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Determinants of male territorial behavior in a Hungarian collared flycatcher population: plumage traits of residents and challengers

Abstract In intrasexual conflicts, contestants can rely on relative or absolute size of status badges to mediate aggressive behavior. Most studies focus on the response of focal animals to variation in status badges of their competitors; few have simultaneously considered the traits of both participants under experimental conditions. By simulating territorial intrusions, we tested the importance of two sexual traits [forehead patch size (FPS) and wing patch size (WPS)] in territorial behavior of males in a Hungarian population of the collared flycatcher, *Ficedula albicollis*. We presented a stimulus male to an unpaired resident male to examine whether the characteristics of the territory owner or those of the challenger were associated with the latency of the first attack of the owner, which is a good predictor of the territorial behavior in general. WPS of the stimulus male was a significant determinant of the latency of the first attack, as males with a larger WPS elicited quicker attacks from the residents than males with a small WPS. From the residents' perspective, age appeared to influence their territorial behavior, as yearlings had shorter attack latencies than older males. Additionally, latency could be considered an individual-specific attribute because it varied consistently among males, even when the WPS of the stimulus male was controlled, and it was associated with pairing success. Contrary to findings in a Swedish population, FPS seemed to be unimportant in male–male competition in our population, which suggests population differences in the role of the two plumage traits. Our results indicate that in a territorial conflict, the characteristics of both participants are important.

Keywords Aggression · Male–male competition · Personalities · Plumage coloration · Territoriality · Sexual traits

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Introduction

In animal contests, signals of fighting ability are beneficial for both participants, as costly fights with a predictable outcome can be avoided (Maynard-Smith 1982). The probability of winning may be reflected by potential asymmetries between the competing parties (Maynard-Smith and Parker 1976; Reichert 1998). Accordingly, participants assess the degree of these asymmetries to determine the most likely outcome of the fight. For example, in birds, opponents may differ in body size, experience, success in prior encounters, residence-status and motivation, or in the expression of certain traits, and any of these asymmetries may predict the chances of winning by influencing contest results, durations, or the levels of escalations (e.g., Smith 1972; Searcy 1979; Yasukawa 1979b; Krebs 1982; Hansen and Rohwer 1986; Beletsky and Orians 1987; Røskaft and Rohwer 1987; Jakobsson 1988; Radesäter and Jakobsson 1989; Jackson 1991; Pärt and Qvarnström 1997; Tobias 1997; Pryke et al. 2001, 2002; Pryke and Andersson 2003b). Differences between contestants in traits or states that determine the success of the territorial challenge are termed as correlated asymmetries.

The most common avian mating system is based on resource defense, in which males compete for these resources that are necessary for mate attraction (Lack 1968; Møller 1986). In these intrasexual conflicts, male sexual traits may partially be used to assess the quality of competitors (Andersson 1994). For instance, patches of conspicuous feather coloration, so-called badges, may function as reliable signals of male fighting abilities with

larger/brighter patches indicating better fighting ability than smaller/duller patches (Dawkins and Krebs 1978; Butcher and Rohwer 1989). Theoretically, for such a signaling system to evolve, the traits should be costly when the value of the contested resource is high in relation to the cost of fighting (Maynard-Smith and Harper 1988). The reliability of badges is maintained via either production costs due to the metabolic needs of trait expression (Badyaev and Hill 2000), or via maintenance costs due to the social costs of repeated fights (Qvarnström 1997) or due to mechanical costs of plumage abrasion (Kose and Møller 1999).

When judging the chances of winning, contestants may rely on the relative or absolute size of their badges. Correlated asymmetries are always limited to the current conflict, and an individual that has a more elaborated trait than a given opponent may appear less elaborated than another. A typical example is the great tit *Parus major*, in which males possessing a breast stripe wider than that of an experimental dummy opponent approached the dummy more aggressively than males having smaller badges than the experimental bird (Järvi and Bakken 1984). If correlative asymmetries are important only when lower than a difference threshold, an average male contestant may be expected to show similar responses irrespective of his own badge size when challenged by males with extreme badges. Accordingly, in the red-winged blackbirds *Agelaius phoeniceus*, territorial males consistently responded with more aggression toward redwing mounts with the largest epaulettes (Hansen and Rohwer 1986). On the other hand, individuals bearing extremely large or small traits may always be certain about their success independent of the characteristics of the opponents, so they may apply a consistent strategy against all other males. In the red-shouldered widowbirds *Euplectes axillaris*, males with enlarged epaulettes generally changed their territorial behavior and defeated other males (Pryke and Andersson 2003b). Hence, the importance of relative or absolute badge sizes may vary among experimental situations and species. To distinguish between these roles, one needs to consider the expression of traits in both contestants simultaneously.

The relative value of the contested territory is different for the current owner and for the intruder, as the balance between their potential benefits and costs is different (Krebs 1982; Beletsky and Orians 1987; Jakobsson 1988; Shutler and Weatherhead 1991; Tobias 1997). This is also a correlated asymmetry that influences the probability of winning. For example, the threshold limits for starting or finishing a gradually escalating contest may be different for the owner and the challenger, so they may rely on different cues or use different thresholds depending on their status. The relative value of the defended territory is usually higher for the owner than for the challenger due to past investment in occupation and defense, and due to familiarity with the territory and the neighborhood allowing efficient foraging, predator avoidance, and fightless cohabitation with the neighbors (Krebs 1982; Beletsky and Orians 1989). On the contrary, for the challenger male, the value of the desired territory will depend on the availability of other breeding sites. If there are many vacant territories of similar quality nearby, or the male can easily find other territories due to his experience, the value of a certain place will probably be relatively low (Pärt and Qvarnström 1997).

