

## Risk-taking and survival in the House Sparrow *Passer domesticus*: are plumage ornaments costly?

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An important cost of sexual and social colour signals may be increased conspicuousness of the animals to visual predators. Although such predation costs have repeatedly been proposed for various ornaments of birds, especially for melanised and depigmented signals with low presumed production costs, tests of this hypothesis are rare and inconclusive. In this study we investigated whether individual variation in plumage ornamentation was associated with predator-related risk-taking behaviour and short-term survival in free-living House Sparrows *Passer domesticus*. In a large sample of birds we measured three aspects of coloration used in sexual and social signalling: the size of the melanised black throat patch in males, and the area and conspicuousness of the depigmented wing-bar in both sexes. We measured risk-taking by manipulating the distance of feeders from shelters, and recorded individually ringed birds feeding close to and far from shelter. Sparrows seemed to perceive the farther feeders as more risky, as indicated by the shorter time spent and smaller groups feeding far from rather than close to shelter. However, the use of the more risky (farther) feeders was not related to any of the colour traits we measured, suggesting that Sparrows do not adjust their risk-taking behaviour to their ornamentation. Males (the more ornamented sex) did not take less risk than females. Furthermore, we found no evidence that larger throat patches or more ornamented wing-bars reduced the probability of survival. Our findings were robust and consistent across multiple approaches, even when we controlled for several potential confounding effects. These results do not support the suggestion that melanised and depigmented plumage ornaments have significant predation costs in House Sparrows.

**Keywords:** melanin, pigmentation, predation risk, sexual selection.

The costs of sexual signals are of central importance to the theory of sexual selection, because sex traits that increase mating success are expected to be constrained by costs that reduce the fitness of the trait bearer (reviewed by Kotiaho 2001). One frequently suggested cost of colour signals is reduced survival due to conspicuousness to predators (Andersson 1994, Kotiaho 2001). Costs of increased predation may be especially important for maintaining melanin-based signals that are often considered condition-independent (Senar 2006, but see Griffith *et al.* 2006) and depigmented ornaments that are devoid of all known costs of pigment production (Török

*et al.* 2003). Tests of this idea are rare in general (Götmark 1999, Kotiaho 2001, Godin & McDonough 2003, Husak *et al.* 2006), and especially inconclusive for avian plumage ornaments. For example, in Pied Flycatchers *Ficedula hypoleuca* one study found that predation selects against black-and-white male plumage (Slagsvold *et al.* 1995), whereas other work suggested that predators avoid black males and preferentially attack less ornamented conspecifics (reviewed in Götmark 1999). Surprisingly, recent experiments showed that the depigmented white rump patch of Feral Pigeons *Columba livia* reduces their vulnerability to raptor attacks (Palleroni *et al.* 2005). Comparative studies of melanin-based ornaments did not support the hypothesis that selection for crypsis influenced interspecific variation in the

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extent of black plumage in shorebirds (Bókonyi *et al.* 2003) and finches (Bókonyi & Liker 2005).

Since it is difficult to measure predation rates directly in the field, researchers usually use experiments with dummy birds and prey remains collected at raptor nests to study the effects of coloration on predation hazard (Götmark 1999, Huhta *et al.* 2003), or they monitor the survival of differently coloured prey individuals (e.g. Møller 1989). In this study we used an alternative approach by investigating the behavioural responses of prey birds to different levels of vulnerability to predators. Avoiding situations that expose animals to predators is often an important component of anti-predator strategies, and animals are expected to adjust their level of risk-taking according to their vulnerability (e.g. Godin & Clark 1997, Stankowich & Blumstein 2005, Fernández-Juricic *et al.* 2006). Thus, if larger or more conspicuous ornaments pose a significant predation risk to their bearers, more ornamented individuals should prefer less risky situations such as safer feeding places. One potential pitfall of this approach is that if the risk of predation is compensated by superior escape ability in highly-ornamented individuals, then a study of natural coloration may not detect any correlation between ornamentation and risk-taking. Therefore traits reflecting escape ability should be taken into account. Nevertheless this approach has also some advantages over colour-manipulation studies: it yields larger sample sizes, and does not impose unintended social costs of ornamentation that are not matched to the individuals' rank and quality (Veiga 1995).

Here we tested in free-living House Sparrows *Passer domesticus* whether natural variation in conspicuous plumage traits is related to the level of predation risk taken by differently ornamented individuals. The House Sparrow is an ideal species for investigating the predation costs of plumage colours, as it is the principal prey of several predator species (e.g. Götmark & Post 1996, Baker *et al.* 2005), and displays both melanin-based and depigmented ornaments. The male Sparrows' black throat patch (the bib) is one of the most thoroughly studied melanin-based plumage traits in both intra- and intersexual signalling (e.g. Møller 1987, Griffith *et al.* 1999, Liker & Barta 2001). Despite much research, the costs associated with large bibs, including risk of predation, remain unclear (Johnstone & Norris 1993, Buchanan *et al.* 2003). For example, Møller (1989) found increased mortality and, in particular, increased predation for adult males with larger bibs in autumn, although his sample sizes were very small. Veiga (1995) reported

that bib-enlargement reduced the survival of breeding yearlings, but this was attributed to over-investment in social and sexual competition rather than selective predation. In a larger sample however, Jensen *et al.* (2004) found no relationship between lifespan and bib size. House Sparrows also possess a bright depigmented wing-bar that they apparently use in dominance signalling (Bókonyi *et al.* 2006). Predation costs associated with the conspicuousness of the wing-bar have not been examined.

In this study we tested three predictions of the idea that plumage ornamentation has significant predation costs. First, we studied whether the coloration of male and female Sparrows was related to their risk-taking during foraging in winter. We quantified risk-taking by measuring the frequency of feeding at risky foraging places, i.e. far from shelter, as distance from shelter is a major determinant of perceived predation risk (Stankowich & Blumstein 2005). Since risk-taking may be affected by environmental and individual factors such as time of day, dominance status, escape ability or body condition (Stankowich & Blumstein 2005), we used multivariate statistical models to control for such confounding effects. Secondly, we tested whether risk-taking differed between the sexes: because male Sparrows are more ornamented than females, higher vulnerability may select males to prefer safer feeding sites than females. Although the behaviour of the sexes may differ due to other reasons such as hormonal differences or sex roles in parental care, these may be less important during the non-breeding season when sex hormone levels are low (Hegner & Wingfield 1987), and there are only limited sex-differences in aggressive and foraging behaviour with no marked intersexual dominance (Liker & Barta 2001, Lendvai *et al.* 2004). Finally, we used capture-mark-recapture analysis to test whether variability in plumage ornaments is related to short-term survival of the individuals. Although mortality may have other causes, predation is one of the major causes of death in House Sparrows (Møller 1989, Götmark & Post 1996, Baker *et al.* 2005). Thus if more ornamented birds are at greater predation risk, they are also expected to have lower chances of survival.

