Evidence for differential maternal allocation to eggs in relation to manipulated male attractiveness in the pied flycatcher (*Ficedula hypoleuca*)

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Abstract   We present evidence of differential maternal allocation to eggs in response to manipulated male attractiveness in the migratory pied flycatcher (*Ficedula hypoleuca*). We manipulated the size of a male secondary sexual trait, the white forehead patch, right after male arrival to the breeding area and before female arrival. Patch size was (1) enlarged to the maximum observed in the population, (2) reduced by 40% or (3) kept constant by painting with indelible felt markers over the natural feather patch. Male behaviour was affected by the experimental manipulation, as individuals with enlarged patches performed more approaches to the nestbox in response to song playback during the territory occupation and nest-site presentation phases. Females paired with males with reduced forehead patches laid significantly smaller eggs than those paired with males in the control and enlarged-patch treatments. Laying date and clutch size did not differ among the experimental groups. We discuss that manipulations of ornaments designed to study differential allocation at laying should reduce as well as enlarge their expression.

Introduction

Darwin (1871) first suggested that display characters evolve in response to the aesthetic mate preferences of females. Burley (1986) proposed the differential allocation hypothesis as an explanation for differences in reproductive success resulting from the possession of aesthetic traits in species with biparental care. Differential allocation occurs when parents adjust their reproductive investment decisions to the attractiveness of their mates. A good test of this hypothesis can be provided by manipulating the attractiveness of such traits or by experimentally assigning mates of different attractiveness (reviewed by Sheldon 2000). Studies applying this experimental approach reported that when paired with attractive individuals females may start breeding earlier (De Lope and Møller 1993), lay more eggs (Balzer and Williams 1998) and enhance egg size or quality (Gil et al. 1999; Cunningham and Russell 2000). In addition, manipulated individuals may perceive their own relative attractiveness and this may influence either their own reproductive investment or their social behaviour (Burley 1986; Møller 1987; Qvarnström 1997; Sanz 2001).

Pied flycatcher (*Ficedula hypoleuca*) males have a conspicuous forehead patch of white feathers (Lundberg and Alatalo 1992) that exhibits phenotypic

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plasticity (Kilpimaa et al. 2004) and may play an important role in female choice (Potti and Montalvo 1991). In a closely related species, the collared flycatcher (*F. albicollis*), evidence suggested that the relatively high expression of this secondary sexual trait might function as a badge of status, conferring competitive advantage in male contests over territories (Pärt and Qvarnström 1997). In the same species, the forehead patch size is heritable (Qvarström 1999), positively correlated to the proportion of nestlings within a brood sired by males (Sheldon et al. 1997) and to their lifetime reproductive success (Gustafsson et al. 1995). A few studies exploring the potential role of the forehead patch in signalling parasite resistance in *Ficedula* males revealed that this secondary sexual trait might indicate immune capacity (Andersson 2001) or might be traded-off against it (Kilpimaa et al. 2004). The different findings of these two studies (Andersson 2001; Kilpimaa 2004) could be explained by the correlative nature of the former and the experimental approach of the latter. In addition, collared flycatcher males with larger patches had lower levels of infection by *Haemoproteus* (Andersson 2001) and Potti and Merino (1996a) reported that pied flycatcher females expressing this male secondary sexual trait suffered less from trypanosome infection. According to these studies, the male forehead patch in *Ficedula* flycatchers could operate as a sexual signal in mate attraction as well as a badge of status in social competition by being associated with parasite resistance.

However, sexual attractiveness and social status may in fact be related to other male traits that are, in turn, linked to the expression of patch size. Only experiments manipulating the trait itself are able to clearly reveal the importance of the trait for sexual selection (e.g. Andersson 1982; Møller 1988). Experimentally increased patch size reduced male parental care and increased male competition in the collared flycatcher (Qvarnström 1997). In pied flycatcher males, experimentally reduced patch size resulted in increased parental effort by relatively less attractive individuals while feeding their nestlings, and they also had a larger breeding dispersal distance between two successive years (Sanz 2001). These experiments reveal that patch size itself is involved in social competition and affects the differential allocation of parental effort between mates. Sanz (2001) manipulated patch size after hatching of the young, so differential allocation by females prior to the nestling stage could not be evaluated. Moreover, Qvarnström (1997) only enlarged patch size, while Sanz (2001) only reduced it. As attractiveness may not show a linear relationship with ornament size, effects of manipulation may be different according to the direction of change. Furthermore, enlarging and reducing patch size at the pre-breeding stage may better explore the full attractiveness function and allow an improved consideration of differential maternal allocation to eggs. Dale et al. (1999) manipulated forehead patch size in the pied flycatcher either by enlarging or reducing it and although patch size manipulation seemed not to affect female mate choice, the reproductive investment of females was not studied as the effects of the experiment were only tested during the mating period.