Males of the collared flycatcher *Ficedula albicollis* are very territorial and, hence, are excellent subjects to study the importance of badges in male–male conflicts (Pärt and Qvarnström 1997; Qvarnström 1997; Qvarnström et al. 2000). They are mainly black on the upper parts with prominent white forehead and wing patches, nape, and rump (Svensson 1984). Contesting males display their white patches by fluffing the feathers on the forehead and by flicking the wings (Cramp and Perrins 1993). Studies in a Swedish population showed that the size of the forehead patch (FPS) predicted the outcome of competition over territories (Pärt and Qvarnström 1997). Males with larger forehead patches were more successful in gaining experimentally vacated territories. Additionally, experimentally increased FPS affected the likelihood of territory establishment depending on the original FPS and on age (Qvarnström 1997). However, the wing patch size (WPS) appeared to have minor importance in territoriality at the Scandinavian breeding sites (Pärt and Qvarnström 1997). It is interesting to note that the proximate determination of these plumage traits is different, as FPS is largely age- and condition-dependent (Gustafsson et al. 1995), while WPS expression appears to be independent of condition (Garant et al. 2004). These differences may explain, at least partly, why FPS is the primary signal in male–male competition in the Swedish population.

In this study, we explored the importance of the two white patches during territorial fights in a Hungarian population of the collared flycatcher. We performed simulated territorial challenges by presenting different stimulus males with varying badge sizes in the territory of resident males. We monitored the behavioral response of the residents towards different stimulus males in relation to the absolute and relative sizes of the WPS and FPS of both participants. To our knowledge, few studies have assessed the importance of the relative and absolute expression of several potential traits in sexually selected contests in birds (but see Järvi and Bakken 1984; Pryke et al. 2001), although such situations often involve simultaneous asymmetries. We predicted that if absolute trait values determine the territorial behavior of the resident, only the attributes of one contestant should explain variation in the territorial response elicited. Contrary, if relative relationships are important, we predicted that the role played by the WPS or the FPS of one party should be conditional to the expression of WPS or FPS of the other party. Accordingly, badge size of both the resident and the stimulus males, and also their interaction, should simultaneously forecast the resident's behavior. We also predicted that the role for WPS and FPS in male–male competition might be substantially different in the Hungarian and Swedish populations because the proximate determination

of these traits appears remarkably different in the two breeding sites (Hegyi et al. 2002; Török et al. 2003).

Materials and methods

Study species and field procedures

After migrating from southern African wintering sites, male collared flycatchers arrive at the European breeding grounds before females (Cramp and Perrins 1993). They immediately start to occupy and defend nestboxes or natural cavities, around which they establish small territories where they sing and display to arriving females. The quality of the nest hole and its surroundings influence male mating and reproductive success (Pärt 1994). Males often engage in territorial disputes. Later arriving, poly-territorial or floater birds may either seek unoccupied breeding sites that are quite abundant in artificial nest box plots, or may try to obtain an occupied hole from a resident male. Resident males are highly intolerant of such conspecific rivals and potential nest-hole competitors intruding onto a territory (Cramp and Perrins 1993).

The fieldwork for this study was carried out in a Hungarian breeding population of the collared flycatcher in 2003, 2004, and 2005. The study plot is a part of a continuous, unmanaged, oak-dominated woodland, a strictly protected area of Duna-Ipoly National Park that has been investigated for more than 20 years. From the middle of April, when males start to arrive at the breeding grounds, we daily searched for newly arrived, territory-defending birds, and continuously mapped territory occupation. Due to the intensity of the fieldwork and the standard approaches applied, it was reasonable to assume that newly found males had arrived just before the given date. Hence, the date of the experiment detailed below corresponds to the date of arrival. This procedure was carried out until the majority of birds arrived (middle of May). All males included in this study were unpaired.

If a displaying (i.e., singing or nest box presenting) male was found, we presented it with a live stimulus bird in a small wire cage (15×20 and 15 cm high). Experiments were made during the most active period (usually 0500–1000, but no later than 1200 h), and only in good weather conditions. The time and the date of the experiments were always recorded, so they could later be controlled for statistically (see below).

In 2003 and 2004, by using a digital video camera, we characterized the territorial behavior of 48 resident males towards a stimulus male (see more below) for 20 min, blind to the identity of the stimulus and resident males. To quantify the territory defense behavior of the resident male, we measured the following variables: (1) the time elapsed between the detection of the stimulus male and the first attack (latency of the first attack); (2) the number of attacks during the observation; and (3) the average duration of attacks. Detection was defined as the appearance of the resident male on its territory, while attack was the event when the resident male touched the cage of the stimulus

male, usually showing clear intention to fight. The behavioral variables were chosen based on the observed typical territorial responses of resident males we described in a pilot study, and also on considerations from similar territorial experiments (e.g., Rohwer 1978; Hansen and Rohwer 1983; Eckert and Weatherhead 1987; Slagsvold 1993; Tobias and Seddon 2000; Pryke et al. 2001; Nowicki et al. 2002; Van Duyse et al. 2002; Mays and Hopper 2004). None of the focal birds continued their female attraction displays, and according to our judgment, all of them responded to the presentation of the stimulus male. Five males did not attack the stimulus bird as defined above, although they were obviously aware of the situation (e.g., they frequently approached the stimulus bird). Because the behavior of these males holds biological information, we used them in the analyses. Accordingly, the number and the duration of their attacks were set to zero, while, considering the length of the observations, 1,201 s was used for latency of the first attack (if we excluded these males or used alternative estimates for their latency, the results are similar). The reliability of the average length of time spent attacking could be assessed by repeatability, as within one observation, a male usually attacked more than once. The repeatability was significant ($R=0.48$; $F_{47,806}=10.18$, $P<0.001$), and comparable to that of other behavioral traits, such as a song (e.g., Gil and Slater 2000; Forstmeier et al. 2002; Garamszegi et al. 2004). The significant repeatability of the average duration of attacks indicates that this behavior consistently varied between experimental situations. In the "Results" section, we show a consistent variation for the latency of the first attack within males and between experimental situations, which implies that this variable is also reliable.