## METHODS

### Study site and general procedures

We conducted the study in the Zoo of Veszprém, north-west Hungary, between September 2004 and

September 2005. Several hundred House Sparrows live year-round at the study site, and during winter they usually can be found in flocks of up to *c.* 100 around feeding places. Eurasian Sparrowhawks *Accipiter nisus* and Northern Goshawks *Accipiter gentilis* regularly visit the Zoo, and we often observed Sparrowhawks attacking foraging Sparrow flocks and taking victims. Feral Cats *Felis catus* also hunt in the Zoo, and even captive predators such as the Lynx *Lynx lynx* occasionally take House Sparrows.

We captured Sparrows using mist-nets, and marked all birds ( $n = 662$ ) with a numbered metal ring and three colour rings. By the start of the observations on risk-taking behaviour (January 2005), we had marked 410 Sparrows. One researcher (A.L.) measured the body mass ( $\pm 0.1$  g), tarsus ( $\pm 0.1$  mm) and wing length ( $\pm 1$  mm) of all birds. Body condition at capture was calculated by dividing body mass by (tarsus length)<sup>3</sup> (note that we obtained qualitatively identical results using the residuals from a regression of body mass on tarsus length). The repeatability (Lessells & Boag 1987) of both body mass and condition was high between recaptures (using recaptures with the minimum and maximum values of each individual; mass:  $r = 0.64$ ,  $F_{207,208} = 4.48$ ,  $P < 0.001$ , condition:  $r = 0.63$ ,  $F_{207,208} = 4.48$ ,  $P < 0.001$ ), indicating that our birds maintained relatively consistent body weights during the study.

### Measuring coloration

We measured the bib size of males and the area and conspicuousness of the wing-bar of both sexes from digital photographs taken at capture. We photographed bibs with the birds' beak held perpendicular to body axis, and wing-bars on the left wings flattened in a standardized indoor set-up with constant lighting conditions. We used Scion Image software (Scion Corporation, Frederick, MD, USA) to measure the area of the bib and wing-bar (in cm<sup>2</sup>), and wing-bar conspicuousness as a measure of achromatic contrast between the wing-bar and the brown lesser coverts (for details see Bókonyi *et al.* 2006). Coloration was not measured for moulting birds.

We tested the reliability of our colour measurements in several ways (see also Bókonyi *et al.* 2006). First, we measured a number of photographs three times and calculated the repeatability of measurements. Repeatability proved very high for all colour traits (bib size:  $r = 0.99$ ,  $F_{124,250} = 283.0$ ,  $P < 0.001$ ; wing-bar area:  $r = 0.99$ ,  $F_{198,398} = 766.0$ ,  $P < 0.001$ ; wing-bar conspicuousness:  $r = 0.99$ ,  $F_{198,398} = 388.0$ ,

$P < 0.001$ ). Secondly, we assessed repositioning error by repositioning (i.e. taking from the photo set-up, putting back again, and re-photographing) a number of birds three times. Repeatability among these photos was also high (bib size:  $r = 0.74$ ,  $F_{25,52} = 9.7$ ,  $P < 0.001$ ; wing-bar area:  $r = 0.87$ ,  $F_{37,76} = 20.2$ ,  $P < 0.001$ ; wing-bar conspicuousness:  $r = 0.68$ ,  $F_{37,76} = 7.5$ ,  $P < 0.001$ ). All these measurements were recorded by A.K. Additionally, some photographs were re-measured by V.B. Inter-personal repeatability was high for bib size ( $r = 0.90$ ,  $F_{15,16} = 18.2$ ,  $P < 0.001$ ), wing-bar area ( $r = 0.88$ ,  $F_{34,35} = 15.0$ ,  $P < 0.001$ ) and wing-bar conspicuousness ( $r = 0.81$ ,  $F_{34,35} = 9.3$ ,  $P < 0.001$ ). Finally, both wing-bar measures were repeatable between subsequent recaptures (area:  $r = 0.89$ ,  $F_{80,81} = 16.6$ ,  $P < 0.001$ ; conspicuousness:  $r = 0.57$ ,  $F_{80,81} = 3.7$ ,  $P < 0.001$ ). Although bib size increases as the season progresses due to the abrasion of white feather tips, this increase accelerates after the end of winter (Møller & Erritzøe 1992), whereas we took most photographs (88%) in autumn–winter, and all before the end of April. The increase in bib size in males between their earliest and latest recaptures was significant (paired *t*-test:  $t_{53} = 2.76$ ,  $P = 0.008$ ), but the change was small (mean  $\pm$  se:  $0.19 \pm 0.07$  cm<sup>2</sup>) relative to the range of bib sizes (see Results) and comparable to repositioning error ( $0.18 \pm 0.02$  cm<sup>2</sup>). For birds with multiple colour measurements (from recaptures) we used mean values of all measurements for the survival analyses, and means of measurements taken prior to January 2005 (i.e. before the start of observations) for the analyses of risk-taking.

### Observation of risk-taking

We conducted observations of colour-ringed feeding Sparrows in January–February 2005. Risk-taking was studied at two sites where we manipulated the feeders' distance to cover (platform site) and at another site with fixed position feeders (container site). The two feeding platforms (one at each site) were established in late December 2004 and early January 2005, respectively. They were made of fibreboard sheet (80 × 80 cm) and placed on the ground near bushes. From installation until the start of the observations we regularly provided seed mixture (sunflower seed, wheat, millet, corn grit) on the platforms, and Sparrows quickly learned to feed on them at both sites. During this period, the platforms' edge was 1 m from the nearest bush. At the container site the birds were accustomed to feed from three plastic food containers (diameter 15 cm, height 20 cm, placed on the top of

1.2 m-high wooden pillars), in which food was provided for the Zoo's Raccoons *Procyon lotor*. The containers were c. 0.5, 1.5, and 2 m away, respectively, from the nearest bush and were filled with a food mixture (meat, carrots, apples, boiled eggs, jam) each morning. Raccoons very rarely used the feeders during daytime. The container site was close to (c. 70 m) and used by the same flock as one of the platform sites, while the two platforms were c. 500 m apart with little movement between them (only five ringed individuals were observed at both platforms).

