Lifetime fitness and age-related female ornament signalling: evidence for survival and fecundity selection in the pied flycatcher

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Abstract

Ornaments displayed by females have often been denied evolutionary interest due to their frequently reduced expression relative to males, habitually attributed to a genetic correlation between the sexes. We estimated annual and lifetime reproductive success of female pied flycatchers (*Ficedula hypoleuca*) and applied capture–mark–recapture models to analyse annual survival rates in relation to the patterns of expression (absence/presence) of an ornament displayed by all males and a fraction of females. Overall, the likelihood of expressing the ornament increased nonlinearly with female age and was due to within-individual variation, not to the selective appearance or disappearance of ornament-related expression of phenotypes in the population. Accordingly, expressing the forehead patch in a given year did not influence survival probability. However, those females expressing the ornament at early ages (1–2 years old) enjoyed survival advantages throughout lifetime. Although ornamented females had higher lifetime fecundity and fledging success, their yearly reproductive performance, in terms of fledging productivity, decreased as they aged so that, late in life, ornamented females reared fewer offspring than nonexpressing females of the same age. In addition, both strategies (expressing vs. not expressing the trait) returned similar fitness payoffs in terms of recruited offspring. Our results support the hypothesis that fecundity and survival selection are involved in the displaying of this 'male' ornament by females.

Introduction

Female ornaments (broadly considered as any conspicuous and decorative character displayed by females; Amundsen, 2000a) have frequently been denied evolutionary importance until recently due to their often reduced ('vestigial') expression relative to males, as postulated by the genetic correlation hypothesis of modern days (Lande, 1980, 1987; Cuervo *et al.*, 1996; Amundsen, 2000a,b; Roulin *et al.*, 2001a; Amundsen and Pärn, 2006; Bonduriansky & Chenoweth, 2009;

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Potti & Canal, 2011; Rosvall, 2011; Tobias *et al.*, 2012) which can be traced back to Darwin (1871). Evolutionary theory states that males and females may be displaced from their different phenotypic optima due to sexual genetic conflict, as alleles of the underlying shared genes may be beneficial to one sex but detrimental to the other (Lande, 1980; Clutton-Brock, 2007; Bonduriansky & Chenoweth, 2009; Bonduriansky, 2011; Mills *et al.*, 2012). Abundant empirical work in the last two decades suggests, however, that in some cases selection may act on male and female traits quite independently, implying no conflict between the genetic correlation and functional explanations of female ornamentation (Amundsen and Pärn, 2006; Kraaijeveld *et al.*, 2007), as theoretically supported by Lande's (1980, 1987) models on the evolution of sexual dimorphism (Bonduriansky & Chenoweth, 2009).

According to those models, which are supported by recent experimental work (Doutrelant *et al.*, 2012; Simmons & Emlen, 2008; Morales *et al.*, 2009), attractiveness will at some point become detrimental for females because showiness will be constrained by a trade-off between allocation to fecundity and to female ornamentation (Fitzpatrick *et al.*, 1995). Given directional selection towards greater female showiness, it is expected that only high-quality individuals will afford the more costly expressions of ornaments (Zahavi, 1975).

Although 'quality' is often a difficult concept to be precise about (Wilson & Nussey, 2009), there is little doubt that it should be closely related, if not synonymous, to measurable aspects of fitness, as condition, survival and short- and long-term (lifetime) reproductive success (Clutton-Brock, 1988; Newton, 1989; Cotton *et al.*, 2004). A substantial body of work has examined the relationships between female ornaments, short-term survival and reproductive success and/or surrogates for individual quality in insects (Simmons & Emlen, 2008), fish (Berglund *et al.*, 1997; Amundsen & Forsgren, 2001; Kekäläinen *et al.*, 2010), lizards (Weiss, 2006), birds (Roulin *et al.*, 2001a,b; Jawor *et al.*, 2004; Amundsen and Pärn, 2006; Doutrelant *et al.*, 2008; Gasparini *et al.*, 2009; Martínez-Padilla *et al.*, 2011) and mammals (Robinson *et al.*, 2006; Robinson & Kruuk, 2007; Ezenwa & Jolles, 2008; Stockley & Bro-Jørgensen, 2010), with mixed results. Except for avian plumage colour polymorphisms (reviewed by Roulin, 2004; Brommer *et al.*, 2005), however, only two studies to our knowledge have been able to assess the quantitative genetic basis and lifetime fitness consequences of displaying an ornament common to both sexes (Roulin *et al.*, 1998, 2000, 2010). Roulin *et al.* studied the variation in lifetime reproductive success (LRS) in relation to plumage spotting. They showed that in Barn Owls, *Tyto alba*, the plumage ornament (spottiness) is genetically inherited and that both females and males adjust adaptively their offspring sex ratio according to their own ornamentation to maximize offspring survival.