Based on the data we gathered in the first 2 years of the study, we found that the latency of the first attack is a good predictor of the territorial behavior in general. Specifically, those males that attacked quickly the stimulus bird after its detection also approached it more frequently (latency—number of attacks: $r=-0.62$, $N=48$, $P<0.001$, $\log_{10}$-transformed data), and spent a longer time with attacking it on average (latency—attack duration: $r=-0.46$, $N=48$, $P=0.001$, $\log_{10}$-transformed data). Therefore, in 2005, for ethical and for practical reasons, we only collected data on the latency of the first attack instead of running the experiment for 20 min to obtain the other behavioral variables. Thereafter, to avoid multiple tests of the same questions on correlated data, we used the latency of the first attack ($\log_{10}$-transformed) to reflect the territorial behavior of the residents in all years. This also allowed us to eliminate the potentially confounding effect of the behavior of the stimulus male under the series of attacks. Altogether, we experimentally challenged 63 resident males in 3 years.

After the simulated territorial intrusion, resident males were trapped and their morphological variables were measured. Based on the typical subadult plumage colora-tion of yearling males (brown remiges), we assigned individuals as yearlings or older birds (Svensson 1984). The size of the forehead patch (FPS), which is the product of its maximum height and width, was measured with a

digital caliper to the nearest 0.1 mm. We also estimated the wing patch size (WPS) as the sum of the lengths of white bars on the outer vanes of the 4th–8th primaries measured from the tip of the coverts. As the widths of the white bars on the 4th–8th primaries are strongly correlating with each other ($0.81 < r < 0.96$, $P < 0.001$), we assume that white bars on these five feathers generally reflect the size of the entire wing patch. Hence, our results are comparable from this aspect with that of other studies, which measured wing patch size based on the 1st–8th primaries (e.g., Pärt and Qvarnström 1997). Because the expression of WPS changes when males molt from yearling to adult plumage (Török et al. 2003), WPS was standardized across age categories by bringing the age classes to a common mean of 0 and standard deviation of 1. To assess body size and body condition, we also took measurements of tarsus length with calipers, and body mass with a Pesola spring balance to the nearest 0.1 g. To calculate body-condition index, we calculated residuals from a linear regression of body mass on tarsus length (when we used an alternative index, such as body mass/tarsus length[3], the results were not affected).

After the morphological measurement, some of the resident males ($N = 29$) were kept in captivity for a while (range including all birds: 0–6 days, mean±SE: 0.54±0.17, $N = 63$) to use them as stimulus birds in subsequent experiments, while others were released. By changing the identity of the stimulus birds, we naturally varied the expression of WPS and FPS of the challengers. Having information on the size of plumage traits for both the stimulus and the resident males allowed us to assess statistically the importance of both absolute and relative badge sizes (see below). To avoid any confounding effect arising from male age (e.g., age-dependent plumage characteristics or behavior), we only used older birds to stimulate others. Young birds were released immediately after measurements. The age of resident males was controlled statistically (see below). Altogether 29 males were used as stimulus birds, from which 16 were used more than once. The number of experiments with the same bird used as stimulus male ranged from 1 to 6 (mean±SE: 2.17±0.25, $N = 29$). Presenting the same stimulus males in at least two replicates of the experiment raises issues of pseudoreplication. We avoided this by controlling for multiple measurements for the same stimulus male in the statistical models, in which random factor levels were assigned to each stimulus male (see "Statistical analyses" section). We conducted multiple intrusion trials for 14 resident males. In these cases, we avoided pseudoreplication removing data for resident males that had been already challenged once; thus by using first measurements only to determine which traits affected the latency of first attacks. However, multiple information for the same residents could be used to test how the same males responded to different stimulus males, i.e., to investigate consistent variation within individuals. To ascertain, as much as possible, that the resident male was unfamiliar with the stimulus males, the latter were presented at least 300 m from the territory they had been caught. After using

males in the experiments as stimulus males, we released them at the location of capture. For identification, all released birds (including yearlings) received individual color markings with water resistant pens on their belly plumage. None of the stimulus birds died in captivity. The majority of them were observed breeding after testing, and returned to breed in the next season.

Altogether, 31 resident males were found later as breeders. We used information on pairing success of these males by estimating relative pairing date, which is the time elapsed between the calendar date of release and the start of egg laying.

Statistical analyses

To test the effect of the characteristics of both the resident and the stimulus males on the territorial behavior of the resident male, we used general linear mixed models implemented in Proc MIXED of SAS 8.01 (SAS Institute 1999). We created a starting model with the latency of first attack as the dependent variable, and with WPS, FPS, tarsus length of both males, and with age and body mass of the resident males as independent variables (fixed effects). We also considered biologically meaningful two-way interactions in this initial statistical model (Table 1). As we were interested in determining the role of relative and absolute trait expressions, we included the interaction between the resident and stimulus WPS, FPS, and tarsus length, respectively. To check for potential age-dependent responses, we added the interaction of each main effect with resident age. We included year as a fixed effect, and standardized date and time of the day (the latter two are $\log_{10}$-transformed) as covariates to avoid any confounding effect arising from the between and within seasonal and daily variation in territorial behavior. By including date in the analyses, we also controlled for the differences in male quality due to arrival date. As we often used the same stimulus male in more than one territorial trial that are, thus, pseudoreplicates, we also added the identity of the stimulus birds as a random factor (see Crowder and Hand 1990; Crawley 1993; Grafen and Hails 2002). The age of the resident male, the identity of the experimental male, and year were treated as categorical variables. Because all stimulus birds were old males, we did not consider age from their perspective. A stepwise analysis based on backward deletion procedure allowed us to simplify the full starting model by removing nonsignificant ($p > 0.05$) effects. We removed nonsignificant effects and interactions, starting with the least significant interactions. The removed terms were reentered to the final model one by one, and their effects are given from this model (Table 1). To calculate the degrees of freedom of the models, we used the Satterthwaite correction. Because 14 males were tested twice as residents, in an independent analysis based on a paired t test, we examined how the same males behaved in different territorial situations.

