Heinz-Ulrich Reyer · Wiltrud Fischer · Pascale Steck
Thomas Nabulon · Philip Kessler

Sex-specific nest defense in house sparrows (*Passer domesticus*) varies with badge size of males

Abstract According to indicator models of sexual selection, females can benefit from choosing males with above average epigamic traits, but empirical evidence for such benefits is scarce. Here, we report results from an experiment with 29 pairs of house sparrows (*Passer domesticus*) where the intensity of nest defense against a mounted mustelid predator was related to the size of the black throat and breast patch ("badge") in males. Using principal components analysis (PCA), original response variables of both sexes were reduced to two factors: "Approach" to the predator and "Distant warning". "Approach", the more risky behavior, increased from small- through medium- to large-badged males and decreased in their females. Since large-badged males have a higher certainty of paternity (i.e. greater benefits from defense) and may be older and more experienced (i.e. incur lower costs), the most likely explanation for male defense intensity increasing with badge size is an improving benefit/cost ratio. The resulting optimal response of their females and evolutionarily stable participation in joint parental care is illustrated by a graphical model. It shows that females would, indeed, benefit directly from choosing large-badged males. This, however, is no proof of a direct evolutionary tie between badge size and paternal behavior, as assumed by indicator models of sexual selection. It may simply represent a spurious relationship, originating from the correlation of badge size and defense with confidence of paternity.

H.-U. Reyer (✉) · P. Steck · T. Nabulon
Zoologisches Institut der Universität Zürich,
Winterthurerstrasse 190, CH-8057 Zürich, Switzerland
Fax: +41-1-635 68 17; e-mail: ulireyer@zool.unizh.ch

W. Fischer
Lehrstuhl für Tierphysiologie, Universität Bayreuth,
Postfach 101 251, D-95440 Bayreuth, Germany

P. Kessler
Anthropologisches Institut der Universität Zürich,
Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

Introduction

In birds, one of the most important direct determinants of fitness is nest predation. In some species, 55% of the eggs and 66% of the nestlings are taken by predators (Ricklefs 1969). Nest defense can reduce loss of young (Andersson et al. 1980; Greig-Smith 1980; Knight and Temple 1986), but is costly for parents in terms of time and energy expenditure (Biermann and Robertson 1983), injury, death and reduced future reproductive success (Curio and Regelmann 1985; Roskaft 1985; Gustafsson and Sutherland 1988; Nur 1988, 1990; Dijkstra et al. 1990). The optimal level of defense in a given situation maximizes the difference between these fitness benefits and costs (Andersson et al. 1980; Curio et al. 1984; Winkler 1987; Montgomerie and Weatherhead 1988; Redondo 1989). Because the cost/benefit ratio varies with size, age, experience and other characteristics of the parent, intensity of nest defense should vary accordingly (Montgomerie and Weatherhead 1988; Redondo 1989; Forbes et al. 1994). Where body condition and paternal qualities correlate with plumage characteristics, song features or other male traits (Grant and Grant 1987; Hill 1990, 1991; Norris 1990) females could use such indicators to "predict" future defense intensity of various potential partners in the population and select high quality mates.

Among the most conspicuous traits (at least from a human perspective) is the black throat and breast patch or stripe that occurs in males of many bird species and often correlates with their social status (reviewed by Butcher and Rohwer 1989). In house sparrows (*Passer domesticus*), males with large badges are dominant over small-badged males in winter flocks (Møller 1987a), are in better physical condition (Veiga 1993; Veiga and Puerta 1996), breed earlier in the season (Møller 1989;

Poznik 1993), achieve more extra-pair copulations (Møller 1987b, 1990), may have advantages in sperm competition due to larger testes (Møller and Erritzoe 1988) and seem to be preferred by females (Møller 1988).

It is unclear, however, what benefits females get from this preference and what costs males incur in producing and maintaining large badges. In terms of indirect benefits, genetic covariance between male trait and female preference, as predicted by "run away" and "good-genes" models (reviewed by Andersson 1994), has not yet been demonstrated for house sparrows and even heritability of the badge size itself is disputed (cf. Møller 1987a, 1989 and Veiga 1993). Direct benefits, the essence of "good parent" models (e.g. Heywood 1989; Hoelzer 1989; Grafen 1990; Schluter and Price 1993), are equally equivocal. The reliability of badges as indicators of male age and experience seems to differ among populations because size increases with age in some (Veiga 1993) but not in other locations (Møller 1988). Badge-related differences in nestling feeding were reported by Møller (1988), but not confirmed by Poznik (1993), and badge-related differences in nest site number and quality did not translate into fitness differences (Møller 1988; Veiga 1993).