To investigate the effects of experimentally enhanced or reduced attractiveness of pied flycatcher males at laying, we manipulated the size of the white forehead patch in both directions upon their arrival to the breeding grounds. We checked if the manipulation affected male behaviour, as it could indicate effects on perception of the trait by themselves and presumably by other individuals. We predicted that, according to the differential allocation hypothesis, females mated to more attractive males (those with larger forehead patches) should start breeding earlier and should invest more in terms of egg number and egg size.

Methods

The experiment was conducted during the 2003 breeding season in a deciduous forest of *Quercus pyrenaica* in central Spain (40°48′N, 3°54′E). A study of nestbox breeding birds has been conducted in this area since 1991 (Sanz 1995). The pied flycatcher is a small (12–13 g) hole-nesting migratory passerine of European woodlands (Lundberg and Alatalo 1992). Males exhibit a conspicuous white forehead patch, roughly rectangular in shape in the population under study (mean ± SE: 49.7 mm^2 ± 0.6, range=14.5–107.1, $n = 689$ males), the size of which is determined during a partial moult in the winter quarters.

From mid-April, the study area was exhaustively searched for newly arrived males. Forty-five males were captured with nestbox traps on their first day of observation in the study area. Their original forehead patch size was calculated by multiplying the width and height as measured with a digital calliper (accuracy of 0.01 mm). Males were randomly assigned to one of three experimental groups (15 males per group). Already paired males (cessation of singing indicates pairing in this species; Lundberg and Alatalo 1992) were not included in the experiment. The enlarged-patch group had their original forehead patch enlarged up to the maximum width and height reached in the population (i.e. 11.50 mm and 9.64 mm respectively;

$n=689$ males) with a white permanent paint marker (Edding 751). The reduced-patch group had their original patch size width and height reduced by 40% with a black permanent paint marker. The original patch size of the control group was unaltered, but it was painted over with the white marker. Original forehead patch size did not differ significantly among the three groups before the experimental treatment ($F_{2,42} = 0.45$, $P = 0.64$; mean $\pm$ SE reduced: 64.9 ± 3.2 mm^2, $n = 15$; control: 63.2 ± 3.3 mm^2, $n = 15$; enlarged: 60.3 ± 4.0 mm^2, $n = 15$). The modified patch size was measured for all birds, resulting in a high significant difference in patch size among the three groups after treatment (reduced: 23.2 ± 2.5 mm^2; control: 65.5 ± 3.2 mm^2; enlarged: 100.3 ± 7.5 mm^2; $F_{2,42} = 61.63$, $P < 0.0001$). In order to investigate the potential effect of either enhanced or reduced attractiveness on male behaviour, all males were individually marked with colour rings to allow subsequent observations on the days following manipulation.

Male UV reflection is supposed to affect female mate choice decisions (Siitari et al. 2002) and one may argue that the white paint may have affected the UV reflectance. Measurements of a surface covered with the white paint used for the patch size manipulations taken with an Ocean Optics USB-2000 spectrophotometer (range 300–780 nm) showed a low reflectance (less than 10%) at UV wavelengths. This confirms that patches of males in the enlarged and control groups did not reflect more light at UV wavelengths than the unpainted patches of males in the reduced group.

Frequent checks of nestboxes provided data on laying date, clutch size and hatching date. Eggs were measured on the day they were laid as to length and width with a digital calliper to the nearest 0.01 mm. Volume was estimated as volume=$-0.042 + 0.4976$ [length $\times$ (width)^2] (Ojanen et al. 1978). On day 12 of nestling age, feeding adults were captured at the nest. Mass was recorded with a Pesola spring balance (accuracy 0.05 g) and tarsus length was measured with a digital calliper to the nearest 0.01 mm. We used mass/tarsus length as a measure of female body condition. Although female body condition was measured only at the end of the nestling period in the study year, data from 2002 indicate that female body condition at laying is positively associated with that at the end of the nestling period ($R = 0.30$, $P = 0.048$, $n = 46$). Male patch size was measured again to estimate changes throughout the season. At this stage (47.5 ± 4.7 days elapsed from the first to the second capture), patch size did not differ among experimental treatments (reduced: 55.5 ± 2.4 mm^2, $n = 13$; control: 56.7 ± 3.7 mm^2, $n = 11$; enlarged: 66.5 ± 5.9 mm^2, $n = 10$; $F_{2,31} = 2.16$,