Multiple measurements on the same males also allowed us to estimate the consistency of the latency of the first

Table 1 Determinants of the latency of the first attack of resident collared flycatcher males against a stimulus male using general linear mixed models with stepwise backward model selection

Effect	F (df^c)	P
$FPS_{stimulus}$	0.01 (1,52)	0.92
$WPS_{stimulus}$	**7.94 (1,53)**	**<0.01**
$Tarsus_{stimulus}$	0.05 (1,52)	0.83
$FPS_{resident}$	1.29 (1, 47)	0.26
$WPS_{resident}^a$	1.72 (1, 47)	0.20
$Tarsus_{resident}$	0.01 (1, 47)	0.92
$Condition_{resident}^b$	0.06 (1, 47)	0.80
$Age_{resident}$	**4.14 (1, 53)**	**<0.05**
Year	0.07 (2, 51)	0.93
Date	0.01 (1, 52)	0.94
Time	2.39 (1, 52)	0.13
$FPS_{stimulus} \times Age_{resident}$	0.86 (1, 51)	0.36
$WPS_{stimulus} \times Age_{resident}$	0.00 (1, 52)	0.98
$Tarsus_{stimulus} \times Age_{resident}$	0.84 (1, 51)	0.37
$FPS_{resident} \times Age_{resident}$	0.47 (1, 46)	0.50
$WPS_{resident}^a \times Age_{resident}$	1.18 (1, 46)	0.28
$Tarsus_{resident} \times Age_{resident}$	1.17 (1, 46)	0.29
$Condition_{resident}^b \times Age_{resident}$	0.36 (1, 46)	0.55
$FPS_{stimulus} \times FPS_{resident}$	0.24 (1, 45)	0.63
$WPS_{stimulus} \times WPS_{resident}^a$	0.01 (1, 46)	0.91
$Tarsus_{stimulus} \times Tarsus_{resident}$	0.32 (1, 45)	0.57

The effect of each nonsignificant term was obtained by adding the given effect to the final model (shown in bold). The identity of the stimulus male was controlled as random effect

[a] Age standardized

[b] Residuals from a linear regression of body mass on tarsus length

[c] Satterthwaite corrected degrees of freedom (effect, error)

attack. To reveal the repeatability of the traits, we used the identity of the resident male as the independent variable. In this approach, we controlled for year, date, and time effects as described above, and considered additional potentially confounding variables based on the result of the previous model. However, the sample size for this model was limited, which constrained the construction of very complex models when testing for repeatability. We also assessed the biological relevance of latency by calculating its association with pairing success in a corresponding general linear mixed model, in which we controlled for the date of release.

The identity of 12 resident males was unknown, as we were unable to capture them after the territorial challenge. However, even without having morphological measurements for these birds, we included information on their territorial behavior in our analyses because the characteristics of the stimulus male were known in the corresponding experiments. In some cases, due to the typical age-dependent plumage coloration, the age of these unknown males could be determined during the experiment, and this information was also taken into account. Hence, data availability was slightly different between variables, which may cause variation in sample size, and the degrees of freedom may differ between models involving variables for the resident male and those with information on the stimulus male only. As we applied color marking, it is highly unlikely that the unidentified birds were later represented in our sample, causing pseudo-replication, so we treated them as independent observations. In any case, when we excluded these unknown males, the results and the conclusions were very similar to those we report below.

Results

We found that the territorial behavior of residents, as reflected by the latency of their first attack was determined by the attributes of both contestants. First, latency was significantly related to the WPS of the stimulus male (Table 1), as stimulus males with a larger WPS elicited a faster aggressive response from the residents than males with a smaller WPS (Fig. 1a). The comparison of the behavior of resident males along successive territorial intrusions supported these results. The same male displayed a shorter latency in the experimental situation, in which it had been challenged with a male that had a larger WPS compared to the other trial (paired t tests: $t_{13}=2.85$, $P=0.01$, Fig. 1b). This result is probably unaffected by date and year effects because the above model showed no significant association with these potentially confounding factors (Table 1). The order of exposure with a large- or small-patched stimulus male varied randomly implying that the observed pattern cannot be due to consistent seasonal effects or habituation. However, we also characterized the difference in latency between trials of the same resident (second–first), in relation to the difference in WPS between the stimulus males (second–first). This relationship was also significant ($r=-0.71$, $N=14$, $P<0.01$), providing no statistical evidence for habituation.

The second significant effect describing variation in the latency of the first attack was the age of the resident male (Table 1). The age effect indicated that yearlings had a shorter latency than older birds (Fig. 2).

Latency of the first attack was not related to the WPS of the territory holder. In addition, neither the FPS of residents, nor that of the stimulus males was a significant predictor of the residents' behavioral response (Table 1). Additionally, no significant interaction term remained in the final model (Table 1).

