaller-badged birds. The large-badged individuals also initiated most of the interactions (79%), a trait typical of dominant siskins (Senar 1985).

The correlation in the captive flock between badge size and social status (i.e. dominance score from CA) was 0.71 ($F = 10.0$, df = 1,10, $P < 0.01$; Fig. 2). Multiple-regression analysis of social status on badge size, age, mass, wing and third-primary length showed that the badge size was the only variable that explained the observed variation in social status when all the other variables were held constant (Table 1).

Discussion.—Since dominance rank within male siskin flocks is positively associated with the size of the badge, irrespective of age (and by definition, sex), the chin patch can potentially be used for signalling status (Whitfield 1987). It has been suggested that such badges of status should be particularly selected for in species with flocks that have an unstable membership, since they would reduce the cost of asserting status each time birds joined a new flock (Rohwer 1982, Whitfield 1987). Lemel and Wallin (1993) have shown that badges have more impact on the outcome of conflicts between unfamiliar birds rather than between birds with prior experience. This is not completely the case in siskins, which appear to live in subflocks that are stable and highly integrated (Senar et al. 1990a). However, given the high mobility of the species, these subflocks can interact with many other groups during the course of a winter (Senar et al. 1992), so that badges may be used primarily in interactions between the members of different subflocks.

TABLE 1. Multiple-regression model fitting data from captive flock, with dominance score as dependent variable.

Independent variable	B	Partial	T
Bib size	0.71	—	3.16*
Third-primary length	0.19	-0.27	0.85
Wing length	0.19	-0.27	0.83
Mass	0.09	0.87	0.37
Age	-0.02	-0.03	0.08

**, $P < 0.01$; all others ns ($P > 0.05$).

Since the Eurasian Siskin chin patch is only present in males, it could be argued that this is a sexual ornament, more important in the breeding season and only used incidentally in the nonbreeding season as a means of assessing and establishing status. We do not have the data to test this hypothesis. However, the clear bimodality in the size of the black bib, characteristic of several sexual ornaments in different animal species (Gadgil 1972), supports this view. Badges used to signal dominance status in agonistic encounters in other species (Great Tit [Järvi and Bakken 1984, Pöysä 1988, Wilson 1992, Lemel and Wallin 1993]; House Sparrow [Møller 1987a]) have also been shown to be clearly and perhaps more significantly related to sexual selection (Great Tit [Norris 1990a, b]; House Sparrow [Møller 1990]). Nonetheless, our results show that even if the character had evolved as a sexual ornament, it is now clearly related to dominance status.

Extensive field sampling has shown that adult male siskins have, on average, larger badges than yearlings. This could be a consequence of either: (1) an increase in badge size after the first total molt (i.e. when birds molt into an adult plumage); or (2) differential survival favoring more dominant (and, hence, larger-badged) birds, so that the adult class contains more larger-badged birds than would be expected if there were no directional selection. A direct test of these two possibilities would be to determine changes in badge size from yearling to adult age classes. Unfortunately, the low number of recaptures from one winter to the next in this species (Newton 1972) precludes this analysis. Comparison of the mortality rates of yearling male siskins in relation to badge size also is not feasible due to the high mobility and nomadic tendency of siskins (Senar et al. 1992). The remaining available data are highly contradictory. On the one hand, the fact that only adults were found to have bib sizes above 50 mm^2 (Fig. 1) suggests that individuals do increase their bib size with age. However, this explanation implies a relationship between dominance and age that is not supported by the available data (note that Senar [1985] also found no correlation between age and dominance in 13 captive Eurasian Siskins). Figure 1 also shows that there is no simple relationship between age and bib size, both age class-

es having high numbers of individuals at both extremes of the distribution. These two points suggest that the greater mean badge size of adult birds may be due to dominant birds being more likely to survive to adulthood, rather than to adults being dominant per se. Nevertheless, further work is required before either hypothesis can be convincingly rejected.

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Shorebird Predation on Eggs of Horseshoe Crabs During Spring Stopover on Delaware Bay

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Most species of shorebirds migrate long distances and stop at only a few selected sites (stopovers) to replenish fat deposits that will fuel the remainder of the migratory flight (Myers 1983, Davidson 1984, Senner and Howe 1984, Myers et al. 1987, Piersma 1987). Since great numbers of individuals utilize these stopovers for fattening, it is likely that the collective energy consumption by shorebirds at these stopovers must be large. Delaware Bay located between the states of Delaware and New Jersey in the eastern United States (38°47'N to 39°20'N and 74°50'W to 75°30'W; Clark et al. 1993) is one of these sites in spring. It hosts hundreds of thousands of shorebirds that feed primarily on the eggs of the horseshoe crab (*Limulus polyphemus*; Myers 1986). Birds arrive in synchrony with the horseshoe crabs, which emerge from the sea and lay their eggs in beaches during high tide (Shuster and Botton 1985). As many as 420,000 shorebirds (peak count of all species combined for a 160-km shoreline) have been recorded in a given year (Dunne et al. 1982). A thorough description of Delaware Bay can be found in Clark et al. (1993).

We calculated the total energy consumption by shorebirds during their spring stopover at Delaware Bay by estimating the total energy requirements (energy expenditure and fat deposition), and correcting for the assimilation efficiency of ingested food. Basal metabolic rates (BMR) were calculated using the equations for shorebirds of Kersten and Piersma (1987), which take into account the relatively high BMRs of shorebirds (Castro 1987, Kersten and Piersma 1987, Mathiu et al. 1989). Total energy expenditure was calculated by assuming that the daily energy expenditure is equivalent to 2.5 BMR. This is the average