During the study we divided the days (between 08:00–15:00) into three equal observation periods. Two observers (A.L. and V.B.) watched feeding Sparrows at the platform sites in two periods and at the container site in one period. The order of these observations was chosen randomly each day, with each order-combination occurring equal times during the study.

Platform manipulations were carried out on 7, 11, 13, 18, 19, 21 January and 1, 2, 4, 11 February 2005. Each platform was observed in two periods on each day by one observer (they switched sites between the periods), with each period occurring equal times during the study. At the start of an observation period, we provided food on the platform and shifted its position according to a randomly selected treatment (see below). We left the platform for 30–60 min, then started a 60 min observation. We observed foraging Sparrows from a remote location using spotting scopes and identified as many colour-ringed individuals as possible. After the observation we shifted the platform either according to the next treatment or, at the end of the day, to the 1 m position. We used two treatments: near shelter (the platform's edge was 0.5 m from the bush; low predation risk) or far from shelter (2 m from bush; high predation risk; for similar manipulation of perceived predation risk see Slotow & Rothstein 1995, Barta *et al.* 2004). We allocated treatments such that both were used at both platform sites on each day. During each observation period, a video camera recorded the whole surface of the platform for 30 min (colour-ringed individuals could not be identified from these recordings). We believe that our platform manipulations represented only minor disturbance to the Sparrows, because they were well accustomed to the presence of people and they fed readily from various human-provided objects (e.g. food canisters of many zoo animals) that were moved regularly during the day.

At the container site, observations were conducted on 5, 7, 18, 19, 21 January and 1, 2, 4, 9, 11 February

2005. Two containers were watched simultaneously by the two observers from a remote location, and birds on the third container were recorded by a video camera. After 30 min of observation, we switched the order of observers and camera such that each recorded a different container for another 30 min. The order was chosen randomly, each combination occurring equal times during the study. We identified colour-ringed individuals during observations by scopes, and birds were also reliably sexed and identified from the video recordings at the containers.

### Analyses of risk-taking

To measure the effect of feeder position (near/far) on the behaviour of birds, we analysed all video-recordings as follows. First, we defined a feeding bout as an occasion when at least one Sparrow stayed on the feeder. For each bout we recorded its length (from the landing of the first Sparrow until the departure of the last one, in sec), and the maximum number of birds as a surrogate of group size. We also noted the number of males, females and individuals whose sex could not be determined at the time when the maximum number of birds was on the feeder. For each bout we also recorded whether other bird species were at the feeder. We also noted weather conditions (sunny, cloudy, or snowy) for each observation period; snowfall was mild and occurred in only 3 observation periods. Bout length, group size and sex ratio (expressed as the proportion of females, after excluding unsexed birds) were log-transformed. Platform sites were analysed separately from the container site. In general linear models we tested the effects of distance from shelter, weather, platform site (fixed factors), date, and time of day (covariates) on bout length, group size and sex ratio.

We quantified the risk-taking of individual birds in the following way. In total, we had 3650 records for 186 ringed birds at the three feeding sites (mean  $\pm$  se: 19.62  $\pm$  1.54 records per individual). First, for each bird we counted the number of one-hour observation periods in which the individual was seen to feed near and far from shelter, respectively, and calculated the proportion of all observations that were far from shelter (high-risk feeding hereafter). This measure of risk-taking was calculated separately for the platforms and the container site. Secondly, for colour-ringed individuals identified from video-recordings at the container site we measured the duration of their feeding bouts on the respective containers (in sec), and calculated the mean time

they spent on the different containers. Then we expressed the proportion of time spent on the two farther containers relative to all time spent on containers (high-risk time hereafter).

We used generalized linear models (GLM) with binomial error distribution and logit link function (Dalggaard 2002) to test the bivariate relationships between colour traits and the probability that a bird engaged in high-risk feeding. Then we tested the multiple effects of coloration and possible confounding variables on the probability of high-risk feeding in multivariate mixed GLMs. Because environmental factors such as weather or time of day varied across observation periods, here we used observation periods instead of individuals as measurement units, and entered 'individual' as a random factor. Initial full models included date, time of day, body condition, wing length, and all colour variables as covariates. We used wing length as a proxy of escape ability (Moreno-Rueda 2003). Additionally, platform models included weather as fixed factor. We eliminated non-significant effects stepwise by removing the predictor with the largest *P*-value in each step, but never excluding the random factor. We also assessed the relative importance of colour variables in explaining variation in risk-taking by the information-theory approach (Anderson *et al.* 2000) based on Akaike's Information Criterion corrected for sample size (AICc). We built mixed GLM models that included all possible combinations of colour traits while controlling for all confounding effects, and evaluated these candidate models by their relative Akaike weights ( $\omega_i$ ).

To control for the possible influence of dominance on feeder choice, we used our video and observation records of aggressive interactions among the birds on the containers to calculate fighting success (i.e. the number of wins divided by the total number of aggressive encounters in which the focal bird was involved) as a measure of dominance rank (Liker & Barta 2001). Note that observations of aggressive interactions were only available for a subset of birds, thus we did not include dominance in the previous multivariate analyses. Instead, we used two kinds of analyses to investigate the effects of dominance (as reflected by fighting success) and coloration on risk-taking in the subset of birds with available information. First, we calculated overall fighting success for each individual, and controlled for this variable in partial correlations between high-risk feeding and colour variables. Secondly, we calculated fighting success of each bird for each feeder within

each observation period, and tested its effect along with the aforementioned confounding variables and coloration on risk-taking (here, the distance of the chosen container) in multivariate mixed GLMs. As above, here we used observation periods as measurement units and 'individual' as random factor. Initial full models included fighting success, date, time of day, body condition, wing length, and all colour variables as covariates, then we eliminated non-significant effects stepwise, never excluding the random factor. This second approach allowed us to take into account daily changes in dominance relations, which may occur in large flocks.