The latency of the first attack appeared to be an individual specific attribute, as other things being equal, the same male responded similarly in different experimental situations. When we controlled for year, date, and time effects, beside the WPS of the stimulus male, the identity of the resident male explained a significant amount of variation in latency ($WPS_{stimulus}$: $F_{(1,10.6)}=23.0$, $P<0.001$; resident: $F_{(13,10.6)}=4.95$, $P<0.01$, we could not assess the importance of age in this model because there was little variation from this aspect in the available sample). Hence, the behavioral response of a resident male to a territorial challenge is partially determined by its individual-specific characteristics and by the WPS of the stimulus male. Such an individual-specific characteristic
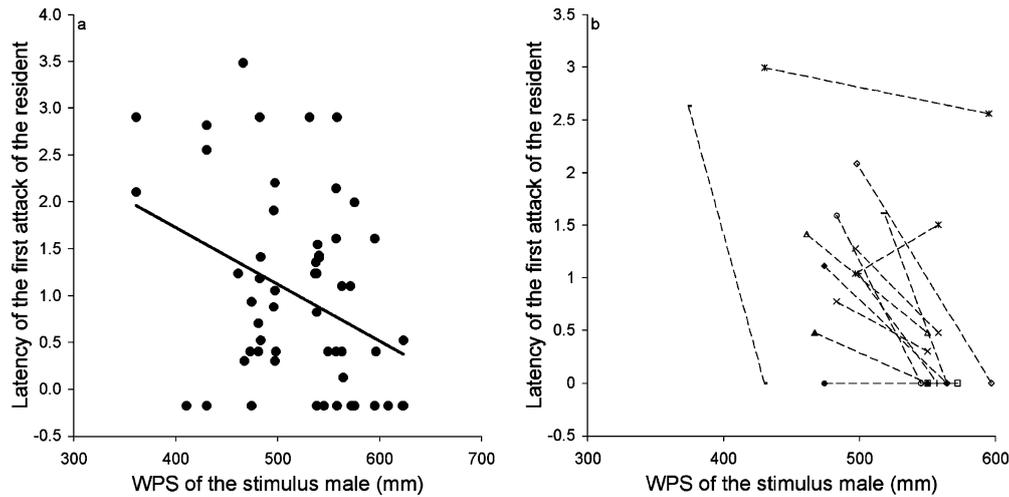
Fig. 1 The relationship between the territorial behavior as reflected by the latency of the first attack of resident collared flycatcher males and the wing patch size (WPS) of the stimulus males in simulated territorial intrusions. **a** The relationship between WPS of stimulus males and $\log_{10}$-transformed latency (in seconds) in 63 resident males. Residuals are shown that are given by the final model in Table 1 (random effects and male age are controlled). **b** The pairwise comparison of the $\log_{10}$-transformed latency of resident males (in seconds) challenged twice with different males with different WPS (N=14)

can be subject to selection and can have an adaptive value. Males that had been observed to attack the stimulus bird quickly, paired significantly later relative to their release after capture than males that had showed a longer latency (latency: $F_{(1,26.7)}$=4.97, P=0.03, Fig. 3; date of release: $F_{(1,20.7)}$=24.77, P<0.001).

Discussion

Although previous studies of status signaling have generally focused on the perspective of one party (e.g., Krebs 1982; Hansen and Rohwer 1986; Røskaft and Rohwer 1987; Pärt and Qvarnström 1997; Pryke and Andersson 2003b), the attributes of both participants may
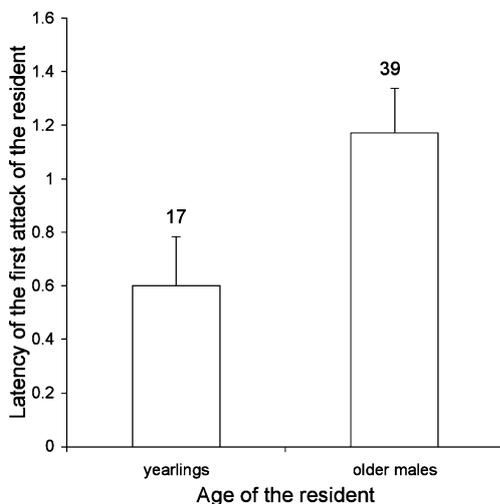

Fig. 2 The age of residents with known identity and the latency of their first attack (in seconds) against the stimulus male, as given by the final model in Table 1 (random effects and WPS$_{stimulus}$ are controlled). Sample sizes and standard errors are given. Data are $\log_{10}$-transformed

be important in a territorial dispute (Järvi and Bakken 1984; Pryke et al. 2001). In the collared flycatcher, our experiment revealed that WPS of the stimulus male was the best predictor of the territorial behavior of resident males. Individuals bearing larger WPS elicited faster attacks, even from the same male, than males with smaller WPS (Table 1 and Fig. 1). Generally, this finding confirms the theory of sexual selection that predicts that male traits are used in male–male competition (Andersson 1994). Particularly, our results concur with the suggestion that WPS is an important status signal in the studied species that is involved in male competition for territories (Török et al. 2003). The age of the resident male was also a significant determinant of its territorial behavior, as yearlings attacked more quickly than older males. The latency of the first attack varied consistently within individuals implying that it is an individual specific attribute, which can potentially show a response to selection. The significant relationship between latency and pairing success supports this implication.

The theory of correlated asymmetries predicts that individuals displaying elaborate signals have increased chances of winning, so such males should be less frequently contested (Reichert 1998). Accordingly, empirical data generally revealed that males with larger badges are more successful in intrasexual conflicts (Smith 1972; Searcy 1979; Järvi and Bakken 1984; Røskaft and Rohwer 1987; Pärt and Qvarnström 1997; Dufour and Weatherhead 1998; Pryke et al. 2001, 2002; Pryke and Andersson 2003a, b, but see Dufour and Weatherhead 1998). In our population, however, males with larger WPS are apparently treated more aggressively than males with smaller WPS, although they may have higher chance to win the fight, if larger WPS indicates superior fighting ability. Similarly, in the red-winged blackbird, territorial males were more aggressive toward redwing mounts with enlarged badge size (Hansen and Rohwer 1986; but see Butcher and Rohwer 1989 for other species). We found that a resident
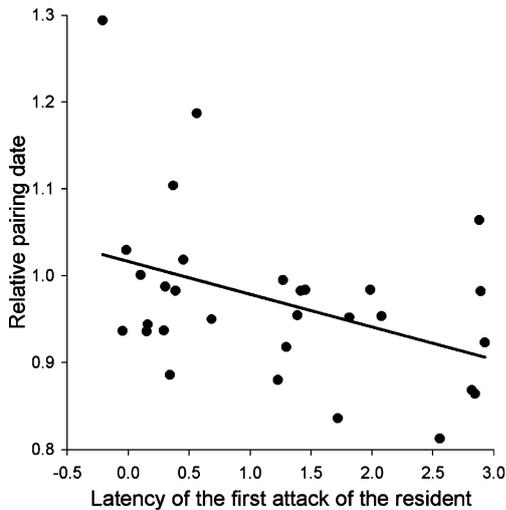
Fig. 3 The relationship between $\log_{10}$-transformed relative pairing date (in days) and $\log_{10}$-transformed latency of the first attack of residents (in seconds), while confounding effects are controlled (see main text)