In Iberian populations of pied flycatchers (*Ficedula hypoleuca* Pallas, 1764), some females express a forehead patch of pale (white or creamy) feathers similar to that all males display, although often smaller (by a half, on average; Potti & Canal, 2011). Both genetic (Potti, 1993; Potti & Canal, 2011) and functional (Potti & Merino, 1996; Morales *et al.*, 2007) hypotheses have been invoked to explain female expression as well as size of the 'male' ornament in these populations. A preference of males for females displaying large forehead patches has been suggested on the basis of the reported assortative mating with respect to trait size (Potti & Merino, 1996; Potti & Canal, 2011) and the signalling of their age and parasite (trypanosome)-free condition by ornamented females (Potti & Merino, 1996) although the possibility that assortative mating may be due to reasons other than mate choice cannot be discarded (Burley, 1983; Roulin, 1999; Kraaijeveld *et al.*, 2007). In addition, as in the congeneric collared flycatcher (*Ficedula albicollis*; Gustafsson *et al.*, 1995; Qvarnström *et al.*, 2006; de Heij *et al.*, 2011), there is positive directional sexual selection in at least some Iberian populations of pied flycatchers on forehead patch size in males. Males with large forehead patches mate more quickly (Potti & Montalvo, 1991a) and sire more extra-pair offspring than males with smaller patches (Canal *et al.*, 2011). Although the magnitude of the cross-sex genetic correlation in trait expression is unknown (all males express the trait, hence there is no variance in male trait expression), once expressed in females there is a strong positive genetic correlation between the sexes in trait size (Potti & Canal, 2011). This sets the potential for genetic conflict between the sexes to occur (Andrés & Morrow, 2003; Bonduriansky & Chenoweth, 2009).

Once assessed the genetic basis of trait size and expression (Potti & Canal, 2011), a second essential step is to answer one of the questions posed by Rosvall (2011) on the 'enigmatic' evolutionary significance of exaggerated traits in females: Are these traits primarily shaped by fecundity and survival selection? Here, we aim to answer this question by examining the significance of female ornament expression (presence/absence), that is, whether it may be explained by lifetime fitness advantages in terms of survival and reproductive success and thus may signal individual quality. When treated as a threshold trait (Falconer & MacKay, 1996), ornament displaying (as opposed to ornament size) in female pied flycatchers has been shown to retain large amounts of unexplained nonadditive genetic and/or environmental variation, with a low (presumably, autosome-based) heritability (Potti & Canal, 2011). Because of the relatively low frequency of ornament expression by females (see Results), that variation renders ornament displaying more suitable than ornament size for dissecting the fitness consequences that developing the trait (to any degree) may have for females. We followed survival and reproductive success from yearly reproductive performance to lifetime fecundity and fledging production until recruitment in relation to the expression of the ornament, so that the short- and long-term benefits and costs accrued from trait expression could be ascertained. As both breeding success and trait expression are age dependent (Lundberg & Alatalo, 1992; Potti, 1993; Potti & Merino, 1996; Morales *et al.*, 2007), variation along the ontogeny must be taken into account for a meaningful analysis of its fitness-related variation (Amundsen and Pärn, 2006; Kraaijeveld *et al.*, 2007). In doing so, we try to distinguish within-individual from populationwide effects (van de Pol & Verhulst, 2006) and then look at the consequences of expressing the ornament at particular ages to highlight some of its likely benefits and costs.