High-risk time on the containers was normally distributed, thus we tested its relationships with colour variables by bivariate Pearson's correlations. Because of small sample size for high-risk time, we did not conduct multivariate analyses in this case.

We used the R statistical computing environment for statistical analyses. All tests were two-tailed with a 95% confidence level. We report means  $\pm$  se followed by range (min – max), and provide *t*-values for independent samples *t*-tests throughout.

### Mark-capture-recapture analyses

Survival analyses were conducted for the whole study period (16 September 2004 – 13 September 2005) during which we had a total of 1073 encounters of 184 male and 144 female birds. After the initial capture, Sparrows were either recaptured or identified by colour rings, and we treated both recaptures and resightings as recapture events ( $n = 745$ ) in the analyses. Recaptures (including resightings) were carried out on a monthly basis, yielding 12 encounter occasions. From this dataset we determined encounter history for each individual (Lebreton *et al.* 1992). Recapture effort was defined as the time spent on observing and capturing the birds in each month (in hours).

We began modelling with the fully parameterised Cormack-Jolly-Seber (CJS) model (Clobert & Lebreton 1987), which assumes differences in survival and recapture probabilities between recapture periods. We then reduced the dimensionality of the models to seek a more parsimonious structure by removing interaction terms and factors. We started modelling by simplifying the recapture parameter, keeping the survival parameter fully parameterised (Lebreton *et al.* 1992). After finding the most parsimonious model for recapture, we simplified the survival parameter without further modifying the recapture parameter. As well as fully time-dependent and

constant survival and recapture probabilities, we also investigated seasonal models using three seasonal categories: non-breeding (October–March), breeding (April–July) and moult (August–September). In the last step, colour variables were added as individual covariates to the most parsimonious model structure. Beside the analyses for the whole study period, we also investigated the effects of individual covariates on survival probability specifically in the non-breeding season, because (i) our observations on risk-taking behaviour were conducted in this period and (ii) increased predation on large-bibbed males had been reported for the non-breeding season (Møller 1989).

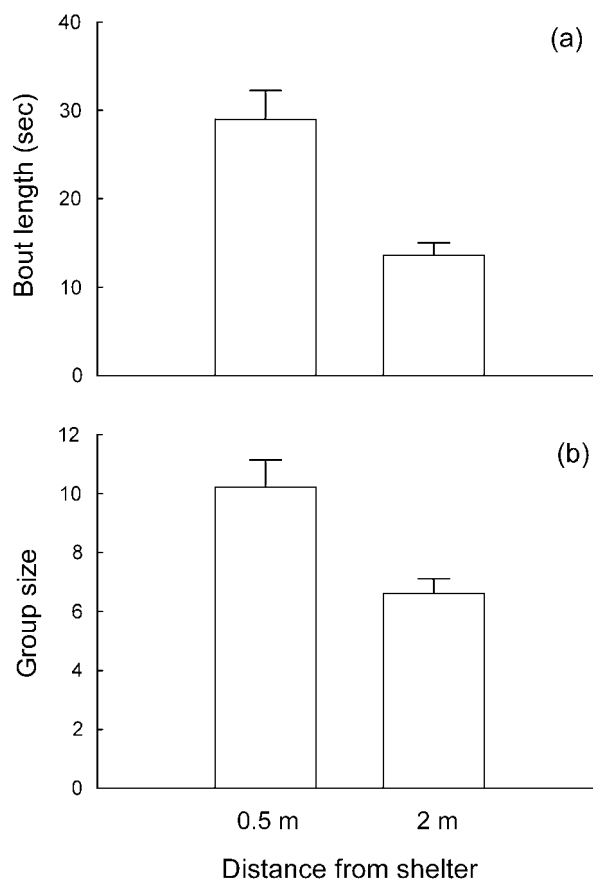
Selection among competing models was based on AICc. We used program Mark (G. C. White, Dept of Fisheries and Wildlife, Colorado State University, Fort Collins, CO, USA) for the model selection (White & Burnham 1999), and U-CARE for goodness-of-fit (GOF) tests for the CJS model (Choquet *et al.* 2003). U-CARE (CEFE-CNRS, Montpellier, France) performs  $\chi^2$  statistics to test the assumptions of the CJS model. These GOF tests (TEST2 and TEST3) are the same as tests in RELEASE (Burnham *et al.* 1987), and we used their overall result to test the fit to the CJS model. In model descriptions  $\Phi$  and  $p$  stand for the survival and recapture parameter, respectively, and subscripts denote the model structure (Lebreton *et al.* 1992, Pradel 1993).

## RESULTS

For birds photographed prior to the risk-taking observations, male bib size ranged 0.13–2.30 cm<sup>2</sup> ( $0.95 \pm 0.04$ ,  $n = 96$ ). Wing-bar area was significantly larger in males ( $1.06 \pm 0.03$ , 0.35–1.64 cm<sup>2</sup>,  $n = 96$ ) than in females ( $0.37 \pm 0.02$ , 0.14–0.73 cm<sup>2</sup>,  $n = 60$ ;  $t_{154} = 21.72$ ,  $P < 0.001$ ). Wing-bar conspicuousness was also significantly higher in males ( $84 \pm 1.29$ , 44–115) than in females ( $65 \pm 1.21$ , 42–87;  $t_{154} = 10.47$ ,  $P < 0.001$ ).