With respect to costs – a precondition for preventing the spread of "cheats" – social control through regular male-male interactions seems to be an insufficient safeguard against the invasion of cheats (Johnstone and Norris 1993) and apparently occurs less often than previously assumed (Slotow et al. 1993; see also Veiga 1993 and literature therein). Two recent studies have indicated that production of the badge itself is costly (Veiga and Puerta 1996) and that susceptibility to infections increases with badge size (Møller et al. 1996), but the precise relationship between badge size and health costs remains obscure. The usually invoked immunodepressive effects of circulating testosterone levels (Grossmann 1985; Folstad and Karter 1992; Wedekind 1992) are an unlikely explanation, because showy plumage in male birds is usually controlled genetically or arises from the lack of oestrogen rather than from the presence of testosterone (Owens and Short 1995).

Thus, the adaptive significance of badge size variation in male house sparrows and female preference for large badged males remains unclear. In this study we present an experiment that addresses two specific questions:

1. Does nest defense of males vary with badge size?
2. If yes, do females benefit from these differences?

Methods

Study area and species

The study area is located on the campus of the University of Zürich-Irchel, where large numbers of sparrows nest under the metal hoods covering the window blinds. The distance between windows restricts adjacent nests to be at least 2 m apart horizontally and 3 m vertically. This allows the assignment of pairs to particular nest sites, even when some birds are not individually

marked or the rings cannot be identified fast enough. Because sparrow pairs in our study area are faithful to their nest sites within and between years (Reyer, H.-U., DelFante, F., Sandor, A., Poznik, C. and Schiegg, K., unpublished work) repeated use of the same pair could be avoided, even for unringed birds, by presenting the predator only once at each nest site. Male nest owners were categorized as small-, medium- or large-badged according to the visually estimated size of their black throat and breast patch. Previous studies have shown that such estimates, relative to other males in the population, correspond well to actual badge size if they are made during the breeding season (Møller 1987a; DelFante 1991). Earlier estimates can be misleading since badges increase in size from winter to spring due to the abrasion of light feather tips (Møller and Erritzoe 1992).

Observational and experimental procedures

Potential nest sites were checked for eggs and young twice a week. This yielded information about clutch size and nestling number, as well as about hatching date, nestling age and time from hatching to fledging in classes of 3 days. All experiments were performed in age classes 1–5 (1–15 days); fledging occurred in classes 5–7 (13–21 days).

The experiments were conducted between 7 June and 2 July 1993 (21 nests) and between 16 May and 24 June 1994 (34 nest). In both years, we used mounted mustelids (Mustelidae) in a crouching position as predators, but the two years differed in details. In 1993 a beech marten (*Martes foina*), was put 2 m below the nest on the windowsill with its face in an angle of 90° towards the nest; in 1994 an ermine (*Mustela erminea*) in summer coat was fixed 0.5 m below the nest, facing the entrance.

Prior to each experiment, the nest was observed for some time in order to habituate the parents to the observer and to ascertain that they were still feeding young. Depending on the frequency of nest visits during this time, the pre-experimental observation period lasted 30–120 min. Once, the predator had been fixed close to the nest during a break of parental feeding, two people, one observing the male, the other the female, started observations from a distance of 10–30 m and recorded the following response variables:

1. *Latency* time (min) between the predator becoming visible and the first appearance of a nest owner.

Thereafter, we noted every 15 s for a period of 20 min the following four variables:

2. *Attacks* number of all direct flights towards the predator to within a distance of 30–200 cm before changing direction.
3. *Alarm call* occurrence (yes or no) of warning calls within each 15-s interval.
4. *Distance* (m) between a perching bird and the predator during each 15-s interval, estimated in three categories of 0–2, 2–5 and >5 m.
5. *Out of sight* 15-s intervals in which the bird could neither be seen nor heard. Data for variables 3–5 were later converted into minutes by multiplying the length (15 s) with the number of intervals in which the event occurred.