male responded to intruders irrespective of his own badge size, and that the same male more quickly directed aggression towards a male bearing larger WPS than with smaller WPS. These findings suggest that absolute rather than relative trait values are important, which is in conflict with the expectation of correlated asymmetries.

It is likely that male collared flycatchers are unable to estimate relative trait ratios because they do not know the size of their own badges. For example, a male may find it difficult to "remember" his own badge size, which was developed months before its use as a dominance signal. However, individuals may learn their relative status from previous territorial experiences, and they may sense themselves dominant, if they are repeatedly successful in territorial conflicts due to their superior fighting ability or condition (see Jackson 1991). Latency was consistent within males implying that residents may apply similar levels of aggression, which is independent of the size of their own badges. At the same time, they will attack larger badged intruders more aggressively than smaller badged intruders, probably because the formers are perceived as larger threats (see also Røskaft and Rohwer 1987). Hence, their territorial behavior is partly determined by intrinsic attributes, such as fighting ability or condition, but can still be adjusted according to the signal displayed by their opponent.

The relative value of the contested territory is presumably higher for the owner than for the challenger. Differences in the extent of knowledge or investment in an area and, hence, willingness to escalate contests, contribute to territorial dominance (Beletsky and Orians 1989, 1993; Tobias 1997). Such residence biases can be essential determinants of contest outcome that may sometimes override other asymmetry rules (Reichert 1998). For example, prior residency history may blur age-related rules in the dominance hierarchies of great tits, as juvenile birds with prior residency advantage may become domi-

nant above adults (Sandell and Smith 1991). A resident collared flycatcher male may benefit by intense territory defense because of the relatively high value of the territory. However, a challenger may be less interested in the given territory, as others are still available; thus, it may leave the territory without a fight or give up the current contest easier when confronted with aggressive territory defense, if the cost of injury is high. Hence, the differential cost-benefit balance due to the residence asymmetry may result in resident males "always winning" (see also Krebs 1982), but only if they invest more in more threatening situations, e.g., when defending against males with larger WPS. Notably, residence asymmetry drives the red epaulette in the red-winged blackbirds to function differently from the perspective of the territory holder and intruder. Mounts with enlarged badge size elicited escalated aggression from resident males (Hansen and Rohwer 1983), but in the reciprocal experimental situation, they were more threatening to intruders (Røskaft and Rohwer 1987). Additionally, epaulette-blackened males had great difficulty holding their territories and were frequently evicted by floating males (Peek 1972; Smith 1972; Morris 1975). However, such status dependent roles reflect the two sides of the same coin, and indicate that a larger badge size is more threatening (Hansen and Rohwer 1983; Røskaft and Rohwer 1987).

Nonetheless, resident males do not always win (see Pärt and Qvarnström 1997; Garamszegi et al. 2004). It may happen that the cost-benefit patterns change for the challenger males because there are fewer alternative breeding sites available later in the season, or because the challenger male is already familiar with the contested territory. Generally, if the value of a given territory increases, residency asymmetries become less important, and other correlated asymmetries may rule the contest. We have no data to test this hypothesis directly.

Body condition seems one of the major proximate determinants of WPS in the observed population suggesting that WPS involves some production costs (Török et al. 2003), whereas FPS shows a weak correlation with condition (Hegyi et al. 2002). Additionally, as large WPS may more frequently elicit aggressive responses from other males than small WPS, social costs due to frequent punishments may represent maintenance costs. It has been suggested that condition-dependence may develop, at least partly, due to the large badge size increasing male–male aggression, so that reliability is controlled by repeated fights (Pärt and Qvarnström 1997; Qvarnström 1997). It is interesting to note that in the Swedish population, FPS is the condition-dependent trait (Gustafsson et al. 1994, 1995; Qvarnström 1999; Hegyi et al. 2002), and FPS predicts the outcome of competition over nestboxes, while WPS is not used in such a male–male context (Pärt and Qvarnström 1997). Therefore, the different determination and function of the two white patches in different populations of the same species suggests a link between the role of a signal and the information it conveys. Considering the possible evolutionary mechanisms acting in our population, probably either the expression of the wing-patch became condition-dependent due to social

costs, or the size of trait started to function as a badge because it reliably signals condition.

Male age was associated with territorial behavior, as yearlings attacked their challengers more quickly than older males. Whether this difference results in dissimilar success in territorial fights remains unclear. Perhaps, older males with more experience are better in repelling competitors (see Yasukawa 1979a; Jakobsson 1988; Tobias 1997; Hyman et al. 2004), and yearlings are keener to fight for a given territory, which is more valuable to them. Inexperienced younger birds may have more difficulties in regaining a territory than older males, which increases the value of an already obtained territory in their eyes. Additionally, young males are less familiar with other territories due to the lack of previous breeding experience. These factors may shift the cost-benefit balance of territory defense towards a predisposition to fight more aggressively.