### Effects of distance from shelter

On the platforms, Sparrows spent significantly more time in the near than in the far position ( $t_{158} = 4.32$ ,  $P < 0.001$ ; Fig. 1a), and group size was also significantly larger near than far from shelter ( $t_{149} = 2.30$ ,  $P = 0.023$ ; Fig. 1b). These results remained unchanged when we included several potentially confounding variables in the models (Table 1), and when we excluded bouts in which other species were present (not shown). Sex ratio on the platforms did not differ



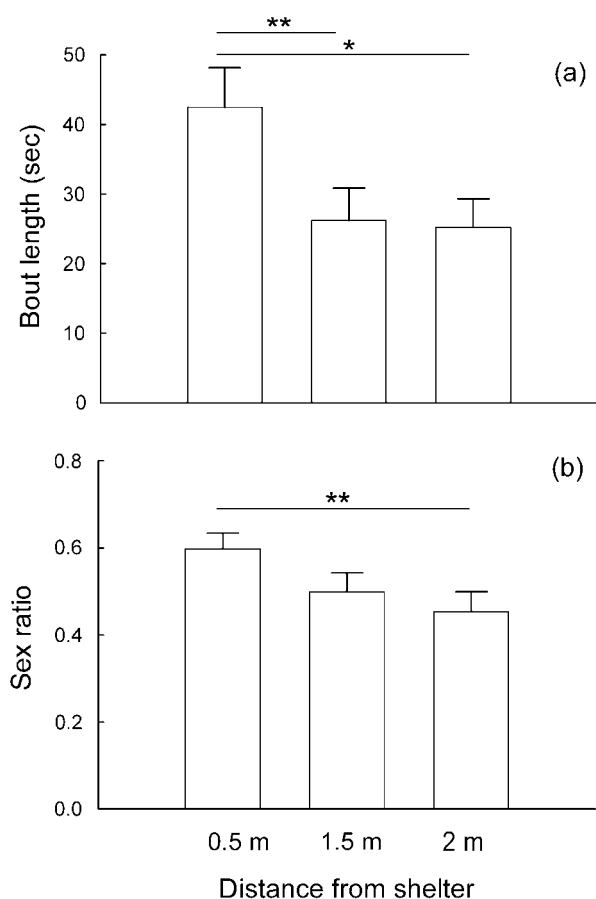
**Figure 1.** (a) Feeding bout length (mean + SE) and (b) group size (maximum number of individuals per feeding bout; mean + SE) of House Sparrow flocks on the platforms near and far from shelter (data from the two platform sites combined). See text for statistics.

between the far and near positions ( $t_{160} = 0.72$ ,  $P = 0.471$ ; Table 1). The latter result should be treated with caution, however, because on average 16% of the birds could not be sexed from the videos, although groups near and far from shelter did not differ in the proportion of unsexed birds ( $t_{92} = -0.30$ ,  $P = 0.768$ ).

At the container site, Sparrows spent significantly more time feeding on the nearest container than on the farther containers ( $F_{2,273} = 6.32$ ,  $P = 0.002$ ; Fig. 2a). Group size did not differ between containers ( $F_{2,273} = 1.23$ ,  $P = 0.295$ ); note however that maximal group size was limited to *c.* 10 birds due to small container size. These results were not altered when we included date and time of day in the models (Table 1; weather was constantly sunny during container observations), or when we excluded bouts in which other species were present (not shown). The proportion of females was higher on the nearest than

**Table 1.** Feeding bout length (sec), maximum group size (number of birds), and sex ratio (proportion of females) of Sparrow flocks feeding on two types of feeders, in relation to the feeder's distance from shelter and possible confounding variables. Effect sizes ( $\eta^2$ ) are given for the initial full general linear models. Asterisks (\*) mark the predictors included in the final models obtained by stepwise backward elimination of non-significant effects.

	Feeding bout length		Maximal group size		Sex ratio	
	Platforms	Containers	Platforms	Containers	Platforms	Containers
Distance from shelter	0.088*	0.049*	0.098*	0.014	0.014	0.031*
Date	< 0.001	0.006	0.050*	0.019*	0.074*	0.003
Time of day	0.095*	0.034*	0.009	0.001	0.002	0.031*
Platform site	0.145*		0.018		0.114*	
Weather	0.039*		0.068*		0.038	



**Figure 2.** (a) Feeding bout length (mean + SE) and (b) sex ratio (proportion of females, mean + SE) of House Sparrow flocks on the three containers. Asterisks mark the significant pairwise differences (Dunnnett's post-hoc *t*-tests; \*\**P* < 0.050, \**P* = 0.056).

on the farthest container ( $F_{2,273} = 3.19, P = 0.043$ ; Table 1, Fig. 2b).

The shorter feeding bouts and smaller groups supported our expectation that Sparrows perceived

the feeders far from shelter as more risky. Thus, in the following analyses we assumed that greater frequency and time using the farther feeders reflected greater levels of risk taken by the birds.

### Coloration and risk-taking

On the platforms, high-risk feeding was not related to bib size, wing-bar area or wing-bar conspicuousness in males and females (Table 2). The two platform sites did not differ in high-risk feeding ( $t_{80} = 0.86, P = 0.391$ ), hence we pooled data from the two platform sites in the analyses. Note however that we obtained identical results when platform site was included in the models (not shown). In multivariate analyses, the effects of all colour variables remained non-significant. The final model for males included date ( $\beta \pm se: 0.09 \pm 0.02, P < 0.001$ ) and weather ( $\beta_1 \pm se: -1.34 \pm 0.35, P < 0.001; \beta_2 \pm se: -0.51 \pm 0.30, P = 0.092$ ). The final model for females contained the time of day ( $\beta \pm se: 0.16 \pm 0.08, P = 0.047$ ), date ( $\beta \pm se: 0.06 \pm 0.02, P = 0.001$ ) and weather ( $\beta_1 \pm se: -0.83 \pm 0.36, P = 0.021; \beta_2 \pm se: 0.54 \pm 0.36, P = 0.131$ ). These results of stepwise GLMs were supported by AICc-based model comparison: in neither sex did the best model for high-risk feeding include any of the colour variables (Table 3a).

At the container site, high-risk feeding was again unrelated to bib size, wing-bar area and wing-bar conspicuousness in both sexes (Table 2). In multivariate analyses, the effects of all colour variables remained non-significant again, and the final models contained no significant predictors for high-risk feeding. Consistently with stepwise GLMs, AICc-based model comparison indicated that colour traits were of minor importance in explaining high-risk feeding (Table 3b).

Fighting success was not related to high-risk feeding at the container site (males:  $\beta \pm se: 0.75 \pm 0.67,$

**Table 2.** Relationships of high-risk feeding with colour traits in male and female House Sparrows feeding on two types of feeders. Parameter estimates ( $\beta \pm SE$ ) are given for bivariate generalized linear models with binomial error distribution.

