

## Badge size in collared flycatchers predicts outcome of male competition over territories

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**Abstract.** The evolution of conspicuous coloration is often hypothesized to be driven by sexual selection, where colour traits may function as honest signals of individual abilities in male contest competition and female choice. However, game theory models suggest that colourful badges (i.e. energetically cheap signals) may have no function in sexually selected contests, because the value of the contested resource is too high relative to the costs of fighting. We investigated this assertion by experimentally staging male contests over nest sites (a crucial resource for attracting females) in old ( $\geq 2$  years) male collared flycatchers, *Ficedula albicollis*. Males with a relatively large white forehead patch (i.e. a condition-dependent plumage trait displayed in male contests) enjoyed a competitive advantage in disputes over experimentally vacated territories. No other measured morphological variable predicted the outcome of such a dispute. Furthermore, the winners of the disputes acquired a female more quickly than did the losers. Thus, our results suggest that the white forehead patch of male collared flycatchers may function as a badge of status that is also used in sexually selected contests over resources. We suggest that this is because the value of the contested territory may be relatively low compared with the cost of fighting when alternative vacant sites exist in the neighbourhood.

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Bright coloration has been suggested to evolve through predation (Baker & Parker 1979), intraspecific competition for resources (Rohwer 1975, 1982), sexual selection (Darwin 1871) or reinforcement in sympatric speciation (Moynihan 1960). In many species, males are more conspicuous or distinctively coloured than females suggesting that sexual selection may be an important selective mechanism promoting bright coloration. Also, several studies have shown that females prefer males with larger or more intensively coloured traits while the effect of male contest competition for access to females has been given less attention (for a review see Andersson 1994). The function of conspicuous coloration in contest competition has mainly been studied in competition for resources during the non-breeding season,

where it is suggested to signal social status (the status signalling hypothesis; Rohwer 1975, 1982; Whitfield 1987). However, status signalling may be equally applicable in sexually selected contests (Butcher & Rohwer 1989; Andersson 1994).

In birds, the most common mating system is based on resource defence where males compete for resources that are necessary for attracting females, such as nesting sites or territories. Competition for the best resources may be severe and a male's competitive ability in situations of contests will therefore affect his mating success. Signalling fighting ability may be advantageous for both contestants since costly fights with a predictable outcome are avoided (Maynard Smith 1982), and it is often assumed that coloration may function as a reliable signal of male abilities in contests. However, many conspicuous colour traits are probably energetically cheap to produce (Butcher & Rohwer 1989; but see Hill 1991), and theoretical models suggest that such badges of status (i.e. energetically cheap signals) have no value when the value of a contested resource is high relative to

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the costs of fighting (Maynard Smith & Harper 1988). Therefore, it has been suggested that badges of fighting ability have no function in male contests over territories (Maynard Smith & Harper 1988; Wilson 1992; Johnstone & Norris 1993). Thus, the function of badges in male contest competition for access to mates could be questioned.

Here we investigate whether the size of the white forehead patch (a trait that is displayed in male contests), among other morphological traits, predicts the outcome of territorial contests between male collared flycatchers, *Ficedula albicollis*, by experimentally staging male-male interactions during the phase of territory establishment. We also investigate whether the outcome of these territorial disputes is associated with a mating advantage and with reproductive success.

### The Collared Flycatcher

The collared flycatcher is a sexually dichromatic migratory passerine bird species breeding in central and eastern Europe and wintering in southern Africa. Males arrive at the breeding grounds a few days before the females and immediately start to defend a nest hole. They quickly develop site-dominance and have never been observed to be expelled from their territories by intruders after one or a few days' ownership (Pärt 1994). Previous data suggest that the quality of the nest hole and its surroundings influence male mating and reproductive success (Pärt 1994). The male is mainly black on the upper parts with a prominent white forehead patch and nape and a whitish rump, while the female is greyish-brown on the upper parts. Furthermore, males have a larger white wing patch (on the inner part of the primaries) and more white on the greater coverts and tertials than females (Svensson 1992). Males display their white forehead patch (fluffing the feathers on the forehead) in disputes over territories until one bird retreats or starts to fight (Cramp & Perrins 1993). Recent results show that the size of the patch is positively related to the male's physiological condition (see Gustafsson et al. 1995) suggesting that it may function as an honest badge of fighting ability.