Statistical procedures

Statistical analyses were performed only with response variables 2–4. Latency (1) was excluded because parents usually encountered the predator accidentally when returning to the nest with food. In such a situation, the time until the first approach is more influenced by the foraging pattern than by nest defense. Out of sight (5) was not considered because its duration results directly from the total observation time minus the summed time spent in the three distance categories. With the remaining variables we first performed a principal components analysis (PCA) with subsequent varimax rotation to reduce potentially correlating responses to a smaller number of independent factors (Sokal and Rohlf 1969). Since correlation coefficients between frequencies of any two response

variables – which form the basis for PCAs – did not differ between males and females ($P \geq 0.129$, $t_s \leq 1.522$; test of homogeneity; Sokal and Rohlf 1969) we pooled data from both sexes for the PCA. We ln-transformed all variables to achieve a better approximation of the required normal distribution, extracted only factors with eigenvalues ≥ 1 (Kaiser criterion, Bauer 1986) and used factor loadings of $\geq |0.55|$ for interpreting the factors (Aspey and Blankenship 1977). The individuals' scores on the resulting two factors were then related to three categorical variables (year, badge size and sex) and four covariables (number and age of young, day of the year and distance between nest and observer) by using multivariate and univariate analyses of variance. Pairwise comparisons were performed using Tukey's method, one of the most powerful unplanned multiple comparison procedures (Day and Quinn 1989). All statistical tests were done with SYSTAT 6.0.1., except for power analyses which were performed according to Cohen (1988).

Results

General observations and conditions

When they detected the predator, usually while flying towards the nest with food, parents changed direction, often at the very last moment, and landed on the windowsill or in a nearby bush. There they moved back and forth, while almost continuously flicking their tails, frequently wiping their beaks and often uttering alarm calls. Occasionally, they approached the predator in direct flight (attack), returned to the same or another perch, and continued their restless behavior and calling until the next approach.

While the predator was visible, parents did not feed their young. In order to keep the time without food provisioning short, the predator was removed no later than 30 min after exposing it, even when – due to latencies longer than 10 min – the 20-min observation period was not yet over. For the actual data analysis we only used experiments in which birds of both sexes had arrived and at least one had been present for more than 10 min. This criterion left us with data from 29 nests, 11 of the 21 observed in 1993 and 18 of the 34 watched in 1994. Average observation time at the 29 nests was 19.6 min (± 1.4 SD). Five of the nests belonged to small-, 13 to medium- and 11 to large-badged males. Mean clutch size ($\pm$ SD) for the 29 nests was 4.30 (± 0.82). At the time of the experiments, average values were 2.76 (± 0.83) for absolute nestling number, 0.66 (± 0.22) for number relative to clutch size, 3.07 (± 1.16) for age class and 0.54 (± 0.20) for nestling age relative to age at fledging. There was no significant difference between nests of small-, medium- and large-badged males in any of these five brood parameters (ANOVAs, all $P > 0.14$). However, the power of detecting significant differences in brood parameters with our sample sizes ranged between only 0.10 and 0.27.

Determinants of brood defense

Values of the recorded response variables varied widely among nests. The lowest values were 0 for all five vari-

ables; the highest values were 9 attacks on the predator, 20 min with warning, and 7.5, 10.5 and 20 min, respectively, spent at distances of 0–2, 2–5 and >5 m from the predator.

A principal components analysis (PCA), based on the responses of all males and females from the 29 pairs, reduced the five original variables to two independent factors, explaining 65.4% of the total variance (Table 1). The first factor was called "approach", because it includes attacks on the predator and perching distances between 0 and 5 m from it. The second factor was called "Distant warning", because it is characterized by alarm calls given at distances of >5 m from the predator.

Scores for approach and distant warning factors (dependent variables) were then subjected to a multivariate analysis of variance (MANOVA). We tested simultaneously for the effects of seven independent variables, consisting of four covariates (observer distance, day of the season, number of young and age of young) and three categories (year, badge size and sex) plus their two- and three-way interactions.

Most of the independent variables produced no significant differences in the parental response to the predator (Table 2a). Approach and distant warning did not differ between badge sizes, years (i.e. predator types), day of the season, distance of the observers, or the number and age of nestlings. The same lack of effects was found when relative rather than absolute values for nestling number and age were used.