	Platforms			Containers		
	$\beta \pm SE$	<i>P</i>	<i>n</i>	$\beta \pm SE$	<i>P</i>	<i>n</i>
Bib size	0.23 ± 0.50	0.641	84	0.88 ± 0.80	0.271	55
Wing-bar area						
Males	-0.44 ± 1.79	0.806	84	-1.48 ± 2.13	0.489	53
Females	5.27 ± 4.92	0.284	57	0.95 ± 5.34	0.859	46
Wing-bar conspicuousness						
Males	-0.01 ± 0.01	0.289	85	-0.01 ± 0.01	0.398	54
Females	0.01 ± 0.01	0.884	57	-0.01 ± 0.01	0.574	46

**Table 3.** Comparison of candidate models for high-risk feeding in male and female House Sparrows. Akaike's Information Criterion (AICc), number of estimated parameters (K), and relative Akaike weights ( $\omega_i$ ) of the candidate models are given for (a) the platform sites and (b) the container site. The best model for each case is shown in bold. Predictors are bib size (B), wing-bar area (A), wing-bar conspicuousness (C), and confounding variables (Conf): date, time of day, weather (only for the platform models), body condition, and wing length.

Predictors	Males			Females	
	K	AICc	$\omega_i$	AICc	$\omega_i$
<b>Conf</b>	<b>7</b>	<b>387.38</b>	<b>0.36</b>	<b>315.79</b>	<b>0.54</b>
Conf, C	8	389.49	0.13	317.73	0.20
Conf, A	8	388.89	0.17	317.93	0.18
Conf, B	8	389.29	0.14	–	–
Conf, A, C	9	390.91	0.06	319.79	0.07
Conf, B, C	9	391.41	0.05	–	–
Conf, B, A	9	390.81	0.07	–	–
Conf, B, A, C	10	392.95	0.02	–	–

Predictors	Males			Females	
	K	AICc	$\omega_i$	AICc	$\omega_i$
<b>Conf</b>	<b>5</b>	<b>378.73</b>	<b>0.31</b>	<b>453.19</b>	<b>0.50</b>
Conf, C	6	380.62	0.12	454.86	0.22
Conf, A	6	379.72	0.19	455.06	0.20
Conf, B	6	380.32	0.14	–	–
Conf, A, C	7	381.83	0.07	456.75	0.08
Conf, B, C	7	382.33	0.05	–	–
Conf, B, A	7	381.23	0.09	–	–
Conf, B, A, C	8	383.36	0.03	–	–

$P = 0.261$ ,  $n = 32$ ; females:  $\beta \pm se$ :  $-0.50 \pm 0.62$ ,  $P = 0.414$ ,  $n = 35$ ). Moreover, when controlling for fighting success in partial correlations, high-risk feeding remained unrelated to bib size ( $r_p = -0.08$ ,  $P = 0.688$ ,

$n = 25$ ), wing-bar area (males:  $r_p = -0.18$ ,  $P = 0.381$ ,  $n = 25$ ; females:  $r_p = 0.25$ ,  $P = 0.2158$ ,  $n = 24$ ) or wing-bar conspicuousness (males:  $r_p = -0.14$ ,  $P = 0.476$ ,  $n = 25$ ; females:  $r_p = -0.23$ ,  $P = 0.252$ ,  $n = 24$ ). These results were unchanged when we restricted the analyses to those individuals for which we had recorded more than five fights (bib size:  $r_p = 0.20$ ,  $P = 0.513$ ,  $n = 11$ ; wing-bar area: males:  $r_p = 0.32$ ,  $P = 0.282$ ,  $n = 11$ ; females:  $r_p = 0.13$ ,  $P = 0.687$ ,  $n = 10$ ; wing-bar conspicuousness: males:  $r_p = 0.08$ ,  $P = 0.796$ ,  $n = 11$ ; females:  $r_p = -0.41$ ,  $P = 0.190$ ,  $n = 10$ ). In multivariate mixed GLMs containing fighting success, none of the colour variables had significant effect on risk-taking: the final model for males contained no significant predictors for high-risk feeding, while for females it included only the time of day ( $\beta \pm se$ :  $-0.44 \pm 0.17$ ,  $P = 0.009$ ).

As with high-risk feeding, high-risk time on the containers was not related to bib size ( $r = -0.11$ ,  $P = 0.764$ ,  $n = 10$ ), wing-bar area (males:  $r = -0.02$ ,  $P = 0.957$ ,  $n = 11$ ; females:  $r = -0.11$ ,  $P = 0.665$ ,  $n = 17$ ) or wing-bar conspicuousness (males:  $r < 0.001$ ,  $P > 0.999$ ,  $n = 11$ ; females:  $r = -0.03$ ,  $P = 0.908$ ,  $n = 17$ ).

Males and females did not differ in high-risk feeding (platforms:  $t_{85} = 0.03$ ,  $P = 0.975$ ; containers:  $t_{76} = 0.17$ ,  $P = 0.869$ ) or in high-risk time ( $t_{29} = -1.13$ ,  $P = 0.267$ ). For birds that we observed both at the platform and container sites, high-risk feeding was not correlated between the two feeder types ( $r = -0.02$ ,  $P = 0.879$ ,  $n = 66$ ).

### Coloration and survival

The goodness-of-fit test showed significant deviation from the general Cormack-Jolly-Seber model ( $\Phi_t p_t$ ) for both the male and the female data (males:  $\chi^2_{30} = 51.08$ ,  $P = 0.010$ ; females:  $\chi^2_{31} = 83.85$ ,  $P < 0.001$ ). This lack of fit was due to heterogeneity in the short-term recapture probabilities as indicated by a



significant component of the GOF tests (TEST2.CT, males:  $\chi^2_9 = 25.42$ ,  $P = 0.002$ , females:  $\chi^2_9 = 70.38$ ,  $P < 0.001$ ). The  $z$  statistic in the program U-CARE (Choquet *et al.* 2003) revealed significant trap-dependence (Pradel 1993). In other words, the probability of being encountered differed between the animals encountered and not encountered at the previous occasion (males:  $z = -2.26$ ,  $P = 0.024$ , females:  $z = -6.11$ ,  $P < 0.001$ ). To deal with trap-dependence, we created a new global starting model with two-level dummy age-class model structure in the recapture probability:  $\Phi_t p_{m+tv}$ , where the subscript 'm' denotes that the model accounts for the heterogeneity in recapture probability (Pradel 1993).