Apparently, latency is an individual specific behavioral trait, and males behave repeatably in different territorial challenges (see also Lack 1946; Nowicki et al. 2002). This can happen, for example, if high quality males always invest less in direct attacks, and if low quality males apply a more stringent defense strategy to maintain the territory. Male red-winged blackbirds that are successful in establishing territories are less aggressive than those that failed, suggesting that the males of highest resource holding potential can retain their territories with little effort (Yasukawa 1979a). Alternatively, male quality may positively affect the latency of the first attack, if it reflects fighting ability per se. If latency directly determines the success in territoriality, only males in prime quality should be able to attack quickly. However, our results rather imply that longer latency involves superior quality, for three reasons. First, when challenged by high quality males with larger WPS, residents becoming relatively less dominant decrease the latency of the first attack. Second, inexperienced, young males have shorter latency than older males. Third, residents with longer latency seem to have a selective advantage by finding breeding partners faster, as indicated by the negative relationship between mating success and latency. However, this association may also be explained by the trade-off between male aggression and attractiveness, with males investing less in territory defense and being more successful in female attraction (Qvarnström and Forsgren 1998). In any case, its significant repeatability and its linkage with mating success suggest that latency may be an important behavioral trait that reflects aggression or fighting ability and may respond to intrasexual and other selection forces. Perhaps, latency is a manifestation of individual personalities (see Groothuis and Carere 2005 for review), with shy individuals always responding slower than bold individuals with shorter latency. Note that latency is related to a component of male quality that is not signaled via the size of the two white patches, as it was not related significantly to the size of the own badges.

To conclude, the WPS and age of males may function in contests over territories in our population. We have shown that, probably due to both residency bias and the fact that individuals do not know their own badges, absolute and not relative badge size of the stimulus male determined the territorial behavior of the territory holder. Specifically, stimulus males with larger WPS elicited more intense aggressive responses from resident males than did stimulus males with smaller WPS, probably because the formers are perceived as larger threats. There are clear-cut differences between different populations, as in the Hungarian population WPS, being a condition-dependent trait, is used in male–male contest, while in the Swedish population, FPS has similar roles. Our findings emphasize that territorial challenge experiments should consider the characteristics of both participants.

References

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

Badyaev AV, Hill GE (2000) Evolution of sexual dichromatism: contribution of carotenoid- versus melanin-based coloration. Biol J Linn Soc 69:153–172

Beletsky LD, Orians GH (1987) Territoriality among male red-winged blackbirds. 2. Removal experiments and site dominance. Behav Ecol Sociobiol 20:339–349

Beletsky LD, Orians GH (1989) Territoriality among male red-winged blackbirds. III. Testing hypotheses of territorial dominance. Behav Ecol Sociobiol 24:333–339

Beletsky LD, Orians GH (1993) Factors affecting which male red-winged blackbirds acquire territories. Condor 955:782–791

Butcher GS, Rohwer S (1989) The evolution of conspicuous and distinctive coloration in birds. Curr Ornithol 6:51–108

Cramp S, Perrins CM (1993) The birds of the Western Palearctic, vol VII. Flycatchers to shrikes. Oxford University Press, Oxford

Crawley MJ (1993) GLIM for ecologists. Blackwell Scientific Publications, Oxford

Crowder MJ, Hand DJ (1990) Analysis of repeated measures. Chapman & Hall, New York

Dawkins R, Krebs JR (1978) Animal signals: information or manipulation? In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Sinauer Associates, Sunderland, Massachusetts

Dufour KW, Weatherhead PJ (1998) Bilateral symmetry and social dominance in captive male red-winged blackbirds. Behav Ecol Sociobiol 42:71–76

Eckert CG, Weatherhead PJ (1987) Competition for territories in red-winged blackbirds: is resource-holding potential realized. Behav Ecol Sociobiol 20:369–375

Forstmeier W, Kempenaers B, Meyer A, Leisler B (2002) A novel song parameter correlates with extra-pair paternity and reflects male longevity. Proc R Soc Lond B 269:1479–1485

Garamszegi LZ, Møller AP, Török J, Michl G, Péczely P, Richard M (2004) Immune challenge mediates vocal communication in a passerine bird: an experiment. Behav Ecol 15:148–157

Garant D, Sheldon BC, Gustafsson L (2004) Climatic and temporal effects on the expression of secondary sexual characters: genetic and environmental components. Evolution 58:634–644

Gil D, Slater PJB (2000) Song organisation and singing patterns of the willow warbler, *Phylloscopus trochilus*. Behaviour 137:759–782

Grafen A, Hails RS (2002) Modern statistics for the life sciences. Oxford University Press, Oxford

Groothuis TGG, Carere C (2005) Avian personalities: characterization and epigenesis. Neurosci Biobehav Rev 29:137–150

Gustafsson L, Nordling D, Andersson MS, Sheldon BC, Qvarnström A (1994) Infectious diseases, reproductive effort and the cost of reproduction in birds. Philos Trans R Soc Lond B 346:323–331

Gustafsson L, Qvarnström A, Griffith SC (1995) Trade-offs between life-history traits and a secondary sexual character in male collared flycatchers. Nature 375:311–313

Hansen AJ, Rohwer S (1983) Coverable badges in intramale territorial disputes. Am Zool 23:932–932

Hansen AJ, Rohwer S (1986) Coverable badges and resource defense in birds. Anim Behav 34:69–76

Hegyi G, Török J, Tóth L (2002) Qualitative population divergence in proximate determination of a sexually selected trait in the collared flycatcher. J Evol Biol 15:710–719

Hyman J, Hughes M, Searcy WA, Nowicki S (2004) Individual variation in the strength of territory defense in male song sparrows: correlates of age, territory tenure, and neighbor aggressiveness. Behaviour 141:15–27

Jackson WM (1991) Why do winners keep winning. Behav Ecol Sociobiol 28:271–276

Jakobsson S (1988) Territorial fidelity of willow warbler (Phylloscopus trochilus) males and success in competition over territories. Behav Ecol Sociobiol 22:79–84

Järvi T, Bakken M (1984) The function of the variation in the breast stripe of the great tit (Parus major). Anim Behav 32:590–596