Materials and methods

Study system

We studied a population of pied flycatchers breeding in nest boxes in La Hiruela, about 100 km north-east of Madrid, central Spain, in the breeding seasons from 1987 to 2005, except 2003. Pied flycatchers are small (*c.* 12 g) trans-Saharan migrants that start to arrive to the study area around the third week of April (Potti & Montalvo, 1991a). All nests were visited regularly to obtain accurate estimates of breeding date, clutch size and number of fledged young. Most breeding adults were captured during incubation (females) or with a nestbox trap while feeding nestlings (males and females), aged (Potti & Montalvo, 1991a), marked for individual identification with numbered and colour rings and released. Immigrant birds aged as beyond their first year when first captured were ascribed an age of 2 years on the basis of patterns of age at first reproduction observed in birds of exactly known age (Potti & Montalvo, 1991b). We recorded a female as lacking a forehead patch even when occasionally she had a few (1–2) white feathers interspersed among the 'normal' (i.e. buffy or greyish) feathers, but they did not form a measurable, continuous plumage patch (cf. Morales *et al.*, 2007). Ornament expression was never used as a criterion for ageing females.

All fledglings were ringed on day 13 of nestling age. Most pied flycatchers mate monogamously, but some males succeed in becoming polygamous (Lundberg & Alatalo, 1992; Potti & Montalvo, 1993; Canal *et al.*, 2012). The pairing status of social mates in all nests was categorized as either monogamous or primary or secondary in the case of bigamous social bonds (Lundberg & Alatalo, 1992; Potti & Montalvo, 1993).

Fitness estimation

To estimate fitness components (i.e. survival, clutch size, numbers of 13-day-old fledglings and recruits), we used all information on each individual in addition to a database summarizing the female life-history data (i.e. longevity and LRS; see Table 1) from the former, longitudinal data set. In the summary database, females would be ascribed to either of two groups (ornamented vs. nonornamented) on the basis of expression, or lack thereof, of the forehead patch at least once in their lifetimes and then fitness components would be compared between both groups. The same approach was used but categorizing females as ornamented or not at early ages (1–2 years old). Yet, for age-dependent trait expression – as is the case with the female forehead patch (see Results) – a female's longevity obviously influences her likelihood of being classified as ornamented or not. To solve this sampling problem, we used the longitudinal data set, containing all the records on both annual

Table 1 Raw statistics for measurements of lifetime fitness in nonornamented and ornamented female pied flycatchers. These figures, although pointing to a higher quality of ornamented females, should not be taken at face value for the interpretation of ornament expression-related differences in female fitness components. See Fitness estimation in Methods for further explanation.

	Nonornamented				Ornamented			
	Mean	SD	*n*	range	Mean	SD	*n*	Range
Longevity (years)	3.31	1.18	232	2–6	4.41	1.15	113	2–6
Lifetime fecundity (no. eggs)	9.26	5.38	229	3–31	14.97	7.65	113	4–39
Lifetime no. of fledged young	5.91	4.72	232	0–22	10.29	6.01	113	0–31
Lifetime no. of recruits	0.69	1.03	232	0–5	1.38	1.54	113	0–8

female reproductive performance (i.e. clutch size, number of fledglings reared to independence and number of recruits from each breeding attempt) as well as the scores of concurrent (yearly) female ornament expression [0 (absence)/1 (presence)]. These models overcome the problem of circularity caused by lifespan influencing both sampling detectability of trait expression and fitness, with trait expression potentially influencing fitness, by directly testing for influences of ornament expression on yearly reproductive success, independently of female lifespan.

Yearly number of eggs and fledglings were analysed with the entire longitudinal data set. Because of the gap in fieldwork in 2003 and as recruits may postpone their first breeding until the second or, more rarely, third year of life (Potti & Montalvo, 1991b), all breeding events after the year 1999 were excluded from the analysis of annual recruitment. Lifetime analyses were restricted to the fitness components of all females marked for the first time between 1987 and 1996. This time window allows for the time interval (6 years) needed to ascertain recruitment of females marked as fledglings and their offspring for all cohorts. The few females still alive after 1999 were removed from the lifetime analyses in order not to underestimate their performance throughout life.