Table 4a presents the models for males. Recapture probability was strongly time-dependent (model 1 vs. model 2), but this variability was not explained by variation in recapture effort (model 2 vs. model 3). Survival also varied in time (model 1 vs. model 5) but this variation was not explained by seasonal differences (models 5–6). Neither bib size nor wing-bar traits (either alone or together) influenced survival probability of males (models 7–10 vs. model 1). Models containing the effects of colour variables specifically in the non-breeding season received less support than the seasonal model without individual covariates (models 11–13 vs. model 6) and were weaker than the best model (models 11–13 vs. model 1). Models containing quadratic relationships between colour variables and survival were less supported than linear models (models 7–9 vs. models 14–16).

Models of females are summarized in Table 4b. As with males, recapture probability was time-dependent, independently of recapture effort and season (models 1–4). In contrast to males, female survival was constant over time (models 1 and 6 vs. model 5). However, as in males, wing-bar characteristics did not explain variation in survival probability (models 7–10 vs. model 5). Models containing wing-bar variables specifically for the non-breeding season received less support than either the seasonal model without individual covariates (models 10–11 vs. model 6) or the best model (model 5). As in the case of males, models containing quadratic terms of colour variables were less supported than the linear models (models 7–8 vs. models 12–13).

## DISCUSSION

In this study we used multiple approaches to investigate whether melanin-based and depigmented

plumage ornaments may increase the risk of predation and thereby mortality in House Sparrows. Our results consistently failed to support any of the three predictions of the predation-cost hypothesis. First, although we successfully manipulated the predation risk perceived by the birds, we found that Sparrows did not adjust their risk-taking behaviour to their coloration. This result was consistent between the two sexes, for different feeder types, and remained unchanged after controlling for several confounding variables that may account for variation in the motivation of birds (e.g. time of the day, weather, body condition). In addition, although a number of Sparrows used both platforms and containers, their risk-taking was not correlated between these two feeder types, suggesting further that they had no consistent preferences for particular feeder positions (near or far). Secondly, although males are more ornamented than females, they did not use the safer feeders more often than females at either feeder type. Thirdly, in a large sample of birds we found no evidence that coloration influences the probability of survival. In both sexes, the inclusion of colour traits did not improve the fit of the models, and the effects of the bib and the wing-bar on survival were at best weak. Furthermore, this result was independent of the time period for which the effects of coloration were modelled (whole year or non-breeding season), and whether we included the effects of different colour traits separately or in combination. The lack of bib size effects during the non-breeding season is particularly noteworthy, because this is the period for which a predation cost of large bib had been suggested (Møller 1989). Our latter result is consistent with that of Jensen *et al.* (2004) who reported that the lifespan of male Sparrows was unrelated to their bib size. Note that our findings on survival are based on capture-mark-recapture analyses, the most powerful of the available methods for detecting the effects of individual traits (such as coloration) on survival (e.g. Gregoire *et al.* 2004).

How can these results be explained? Although the black bib of male Sparrows contrasts strongly with the surrounding light breast feathers at close view, when viewed at greater distances by predators it may blend in with the brown and grey patterns of the bird and its background (Endler 1978), providing a relatively inconspicuous appearance. Similarly, although the light wing-bar is displayed prominently by Sparrows during aggressive interactions (Bókonyi *et al.* 2006), it can be totally covered by the neighbouring feathers, and we often observed Sparrows

**Table 4.** Comparison of candidate models for survival and recapture probabilities in (a) male and (b) female House Sparrows. Modelling procedure began with the recapture probability ( $p$ ), then the model with the lowest AICc value was selected for modelling the survival probability ( $\Phi$ ). The best model was then selected to model the effects of coloration. In each section, the best model is shown in bold. Akaike's Information Criterion (AICc), number of estimated parameters (K), and the estimated effects of colour traits on survival probability ( $\beta \pm SE$ ) are given. Parameter estimates show the slope of the linear relationship between the given individual covariate (coloration) and the survival probability on the logit scale. Model notation: t, time; m, short-time trap dependence; e, recapture effort; s, season (non-breeding, breeding and moulting); B, bib size; A, wing-bar area; C, wing-bar conspicuousness.  $B^2$ ,  $A^2$  and  $C^2$  represent quadratic terms.

(a)

Models		AICc	K	$\beta \pm SE$
<i>Modelling recapture probability</i>				
<b>(1)</b>	<b><math>\Phi_t p_{t+m}</math></b>	<b>1418.75</b>	<b>22</b>	–
(2) <sup>1</sup>	$\Phi_t p_m$	1460.81	13	–
(3)	$\Phi_t p_{m+e}$	1462.86	14	–
(4)	$\Phi_t p_{s+m}$	1461.57	15	–
<i>Modelling survival probability</i>				
(5)	$\Phi p_{t+m}$	1430.99	13	–
(6)	$\Phi_s p_{t+m}$	1434.45	15	–
<i>Modelling the effects of coloration on survival probability</i>				
(7)	$\Phi_{t+B} p_{t+m}$	1420.64	23	0.56 $\pm$ 1.08
(8)	$\Phi_{t+A} p_{t+m}$	1419.04	23	2.20 $\pm$ 1.61
(9)	$\Phi_{t+C} p_{t+m}$	1420.65	23	0.44 $\pm$ 0.86
(10)	$\Phi_{t+A+C+B} p_{t+m}$	1423.63	25	B: –0.28 $\pm$ 1.15 A: 2.48 $\pm$ 1.77 C: –0.06 $\pm$ 0.96
(11)	$\Phi_{s(B)} p_{t+m}$	1436.49	16	0.35 $\pm$ 1.32
(12)	$\Phi_{s(A)} p_{t+m}$	1435.49	16	1.90 $\pm$ 1.83
(13)	$\Phi_{s(C)} p_{t+m}$	1436.46	16	0.31 $\pm$ 0.98
(14)	$\Phi_{t+B+B^2} p_{t+m}$	1422.08	24	B: –3.04 $\pm$ 4.39 $B^2$ : 6.28 $\pm$ 7.43
(15)	$\Phi_{t+A+A^2} p_{t+m}$	1421.16	24	A: 0.01 $\pm$ 9.68 $A^2$ : 4.25 $\pm$ 18.54
(16)	$\Phi_{t+C+C^2} p_{t+m}$	1421.71	24	C: 10.76 $\pm$ 7.90 $C^2$ : –6.40 $\pm$ 4.80