### METHODS

In 1989 and 1990 we performed a translocation experiment, originally conducted to investigate

age- and sex-differences in site fidelity (Pärt 1995), in several nestbox plots situated in a 33 km<sup>2</sup> study area on the southern part of the island of Gotland (57°10'N, 18°20'E), Sweden. Each day, from early May to early June, we thoroughly searched all plots for newly arrived males and females, established unpaired males and established breeding pairs. The first day an individual was observed was assumed to be the date of arrival. Of all birds arriving on one particular day we randomly captured a number in their nestboxes, held them in captivity in darkness in small cages for 1–4 h and then released them either in the plot of capture (within 200 m from the nestbox of capture) or translocated to another plot (1.5–6 km away). We randomly assigned combinations of colour rings for individual identification in the field (for further details of experimental procedures, see Pärt 1995).

Male collared flycatchers mainly defend nest holes (i.e. a territory) against other males and announce their presence by song. Within the study plots competition for vacant nestboxes was intense on some days, and on several occasions nestboxes of experimentally detained males were seen to be occupied and defended by new singing males within 1 h (in 30% of the cases a new male was observed singing on the territory a few hours after it was vacated). Our experiment therefore created a situation where two males (the detained original owner and the new owner) probably had similar intentions of establishing ownership of a specific territory. That is, males involved in the experiment had probably not been able to develop any strong site-dominance.

We classified an old owner as regaining his territory when a new male had been observed singing on this territory before he had returned and settled on it ( $N=10$  males). Similarly, we classified a returning male (i.e. observed in the plot of capture) as evicted if a new male was seen singing and defending nestboxes on his original territory on the same day (or before) he was observed in a new territory ( $N=21$  cases). Two facts suggest that the detained evicted males had at least tried to regain their old territory. First, return rate to the original territory was much lower when a detained male's original territory was occupied by a new male before he had returned (32%,  $N=31$ ) than when no new male was seen on his old territory (69% of  $N=42$ ;  $\chi^2_1=9.7$ ,  $P<0.01$ ). Second, we observed 15 cases of

**Table I.** Morphological characteristics of old ( $\geq 2$  years old) detained collared flycatcher males that regained their old territory from an intruder and males that failed to regain their old territory and shifted to another in the neighbourhood (i.e. within 150 m)

	Regained			Evicted			$t/U$	$P$
	$N$	$\bar{X}$	SE	$N$	$\bar{X}$	SE		
Tarsus length (mm)	10	19.70	0.01	21	19.33	0.14	1.62	NS
Wing length (mm)	10	82.55	0.46	21	81.88	0.26	1.32	NS
Tail length (mm)	10	50.95	0.58	21	50.45	0.23	0.95	NS
Forehead patch (mm <sup>2</sup> )	10	88.88	2.80	20	80.90	2.78	1.79	<0.1
Wing patch (mm <sup>2</sup> )	8	50.12	2.25	18	49.33	1.51	0.29	NS
Percentage grey	8	0.62	0.62	20	0.40	0.26	75.5	NS
Body weight (g)	8	12.51	0.20	18	12.68	0.16	0.63	NS

$P$ -values refer to Student's  $t$ -test, two-tailed, except for percentage grey where  $P$ -values refer to a Mann-Whitney  $U$ -test.

fight between the new owner and another male (mainly unidentified) after the detained previous owner had been released (either the same day or the day after). Because of the difficulties of observing rings of birds fighting in dense vegetation, we were able to identify returned colour-ringed males in only three cases and unidentified experimental males (i.e. colour ringed) in only four cases in such fights.