Kose M, Møller AP (1999) Sexual selection, feather breakage and parasites: the importance of white spots in the tail of the barn swallow (Hirundo rustica). Behav Ecol Sociobiol 45:430–436

Krebs JR (1982) Territorial defense in the great tit (Parus major): do residents always win? Behav Ecol Sociobiol 11:185–194

Lack D (1946) The life of the robin, revised edn. H. F. and G. Witherby, London

Lack D (1968) Ecological adaptations for breeding in birds. Methuen, London

Maynard-Smith J (1982) Evolution and the theory of games. Cambridge University Press, Cambridge

Maynard-Smith J, Harper DGC (1988) The evolution of aggression: can selection generate variability? Philos Trans R Soc Lond B 319:557–570

Maynard-Smith J, Parker GA (1976) The logic of asymmetric contests. Anim Behav 24:159–175

Mays HL, Hopper KR (2004) Differential responses of yellow-breasted chats, Icteria virens, to male and female conspecific model presentations. Anim Behav 67:21–26

Møller AP (1986) Mating system among European passerines: a review. Ibis 128:234–250

Morris L (1975) Effect of blackened epaulets on the territorial behavior and breeding success of male red-winged blackbirds, Agelaius phoeniceus. Ohio J Sci 75:168–176

Nowicki S, Searcy WA, Krueger T, Hughes M (2002) Individual variation in response to simulated territorial challenge among territory-holding song sparrows. J Avian Biol 33:253–259

Pärt T (1994) Male philopatry confers a mating advantage in the migratory collared flycatcher, Ficedula albicollis. Anim Behav 48:401–409

Pärt T, Qvarnström A (1997) Badge size in collared flycatchers predicts outcome of male competition over territories. Anim Behav 54:893–899

Peek FW (1972) Experimental study of territorial function of vocal and visual display in male red-winged blackbird (Agelaius phoeniceus). Anim Behav 20:112–118

Pryke SR, Andersson S (2003a) Carotenoid-based epaulettes reveal male competitive ability: experiments with resident and floater red-shouldered, widowbirds. Anim Behav 66:217–224

Pryke SR, Andersson S (2003b) Carotenoid-based status signalling in red-shouldered widowbirds (Euplectes axillaris): epaulet size and redness affect captive and territorial competition. Behav Ecol Sociobiol 53:393–401

Pryke SR, Lawes MJ, Andersson S (2001) Agonistic carotenoid signalling in male red-collared widowbirds: aggression related to the colour signal of both the territory owner and model intruder. Anim Behav 62:695–704

Pryke SR, Andersson S, Lawes MJ, Piper SE (2002) Carotenoid status signaling in captive and wild red-collared widowbirds: independent effects of badge size and color. Behav Ecol 13:622–631

Qvarnström A (1997) Experimentally increased badge size increases male competition and reduces male parental care in the collared flycather. Proc R Soc Lond B 264:1225–1231

Qvarnström A (1999) Genotype-by-environment interactions in the determination of the size of a secondary sexual character in the collared flycatcher (Ficedula albicollis). Evolution 53:1564–1572

Qvarnström A, Forsgren E (1998) Should females prefer dominant males? Trends Ecol Evol 13:498–501

Qvarnström A, Griffith SC, Gustafsson L (2000) Male–male competition and parental care in collared flycatchers (Ficedula albicollis): an experiment controlling for differences in territory quality. Proc R Soc Lond B 267:2547–2552

Radesäter T, Jakobsson S (1989) Song rate correlations of replacement territorial willow warblers Phylloscopus trochilus. Ornis Scand 20:71–73

Reichert SE (1998) Game theory and animal contest. In: Dugatkin LE, Reeve HK (eds) Game theory and animal behavior. Oxford University Press, Oxford

Rohwer S (1978) Passerine subadult plumages and the deceptive acquisition of resources: test of a critical assumption. Condor 80:173–179

Røskaft E, Rohwer S (1987) An experimental study of the function of the red epaulettes and the black body colour of male red-winged blackbirds. Anim Behav 35:1070–1077

Sandell M, Smith HG (1991) Dominance, prior occupancy, and winter residency in the great tit (Parus major). Behav Ecol Sociobiol 29:147–152

SAS Institute (1999) The SAS system for Windows, 8.01 edn. SAS Institute Incorporation, Cary, USA

Searcy WA (1979) Morphological correlates of dominance in captive male red-winged blackbirds. Condor 81:417–420

Shutler D, Weatherhead PJ (1991) Owner and floater red-winged blackbirds: determinants of status. Behav Ecol Sociobiol 28:235–241

Slagsvold T (1993) Female–female aggression and monogamy in great tits Parus major. Ornis Scand 24:155–158

Smith DG (1972) The role of the epaulets in red-winged blackbird (Agelaius phoeniceus) social system. Behaviour 41:251–268

Svensson L (1984) Identification guide to European passerines, 3rd edn. British Trust for Ornithology, Stockholm

Tobias J (1997) Asymmetric territorial contests in the European robin: the role of settlement costs. Anim Behav 54:9–21

Tobias J, Seddon N (2000) Territoriality as a paternity guard in the European robin, Erithacus rubecula. Anim Behav 60:165–173

Török J, Hegyi G, Garamszegi LZ (2003) Depigmented wing patch size is a condition-dependent indicator of viability in male collared flycatchers. Behav Ecol 14:382–388

Van Duyse E, Pinxten R, Eens M (2002) Effects of testosterone on song, aggression, and nestling feeding behavior in male great tits, Parus major. Horm Behav 41:178–186

Yasukawa K (1979a) Territory establishment in red-winged blackbirds: importance of aggressive behavior and experience. Condor 81:258–264

Yasukawa K (1979b) Territory establishment in red-winged blackbirds: importance of aggressive-behavior and experience. Condor 81:258–264