$P = 0.13$) as paint marking might have vanished with time. However, the following evidence allowed us to infer that the experimental manipulation lasted throughout the period elapsed from the date of the initial capture of males to the beginning of the incubation period (17.47 ± 0.8 days), when the amount of resources to be invested in the clutch has already been determined:

1. During playback observations with binoculars, we confirmed that the paint lasted at least during the laying stage.
2. The patch size at the end of the nestling period was positively correlated with the modified patch size after manipulation and not with the original patch size (modified patch size: $r = 0.46$, $n = 34$, $P = 0.0065$; original patch size: $r = 0.28$, $n = 34$, $P = 0.11$). Thus, the effect of manipulation was still detectable at the end of the nestling period. This effect was presumably much stronger one month earlier, during the laying period
3. We consider a reasonable assumption that the white paint vanished gradually in a linear fashion throughout the breeding period.

Based on this supposition and the proportion of total time elapsed between manipulation and end of laying with respect to the total period between captures, we estimated that approximately 80% of the magnitude of change (modified patch size–original patch size) lasted until the laying period.

On the days following forehead patch manipulation, each male was observed during 10 min on two separate days before initiation of nest building (values are means$\pm$ SE days elapsed from the experimental manipulation to the first and second observation: 5.5 ± 0.8 and 13.2 ± 1.0, respectively). A digital commercial recorder produced in Great Britain (Mundi Sound PQ10) playing pied flycatcher song performed by the same individual was placed on the ground below the nestbox defended by a certain male. An observer (always the same) hidden at a distance of at least 15 m estimated each male's response. The song rate (number of songs per minute) of the digital recorder (about 40 strophes per 5 min) was in the natural range of song rate typically produced by an adult pied flycatcher male (average of 37.9 strophes per 5 min; Gottlander 1987). The number of times that the male either approached or entered the nestbox and song frequency (number of song phrases) were recorded to quantify the territorial response of males. We also calculated the distance between the nestbox where the male was trapped on arrival and the nestbox subsequently defended.

Sample size and statistical analyses

Of the 45 males assigned to the three experimental groups we recaptured 35 at the nestling stage (11 enlarged, 13 reduced and 11 controls). However, we have data for 36 nests, as from the colour bands we knew the identity of one male that could not be trapped. There was only one case in which we could not accurately measure the patch at recapture because the bird had lost some feathers above the bill. Variables that were normally distributed (Kolmogorov–Smirnov test for continuous variables, $P > 0.05$) were analysed with GLM tests (Statistica 2001) to investigate the effect of treatment, entering male original badge size as a covariate. Variables that were not normally distributed such as clutch size and all male behavioural traits were analysed with non-parametric tests following Zar (1999).

Results

Although male behavioural traits during the first observation period did not differ among the experimental groups (Table 1), during the second observation period males in the enlarged-patch group performed significantly more approaches to the nestbox in response to playback than males in the control and reduced-patch groups (Table 1; Dunn's post-hoc test: difference between the enlarged and the reduced-patch group and between the enlarged-patch and control group, both $P < 0.05$). They also tended to enter the nestbox more times, although not significantly, while they did not differ in the number of songs performed (Table 1). There was no effect of original badge size on the number of times that males approached or entered the nestbox or on song rate (Spearman rank order correlation, all $P > 0.47$). Similarly, there was no effect of time of day (all $P > 0.18$), of the number of days elapsed since the manipulation was carried out (all $P > 0.22$) or of the beginning of nest building (all $P > 0.72$). The experimental groups did not differ in the distance between the nestbox where the male was trapped on arrival and the nestbox subsequently defended (Treatment: $F_{2,32} = 0.60$, $P = 0.55$; original patch size: $F_{1,32} = 0.73$, $P = 0.40$).

The experiment showed that females paired with males in the reduced-patch group laid significantly smaller eggs than those mated with controls or males with enlarged badges (Fig. 1; Fisher Post-hoc test: difference between the reduced and the enlarged-patch group, $P = 0.009$ and between the reduced-patch and the control group, $P = 0.04$). After correcting in the GLM test for female body condition at the end of the nestling period, the effect of treatment on egg volume remained highly significant (treatment: $F_{2,28} = 5.64$, $P = 0.009$; female condition: $F_{1,28} = 6.46$, $P = 0.02$; original badge size: $F_{1,28} = 0.04$, $P = 0.84$). Female age did not differ between treatments either (treatment: $F_{2,29} = 0.50$, $P = 0.61$; original patch size: $F_{1,29} = 0.001$, $P = 0.97$). Laying date was not affected by treatment or original patch size (treatment, $F_{2,32} = 0.72$, $P = 0.49$; original patch size, $F_{1,32} = 0.89$, $P = 0.35$). Clutch size did not differ according to treatment (Kruskal–Wallis test: $H_{2,36} = 1.19$, $P = 0.55$) or to original badge size (Spearman rank correlation: $r_{2,36} = 0.15$, $P = 0.40$). There was no effect of treatment on female condition at the end of the nestling period ($F_{2,29} = 1.03$, $P = 0.37$; original patch size: $F_{1,29} = 0.16$, $P = 0.69$).