However, the way nest defense was partitioned between male and female of a pair differed, as indicated by significant sex ($P = 0.027$) and badge × sex terms ($P = 0.006$) in Table 2a. Averaged over all three badge sizes females scored higher approach ($P = 0.059$) and lower distant warning scores ($P = 0.051$) than males (Table 2b, Fig. 1). When results were broken down by badge size, scores for approach to the predator by parents increased from small through medium to large badges in males, but decreased in their females ($P = 0.010$; Table 2b, Fig. 1a). Distant warning also tended to run in opposite directions in the two sexes ($P = 0.064$;

Table 1 Results from a principal components analyses (PCA), reducing five original response variables to two principal components (PCs). Numbers in the body of the table are factor loadings, i.e. correlations of the original variables with the two PCs. The PCs are named "approach" and "distant warning" after the response variables correlating with them. Relevant loadings (i.e. those $\geq |0.550|$; see Methods) are printed in **bold**

Response variables	PCs:	
	Approach	Distant warning
Distance 0–2 m	**0.809**	−0.024
Distance 2–5 m	**0.767**	0.283
Attacks	**0.641**	−0.190
Distance >5 m	−0.008	**0.832**
Alarm calls	−0.002	**0.898**
Eigenvalue	1.653	1.616
Explained variance (%)	33.1	32.3

Table 2 Summaries of **a** multivariate and **b** univariate analyses of variance with the two defense responses (approach and distant warning) extracted by the PCA from Table 1. Variables with $P \leq 0.05$ are shown in **bold**, those with $P \leq 0.10$ in *italic*. Note that for the two univariate analyses in **b** significance levels are ≤ 0.025, due to the necessary Bonferroni correction (*df* degrees of freedom, *MS* mean squares)

| Source of variation	**a** MANOVA			**b** Univariate ANOVAs						
	Wilks' λ	F	P		Approach			Distant warning		
				df	MS	F	P	MS	F	P
Number of young	0.988	0.244	0.784	1	0.317	0.341	0.562	0.132	0.144	0.706
Age of young	0.914	1.968	0.152	1	1.675	1.799	0.187	1.912	2.093	0.155
Day of season	0.992	0.161	0.852	1	0.036	0.039	0.845	0.271	0.297	0.588
Observer distance	0.975	0.528	0.593	1	0.092	0.098	0.755	0.916	1.003	0.322
Year	0.932	1.554	0.223	1	0.421	0.452	0.505	2.559	2.802	0.101
Badge size	0.945	0.601	0.663	2	0.884	0.949	0.395	0.295	0.323	0.726
Sex	**0.842**	**3.928**	**0.027**	1	*3.499*	*3.758*	*0.059*	*3.665*	*4.013*	*0.051*
Year × Badge	0.979	0.222	0.925	2	0.315	0.338	0.715	0.121	0.133	0.876
Year × Sex	0.957	0.943	0.397	1	0.500	0.537	0.468	1.219	1.335	0.254
Badge × Sex	**0.710**	**3.928**	**0.006**	2	**4.806**	**5.162**	**0.010**	*2.674*	*2.928*	*0.064*
Year × Badge × Sex	0.936	0.711	0.587	2	0.102	0.109	0.897	1.229	1.346	0.271
Error				43	0.931			0.913		
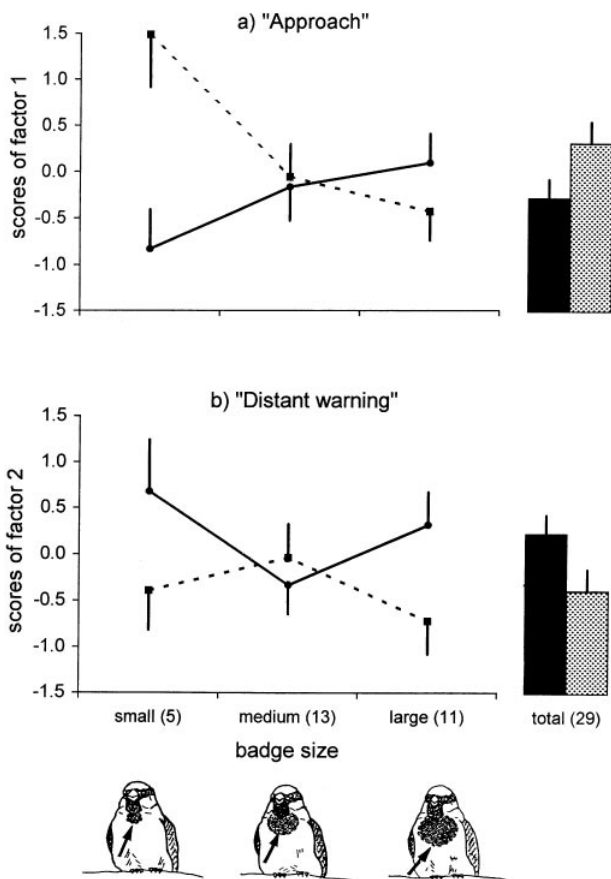
Fig. 1a,b Intensity of brood defense against a mounted predator in relation to sex (*bars*) and badge size × sex interactions (*lines*). **a** "Approach" to the predator, **b** "Distant warning". *Solid lines* and *black bars* are for males, *broken lines* and *stippled bars* for females. Adjusted least square means and 1 SE for factor scores derived from the PCA of Table 1 are shown. Sample sizes are given in parentheses