(b)

Models		AICc	K	$\beta \pm SE$
<i>Modelling recapture probability</i>				
<b>(1)</b>	<b><math>\Phi_t p_{t+m}</math></b>	<b>1067.11</b>	<b>22</b>	–
(2) <sup>1</sup>	$\Phi_t p_m$	1091.33	13	–
(3)	$\Phi_t p_{m+e}$	1110.07	14	–
(4)	$\Phi_t p_{s+m}$	1093.36	15	–
<i>Modelling survival probability</i>				
<b>(5)</b>	<b><math>\Phi p_{t+m}</math></b>	<b>1062.26</b>	<b>13</b>	–
(6)	$\Phi_s p_{t+m}$	1064.9	15	–
<i>Modelling the effects of coloration on survival probability</i>				
(7)	$\Phi_A p_{t+m}$	1064.21	14	–1.44 $\pm$ 3.90
(8)	$\Phi_C p_{t+m}$	1064.26	14	–0.61 $\pm$ 1.44
(9)	$\Phi_{A+C} p_{t+m}$	1066.26	15	A: –1.18 $\pm$ 3.93 C: –0.53 $\pm$ 1.46
(10)	$\Phi_{s(A)} p_{t+m}$	1066.98	16	–1.26 $\pm$ 5.01
(11)	$\Phi_{s(C)} p_{t+m}$	1067.04	16	0.05 $\pm$ 1.79
(12)	$\Phi_{A+A^2} p_{t+m}$	1066.30	15	A: 7.09 $\pm$ 19.04 $A^2$ : 25.28 $\pm$ 83.55
(13)	$\Phi_{C+C^2} p_{t+m}$	1066.35	15	C: –0.28 $\pm$ 14.27 $C^2$ : –0.24 $\pm$ 10.89

<sup>1</sup>Note that 'm' cannot be removed from the model structure because it accounts for trap-dependence.

on the feeders with completely hidden wing-bars (V. Bókony pers. obs.). Male Chaffinches *Fringilla coelebs* also expose their white wing patch, which promotes their detectability to humans, only during social and sexual displays and hide it while foraging (Götmark & Hohlfält 1995). Thus, whereas the presence or absence of some additional square millimetres of melanised plumage or slight differences in its brightness may well be conspicuous and informative to Sparrows during sexual and social interactions (Møller 1987, Griffith *et al.* 1999, Liker & Barta 2001, Bókony *et al.* 2006), it seems unlikely that this variation is relevant to, and constrained by, their typical predators such as Sparrowhawks or cats that rely on surprise attacks (Møller 1989, Baker *et al.* 2005). These results add to recent findings that animals may display their colour signals at reduced predation costs by timing and spacing their display behaviour (e.g. Heindl & Winkler 2003) and by utilising the differences between prey and predator visual systems (Håstad *et al.* 2005).

An alternative explanation is that more ornamented birds might have better escape ability that compensates for increased conspicuousness, so they do not need to reduce their risk-taking during foraging. For example, Moreno-Rueda (2003) reported that bib size was correlated with the capacity to escape from a predator (human) that hunts by chasing Sparrows. However, in that study the main predictor of escape ability of both sexes was wing length (Moreno-Rueda 2003). In our study the relationship between coloration and risk-taking did not change when we included wing length in the analyses, suggesting that our results might not be biased by this aspect of escape ability of the birds. Furthermore, our results remained unchanged when controlling for body condition that may also affect escape ability. Nevertheless we cannot exclude the possibility that some unmeasured aspects of escape ability (e.g. predator-detection skills) influenced our results. Experiments that disentangle the predation-risk effects of colour manipulations from the costs of social 'cheating' are needed to test the predation costs of coloration independently of the individuals' escape ability.

Finally, dominance relationships among the birds could potentially influence our results. In non-breeding flocks, Sparrows establish dominance hierarchies (Møller 1987, Liker & Barta 2001), and dominant birds may exclude subordinates from safer feeding sites (Slotow & Rothstein 1995). However, it is unlikely that such effects masked the relation between coloration and risk-taking. First, dominant

males have larger bibs and more conspicuous wing-bars (Møller 1987, Liker & Barta 2001, Bókony *et al.* 2006), which would predict even less predation risk taken by the more ornamented males than expected due to their conspicuousness alone. Secondly, dominant females are heavier (Liker & Barta 2001), yet body mass did not influence risk-taking or its relation with female coloration (results not shown). Thirdly, the relationship between coloration and risk-taking was consistent between the two feeder types, even though the opportunity to monopolize safer feeding sites was probably smaller on the single large platforms than on the three small, simultaneously available containers. Finally, we did not find any relation between coloration and risk-taking after controlling for fighting success on the containers, even when we investigated it for each feeder choice in each observation period.

A remaining complication is that the costliness of secondary sexual traits may differ between first-year and adult birds (e.g. Grégoire *et al.* 2004). For example, increased mortality was associated with large bibs only in adult Sparrows in one study (Møller 1989), while another study found that bib-enlargement reduced the survival of yearlings but had an opposing effect on older males (Veiga 1995). Being the first year of study in our Sparrow population, we had no information on the age of the majority of birds, so we could not control for age-effects in our analyses. In the sub-sample of birds with known age, however, first-year and older individuals did not differ either in high-risk feeding or in its relation with colour traits (results not shown). Further investigations should clarify how age-differences affect the costs of Sparrow ornaments.

Taken together, we have found no evidence that House Sparrows with more conspicuous melanin-based and depigmented plumage ornaments respond more strongly to increased predation risk or suffer increased mortality than less ornamented individuals. We propose that mechanisms other than predation costs, such as hormonal regulation of the bib size (Buchanan *et al.* 2001, González *et al.* 2001) and condition-dependent production of the wing-bar (Poston *et al.* 2005), are more plausible ways to maintain the reliability of these colour signals in House Sparrows.

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