Table 1 The effect of manipulated forehead patch size on male pied flycatcher (*Ficedula hypoleuca*) behavioural traits during the 10-min period that observations lasted

Observation period	Reduced	n	Control	n	Enlarged	n	H	P
1st[a]								
No. of approaches	1.0 (0–4)	13	0.0 (0–4)	11	1.0 (0–2)	12	4.93	0.09
No. of times inside	0.0 (0–4)	13	0.0 (0–4)	11	0.0 (0–3)	12	2.58	0.28
No. of songs	1.0 (0–55)	13	0.0 (0–19)	11	0.0 (0–25)	12	0.76	0.69
2nd[b]								
No. of approaches	0.0 (0–3)	12	1.0 (0–4)	10	3.0 (0–6)	12	7.27	0.03
No. of times inside	0.0 (0–1)	12	0.0 (0–4)	10	0.5 (0–5)	12	5.29	0.07
No. of songs	0.0 (0–3)	12	0.0 (0–23)	10	0.0 (0–7)	12	1.04	0.60

Note: *H*=Kruskal–Wallis test statistic

Medians (range) are presented

[a] Mean±SE days elapsed from 1st observation period to beginning of nest building and to laying date: 3.1 ± 0.8 and 11.9 ± 0.8, respectively

[b] Mean±SE days elapsed from 2nd observation period to nest building and laying date: –4.4 ± 0.7 and 4.5 ± 0.5, respectively
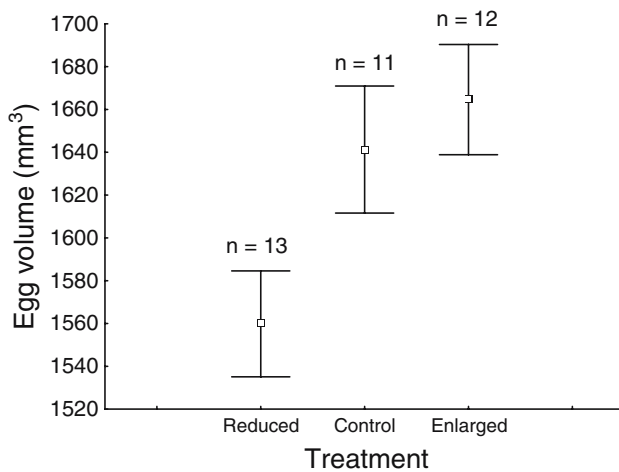
Fig. 1 Mean egg volume per clutch (mean ± SE) in relation to experimental manipulation of male pied flycatcher (*Ficedula hypoleuca*) forehead patch size

Discussion

The manipulation of forehead patch size had significant effects on male territorial behaviour during the mate attraction phase as, during the second observation period, males with enlarged badges performed more approaches to the nestbox and also tended to enter it more frequently in response to playback. These results may reflect that males with enlarged badges perceived their enhanced relative attractiveness or social status and defended their nest-site more vigorously than less attractive ones. However, we did not find evidence for direct benefits derived from this behaviour. Although we expected males with enhanced attractiveness to acquire their mates sooner (Møller 1988), laying date did not differ among experimental groups, though we did not know the exact mating date. Differences in male behaviour were evident only during the second observation period. It may be the case that the first observation period was too early to allow males to perceive their relative patch size, as a likely mechanism of self-perception involves feedback from conspecifics (Burley 1986). It is also plausible that, as the mating period progressed, males intensified their mating display for attracting females and, thus, differences of behaviour among the experimental groups were more evident during the second observation period. Another prediction was that attractive males would show higher song frequency (Balzer and Williams 1998; Lampe and Espmark 2003), but the experimental groups did not differ in song rate throughout the 10-min period that each observation lasted.