Table 2b, Fig. 1b). After Bonferroni correction of the critical *P*-value from 0.05 to 0.25 in the two univariate ANOVAs (Table 2b) only the badge × sex interaction for approaches remained significant. Pairwise comparisons show that small-badged males take a significantly smaller share in risk, nest defense than their females ($P = 0.028$) and score lower on approach than large-badged males ($P = 0.090$), whereas females of small-badged males approach more often than those of large-badged males ($P = 0.047$; Tukey multiple comparisons).

Taken together, our results show that the overall nest defense of house sparrow pairs does not vary with badge size, but the relative contribution of males to risky approaches increases from small- through medium- to large-badged males, while that of their females decreases accordingly.

Discussion

General determinants of nest defense

The costs and benefits, and hence optimal intensity of nest defense, can vary with characteristics of the nest (crypsis, accessibility), the predator (mobility, armament), the young (number, age, quality, vulnerability) and the parents (renesting potential, experience, sex) (reviewed by Montgomerie and Weatherhead 1988; Redondo 1989).

In our study, characteristics of the nest and the predator were not found to affect defense. All nests were of the same type, disturbance by the observer (distance) could be ignored and the two mustelids (year) probably represented similar threats. Contrary to theoretical predictions and results from other empirical studies (Regelmann and Curio 1983 Montgomerie and Weatherhead 1988; Redondo 1989), nestling characteristics

(age, number) were not found to influence defense. Potential explanations for this discrepancy include the fact that we pooled parents with different reproductive potential and that the reproductive value of a brood, normally increasing with size and age, was confounded by nestling quality, vulnerability to thermal conditions and other factors that we did not quantify (for a review see Montgomerie and Weatherhead 1988). Only parental characteristics significantly affected brood defense. Overall, females engaged more in the high-risk "approach" behavior, while males performed more low risk "distant warning" (sex effect). With increasing badge size, however, the proportion of approaches shifted from predominantly female to about equal shares or even a higher contribution by males (badge × sex).

Sex-specific differences in defense

Sex differences in defense intensity have also been found in other studies, but usually with the reverse result, i.e. males risking more than females (see Regelmann and Curio 1986 and literature therein). Explanations include sex-specific differences in (1) ability to raise the brood alone, (2) renesting potential, (3) mortality, (4) perception of risk, (5) value of vital resources and (6) confidence of paternity (Montgomerie and Weatherhead 1988; Redondo 1989; Westneat and Sherman 1993; Westneat and Sargent 1996). Most of these explanations cannot be applied to our results. The ability to raise the brood alone (1) is unlikely to differ among females and males, because after hatching the sexes play an equal role in brooding and food provisioning (Summers-Smith 1988). Renesting potential (2) was not found to be important, as indicated by the lack of a seasonal effect (day). Also, it is unlikely to differ markedly between males and females, because the sex ratio in our population is equal (1.06:1; DelFante 1991). The balanced ratio further indicates that mortality (3) is similar for both sexes. Perception risk (4) is likely to be age- rather than sex-specific. In terms of vital resources (5), retaining a mate and/or a nest is more valuable for males than for females and more valuable for subdominant small- than for dominant large-badged males,

because the latter stand a higher chance of outcompeting the former. Female quality in terms of clutch size production, a further potential resource difference for males, did not differ between badge sizes. Consequently, defense of vital resources would predict either no differences in parental responses to predators or even the reverse of what we found, namely higher male than female investment and a decrease in male defense with badge size.