One of the males that regained his old territory ( $N=10$ ), and three of the males that were evicted ( $N=21$ ) had only been detained while all other males had also been translocated. Thus, whether a male had only been detained or whether he had been translocated did not affect his probability of regaining his original territory (Fisher's exact test:  $P=0.62$ ). All evicted males in the matched-pair comparison (see below) had been translocated.

We measured experimentally detained males when we caught them on the day of arrival and when they were feeding young. New males that had moved into territories of the detained males were caught and measured when they were feeding nestlings (for details see Pärt & Gustafsson 1989). All birds were ringed, and we measured wing length, tail length, tarsus length, area of the white forehead patch, area of the white wing patch and body weight. We estimated percentage of grey on the back by eye (in categories of 10%). The white patch on the forehead is roughly rectangular in shape, and we estimated its area by multiplying width and height (measured to nearest mm). We estimated the area of the wing patch as the sum of the length of white on the inner parts of the outer

web of the first eight primaries (measured from the tips of primary coverts). Since the outer webs of the primaries are of equal width this gives a good estimate of the area of white. Data on reproductive performance of all breeding pairs were collected using standard procedures (see Pärt & Gustafsson 1989).

Because plumage traits often vary with age, any test of status signalling should be restricted to individuals of the same age-class (Whitfield 1987). The size of the white forehead patch as well as other plumage traits of male collared flycatchers differ between 1-year-old and older birds (Svensson 1992; A. Qvarnström, unpublished data). Since the sample size of returning yearlings was too small for statistical testing (see Pärt 1995), we only analysed contests between males 2 or more years old. Sample sizes may vary between different tests because of missing values (some birds were not measured and we failed to catch some of the new males). We used non-parametric tests whenever the assumptions of parametric tests were not met, and all probabilities are two-tailed.

## RESULTS

Among detained old ( $\geq 2$  years) males whose original territory (defined as defended nestboxes at arrival) had been taken over by a new male during the detention, we compared males that regained their old territory with those that were evicted (Table I). Males that regained their old territory tended to have larger forehead patches

**Table II.** A comparison of morphological characteristics of old ( $\geq 2$  years old) male collared flycatchers that failed to re-occupy their territory after being detained and the new owner of their territory

	<i>N</i>	Evicted		New		<i>t</i>	<i>P</i>
		$\bar{X}$	SE	$\bar{X}$	SE		
Tarsus length (mm)	14	19.46	0.17	19.56	0.11	0.49	NS
Wing length (mm)	14	81.93	0.32	82.61	0.40	1.19	NS
Tail length (mm)	14	50.68	0.32	51.89	0.52	1.72	NS
Forehead patch (mm <sup>2</sup> )	13	76.08	3.15	91.86	3.95	3.23	<0.01
Wing patch (mm <sup>2</sup> )	13	46.00	2.88	48.71	3.69	0.51	NS
Percentage grey	12	0.08	0.08	0.77	0.52	1.29	NS
Body weight (g)	13	12.95	0.15	12.93	0.19	0.32	NS

*P*-values refer to a two-tailed paired *t*-test.

**Table III.** Reproductive performance of old ( $\geq 2$  years old) male collared flycatchers that failed to re-occupy their territory after being detained and the new owner of their territory

	<i>N</i>	Evicted		New		<i>t</i>	<i>P</i>
		$\bar{X}$	SE	$\bar{X}$	SE		
Speed of pairing	13	2.08	0.50	0.77	0.32	2.85	<0.01
Date of egg laying	12	19.58	1.54	17.68	1.28	1.69	NS
Clutch size	12	6.25	0.22	6.58	0.19	1.17	NS
No. fledged	12	4.42	0.62	5.42	0.58	2.01	<0.1
No. recruited	12	0.33	0.19	0.33	0.24	0.00	NS

Speed of pairing is defined as the number of days elapsing between the date of pairing and the first day both males were observed singing and defending a territory. Date of egg laying: 1 = 1 May. *P*-values refer to a two-tailed paired *t*-test.

than those failing to do so, while no other morphological trait differed between these two groups of males (Table I). All evicted males established a territory close by, often within 150 m of their original territory.