The experimental manipulation of male forehead patch size resulted in that females paired with less

attractive males laid smaller eggs. Egg size has been shown to enhance nestling growth (Schifferli 1973) and to increase reproductive success (Blomqvist et al. 1997; Potti and Merino 1996b). It is a flexible trait in *Ficedula* flycatchers (Ojanen 1983; Hargitai et al. 2005) and it has been reported that hatchability is higher for clutches of larger eggs and is associated with larger numbers of breeding recruits in a Spanish pied flycatcher population (Potti and Merino 1996b). In addition, the latter authors showed that unsuccessful eggs were only 2.5% smaller than successful ones. We have found that egg size in the reduced group was 4.9% smaller than that of the control group, which suggest that females' decision to allocate more or fewer resources to the eggs might have important fitness consequences. A feasible explanation for why females in the enlarged group did not lay larger eggs could be that females respond in a non-linear way to patch size. Thus, surpassing a certain threshold in the size of the patch would not result in an increase in female stimulation. If the experiment had only included patch enlargements (e.g. Qvarnström 1997), the significant effect on egg size would not have been detected. Experiments performed after laying (e.g. Sanz 2001) could not have resolved the issue either. The differential allocation in egg size in relation to male attractiveness has previously been observed in a precocial species, mallard (*Anas platyrhynchos*) (Cunningham and Russell 2000). Differential allocation in the number of eggs has also been reported (Petrie and Williams 1993) but, in our study, clutch size did not differ according to male badge size. One possibility is that female reproductive decisions about egg size are more flexible than those concerning clutch size, as conditions at the nestling period are unpredictable. As proposed by Hargitai et al. (2005), instead of making irreversible investment decisions, like modifying clutch size, it may be more adaptive for females to alter the egg-size pattern if they do not find reliable cues to prospective food conditions. Besides, altering clutch size might be too drastic in terms of investment compared to modifying egg size, as for instance in our study the egg volume of the whole clutch was reduced by 5%, while laying one egg less for a modal clutch of six eggs would have represented a reduction of 17% in investment. Laying date was not affected by treatment either. This could be explained by the fact that pied flycatcher females suffer time constraints which induce laying as early as possible, as the reproductive period in this migratory species is quite short (Slagsvold and Lifjeld 1989).

As our experiment was conducted before pairing, it may be possible that females mated with

reduced-patch males were of lower quality and laid smaller eggs according to their physiological potential and not according to the size of the male forehead patch. However, females mated with less attractive males did not differ from those mated with control or enlarged ones in laying date, clutch size or body condition. Although female body condition was measured only at the end of the nestling period, we assume that condition at this stage was positively associated with that at laying, as supported by data of 2002 from the same population. Nevertheless, even after correcting for female condition, the effect of treatment on egg volume remained significant. Thus, our results do not seem to support that females paired with reduced males were of lower quality. One may argue that males with reduced patches suffered a reduced competitive ability and occupied poorer breeding territories, with territory quality rather than forehead patch being the reason why females allocated fewer resources to eggs. Although we cannot discard this possibility, as the territory quality was not assessed, it seems unlikely that males with reduced patches suffered reduced competitive ability in territory contests, as they did not mate or start breeding later than the other males.

To conclude, the manipulation of male forehead patch size affected their territorial behaviour and resulted in females paired with less attractive individuals laying similar-sized clutches of smaller eggs, which has been reported to be a cause of hatching failure in this species (Potti and Merino 1996b). Future manipulations of ornaments designed to study maternal differential allocation at laying should reduce as well as enlarge their expression.

Zusammenfassung

Unterschiedliche maternale Investition in Eier bei manipulierter Attraktivität der Männchen des Trauerschnäpper (*Ficedula hypoleuca*)

Wir manipulierten die Größe eines sekundären Geschlechtsmerkmals, des weißen Stirnflecks, bei Männchen des Trauerschnäppers (*Ficedula hypoleuca*) unmittelbar nach ihrer Ankunft im Brutgebiet und vor der Ankunft der Weibchen. Die Größe des Stirnflecks wurde durch übermalen mit einem wasserfesten Filzschreiber (1) vergrößert auf die maximal in der Population vorkommende Größe, (2) um 40 % verringert oder (3) unverändert gelassen. Das Verhalten der Männchen wurde durch die experimentelle Manipulation verändert. Männchen mit vergrößertem Stirnfleck flogen bei Vorspielen von Gesang während Revierbesetzung und

Präsentation Nistkästen häufiger an. Mit Männchen mit reduzierter Größe des Stirnflecks verpaarte Weibchen legten signifikant kleinere Eier als diejenigen, die mit Männchen der Kontrollgruppe oder der Gruppe mit vergrößertem Stirnfleck verpaart waren. Legedatum und Gelegegröße unterschieden sich zwischen den Gruppen nicht. Manipulationen von Gefiederkennzeichen zur experimentellen Untersuchung unterschiedlicher Investition ins Gelege sollten also sowohl Reduzierung wie Verstärkung des Merkmales beinhalten.

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