Brood defense in relation to confidence of paternity

The only explanation compatible with our results lies in the sex-specific confidence of paternity (6). Extra-pair maternity (EPM) has not yet been demonstrated in house sparrows and seems to be rare in most bird species (Petrie and Møller 1991; Hartley et al. 1993; Reyer 1994; Reyer et al. 1997). Extra-pair paternity (EPP), however, is widespread among birds (Birkhead and Møller 1992). In house sparrows, it can occur in as many as 27% of the broods and 14% of the young (Wetton and Parkin 1991). Consequently, a female can be assumed to be the parent of all the young in the nest, but males cannot. Hence the overall higher risk taking of females (sex). Since large-badged males seem to be less affected by EPP than small-badged males, owing to their larger testes and more frequent copulations (Møller and Erritzoe 1988; Møller 1990), certainty of paternity and, hence, benefits from brood defense probably increases with badge size. In contrasts, the risks of a given defense level in terms of life-time re-

Fig. 2a,b Optimal nest defense of males (*solid lines*) and females (*broken lines*) in relation to the contribution of the other sex. *Parallel lines* represent three different benefit/cost ratios which correspond to badge sizes small (*s*), medium (*m*) and large (*l*). In both graphs a badge-size-related change in the contribution of one "acting" sex (*arrows*) is indicated by *three parallel lines*. The resulting opposing change in the contribution of the other sex is indicated by the intersection point moving along the single line. In **a** – the more likely case – the increase in male defense in the direction *s-m-l* leads to a decrease in female defense, while in **b** decreasing female defense in the direction *s-m-l* leads to increased male defense (modified from Houston and Davies 1985)
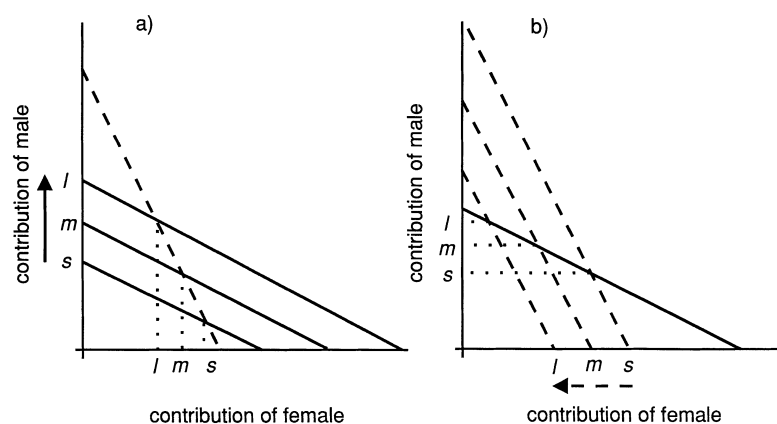
productive success can be assumed to decrease with badge size because males with large and medium badges often, but not always, are older (i.e. more experienced), healthier and/or in better condition than males with small badges (Møller 1988; Veiga 1993; Veiga and Puerta 1996; Møller et al. 1996). As a result, the benefit/cost ratio of defense increases with badge size, and so does the optimal contribution of the male (cf. model by Westneat and Sherman 1993). This is illustrated in Fig. 2a by the set of three parallel lines.

Optimal partitioning of parental care

According to models of joint parental care and sexual conflict an increase in male effort will lead to a decrease in the optimal female effort, provided the total defense of the pair exceeds some threshold level that guarantees survival of the young (Chase 1980; Houston and Davies 1985; Winkler 1987; see also reviews by Clutton-Brock 1991 and Westneat and Sargent 1996). The fact that the summed defense by males and females was similar for all badge classes suggests that this threshold condition was fulfilled in our experiments. As long as this threshold is higher than what a single parent could provide, the evolutionarily stable strategy (ESS) will be one of joint defense, rather than one parent investing nothing and the other defending alone.

The converse scenario, that males respond with an increase to a reduced defense of their females (Fig. 2b), seems less likely, because we see no reason why the females' benefit/cost ratio (and, thus, contribution) should decrease with increasing badge size, i.e. with increasing attractiveness and quality of their males. If anything, there is usually a positive correlation between male attractiveness and relative female effort (Burley 1988; DeLope and Møller 1993). This has been explained through the higher quality of and fitness benefits from offspring sired by attractive males.

No matter which sex is acting and which is reacting, females will benefit from the higher investment of large-badged males, because they can reduce their own effort and risk without decreasing the overall amount of defense. Where badge size increases with age, especially between year one and two (Veiga 1993), and with condition (Veiga and Puerta 1996; Møller et al. 1996) the plumage pattern could theoretically be used by females as an honest early indicator of subsequent paternal investment, as it is assumed by the good parent process of sexual selection (Heywood 1989; Hoelzer 1989; Grafen 1990; Schluter and Price 1993). However, as long as no badge size effect on absolute defense levels is found and age and condition effects on badge size remain equivocal and poorly understood (see Introduction), such a direct evolutionary tie between badge size and paternal behavior cannot be demonstrated. The relationship may simply represent a spurious tie, originating from the correlation of both, badge size and defense, with confidence of paternity.

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