However, it is not the absolute but the relative size of a display trait that is expected to be important in male contests. We therefore made a matched-pair comparison of morphological traits between the new owner and the previous owner failing to re-occupy his old territory. New owners had significantly larger forehead patches than evicted owners, while no other measured morphological trait differed significantly (Table II).

New owners also acquired a female earlier and tended to produce more fledglings than evicted owners (Table III). The difference in speed of acquiring a female did not arise because new owners acquired a female when the previous owner was detained, since all involved males

acquired a female at the earliest on the day after the evicted owner had occupied a new territory. Date of egg laying, clutch size and number of local recruits produced did not differ between the two groups of males (Table III). We could not perform the same matched-pair analyses for detained males that regained their original territories and their evicted combatants since the latter were not identified (see Methods).

One could argue that males with smaller forehead patches suffered more from detention and translocation than males with larger patches and therefore males with small patches were more likely to lose their territorial disputes. However, weight loss during detention increased with increasing forehead patch size of males (partial regression coefficient =  $0.01 \pm 0.003$  SE,  $N=22$ ,  $t_1=3.18$ ,  $P<0.01$ , when controlling for time of detention). Furthermore, forehead patch size was not related to return rate to the plot of capture of translocated males ( $\bar{X} \pm \text{SE} = 83.2 \pm 1.6$  mm<sup>2</sup> and

$82.4 \pm 4.0 \text{ mm}^2$  for returned and not returned, respectively;  $t_{72} = 0.19$ , NS).

## DISCUSSION

### Is Patch Size a Badge of Fighting Ability?

In the context of male contest competition, conspicuous coloration has been hypothesized to signal (1) the presence of a resource owner, especially in territorial species exhibiting strong site-dominance (Peek 1972; Rohwer 1982), or (2) fighting ability (Andersson 1982; Rohwer 1982). Although male collared flycatchers develop a strong site-dominance (Pärt 1994), the fact that males with relatively large forehead patches enjoyed a competitive advantage in disputes over territories cannot be explained by the ownership hypothesis alone. This is because the ownership hypothesis can explain only the occurrence, not the variation, in conspicuous coloration. Furthermore, ownership is probably more efficiently signalled by male song (cf. Lundberg & Alatalo 1992) than by variation in size of the white patch. Since the size of the white forehead patch seems to be a condition-dependent trait sensitive to past reproductive effort and to male rearing environment (Gustafsson et al. 1995), the most likely reason why male forehead patch size predicts the outcome of male–male interactions is that it reflects male fighting ability.

For a trait to be an honest signal of fighting ability it has to be associated with a cost (Maynard Smith & Harper 1988; Grafen 1990). However, the white forehead patch, like many other badges in birds, is probably energetically cheap to produce (Rohwer 1982; Butcher & Rohwer 1989; but see Hill 1991); in fact, the cost of producing an extra few square millimetres of white patch is likely to be negligible. Also, it seems unlikely that variation in the size of the patch could be associated with variation in predation risk. Hence, the honesty of this signal presumably has to be controlled by something other than predation or an energetic cost of producing it. High social costs (e.g. repeated punishment) and a trade-off between aggressive behaviour and metabolic rate and immune defence are possible such mechanisms that may make colour badges honest signals of fighting ability (Maynard Smith & Harper 1988; Grafen 1990; Owens & Hartley 1991; Johnstone & Norris 1993). Male collared

flycatchers frequently engage in territorial disputes, and escalated fights may cause injuries (personal observations). We therefore suggest that the white forehead patch of the male collared flycatcher may function as an honest badge of fighting ability, where the honesty may be controlled, at least partly, by repeated fights.

### Are Badges of Fighting Ability Used in Contests over Territories?

It has been suggested that signals of fighting ability have only a limited value in territorial breeding systems, because, after territories have been established, a signal of fighting ability will decrease in value as knowledge about the neighbours accumulates (Grafen 1990; for empirical evidence, see Lemel & Wallin 1993). However, at the time of territory establishment the fighting ability of most contestants is probably unknown, provided between-year site-fidelity is low or annual mortality high. Collared flycatcher males have a high annual mortality (50%) and a low between-year site-fidelity (<6%; Pärt & Gustafsson 1989), and therefore most contestants encountered are likely to be unfamiliar.

Furthermore, game theory models suggest that badges of fighting ability have no function when the contested resource is of a high value relative to the costs of fighting (e.g. Maynard Smith & Harper 1988). Therefore, it has been suggested that badges of fighting ability are not used in sexually selected contests over valuable resources, such as territories and nesting sites (Maynard Smith & Harper 1988; Wilson 1992). A territory is obviously a valuable resource for males since it is a prerequisite for attracting a female, and in many species individuals value their resource increasingly with their time of ownership (i.e. site dominance; Krebs 1982; Beletsky & Orians 1989). However, when males sample and assess territories, the value of a certain territory is probably relatively low because alternative sites exist and no site-dominance has yet developed. Although site-dominance may develop after 1 day of ownership in the collared flycatcher (Pärt 1994), our experimental results suggest that, on the day of arrival, differences in male abilities (as signalled by the size of the forehead patch) may be more important for the outcome of contests over territories than differences in motivation (e.g. because of site-dominance). We therefore



conclude that the above mentioned assertions may not be true during the phase of territory establishment and that badges of fighting ability may function in sexually selected contests.

Previous studies have shown that conspicuous coloration that is used in contest competition during the non-breeding season is also correlated with mate attraction during the breeding season (Maynard Smith & Harper 1988; Møller 1988). Other studies have investigated the role of conspicuous coloration in male contest competition during the breeding season, but after territory establishment, that is when site-dominance may have developed (e.g. Studd & Robertson 1985; Evans & Hatchwell 1992). Only a few studies have explicitly investigated the function of badges when males sample and assess territories, but these studies suggest colour traits have no function in male contests (Götmark 1993; see also Lundberg & Alatalo 1992; Huhta & Alatalo 1993 for possible cases). Some studies have shown an association between territory quality and male badge size (Studd & Robertson 1985; Maynard Smith & Harper 1988; Møller 1988), suggesting that badges may be used in the phase of territory establishment. However, as long as the evidence is indirect, such associations may also be due to an earlier arrival at the breeding grounds of dominant individuals (see Møller 1988).

### Is an Advantage in Territorial Disputes linked with a Mating Advantage?

In the collared flycatcher, nest site quality is known to influence male mating success (Pärt 1994; see also Alatalo et al. 1986) and reproductive success (Pärt 1994). Because of the order of occupation and because the males fought over a territory in our experiment, it is likely that the new males with a large forehead patch acquired better sites than did the evicted males with a smaller patch. Therefore, one would expect new males to enjoy a mating advantage over the evicted ones. Also, new males with large forehead patches acquired a female more quickly and tended to produce more fledglings than did the expelled owners (Table III). Male traits that signal male abilities in contest competition may be used as indicators of male quality in female choice as well (e.g. Andersson 1994), and recent evidence suggests females prefer large forehead patches per se as judged from data on extra-pair

fertilizations (Sheldon et al. 1997). Thus, present evidence suggests that the forehead patch size of male collared flycatchers may have a function in both male contest competition and female choice.

### Conclusions

To conclude, our data suggest that badges of fighting ability in birds may be used in contests over apparently valuable resources such as territories. This is because the value (i.e. in relation to existing alternatives) of the contested resource may be low compared with the cost of fighting when alternative sites exist in the neighbourhood. Thus, badges of status, such as the white forehead patch of male collared flycatchers, may have an important function in sexually selected contests.

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