Our population has the largest recovery rates for both fledglings and breeding adults (fledglings: 14%; adult males: 52%; adult females: 54%; J. Potti, unpublished data) among those reported across Europe in this well-studied species (Potti & Montalvo, 1991b; Lundberg & Alatalo, 1992; Lehtonen *et al.*, 2009). However, recapture rates were < 1, that is, alive individuals were not

recaptured on all sampling occasions, so apparent survival was estimated within a capture–mark–recapture (CMR) framework (Lebreton *et al.*, 1992; see Statistical Analyses below).

Statistical analyses

Variation with age and annual breeding performance

We used random intercept generalized mixed models (GLMMs, Bolker *et al.*, 2008) as implemented in SAS (v. 9.2; SAS Institute Inc., 2008) to first investigate age-related patterns of forehead patch expression (presence/absence). Within-individual effects were distinguished from between-individual effects (i.e. selective appearance and disappearance of phenotypes) by modelling age of first and last breeding as fixed covariates conditional on the random effect of female identity (van de Pol & Verhulst, 2006). As age was influential in patch expression (see Results), it was also introduced as a covariate to ascertain whether expressing the ornament correlated with annual reproductive parameters. We analysed numbers of eggs (Poisson error, log link function), fledglings reared to independence (Poisson error, log link function) and recruits as breeders (negative binomial error, log link function). We also run similar models accounting for the previous life-history stage as a binomial denominator (fledglings/eggs and recruits/fledglings) and a logit link function. Both type of models showed similar results but, as we were interested in disentangling the independent effect of each life-history stage, we present along the paper the models corresponding to fledging and recruitment rates (see Tables S1 and S2 for the analyses of raw data). In all models, female identity and breeding year were entered as random terms to account for repeated measures of the same female and possible annual differences in patch expression and breeding performance. Laying date was included as a covariate in the models as it is one of the most important determinants of breeding success and recruitment in pied flycatchers (Potti & Montalvo, 1991b; Lundberg & Alatalo, 1992). An association between female ornamentation and productivity could be mediated by territory and/or mate quality, with ornamented females breeding in better territories or being paired with males investing more in their broods than nonornamented females. To account for the potential influence of male quality on reproductive parameters, forehead patch size of the female's social male was introduced as a covariate in early stages of the modelling process. In contrast, male age, another potential predictor of reproductive success, was not included in the models to avoid problems of collinearity due to the strong age-assortative mating reported in this population (Potti, 2000). Regarding territory (nest site) quality, it is unrelated to breeding date or any measured male's secondary sex trait in this population, likely because habitat features are not heterogeneous

enough to cause large difference in fitness in our population (Canal *et al.*, 2012). Thus, we think it is unlikely that territory or male quality may cause severe biases in our results. Female pairing status (i.e. monogamous, primary and secondary females of polygamous males) was also explored in these first steps because pairing status was related to another female ornament in the related collared flycatcher (the wing white patch; Hegyi *et al.*, 2006, 2008). However, pairing status, forehead patch size of the female's social male or their interactions with trait expression did not explain any variation in female fitness components (data not shown) and were not further considered. Therefore, starting models for annual breeding performance included the effects of patch expression (presence/absence), female age, and age at first and last breeding on clutch size, number of fledglings and number of recruits.

We started from models including all main effects and relevant interactions and proceeded iteratively backwards deleting from the models nonsignificant terms until all effects and/or interactions retained significance ($P < 0.05$). The nonsignificance of the removed terms was further confirmed by adding them one by one to the final model. Sample sizes differ among analyses because not all data were known for all individuals.

Annual survival and transition probabilities

Because the expression of the forehead patch varies at the within-individual level, we used multistate CMR models (Nichols & Kendall, 1995; Lebreton & Pradel, 2002) to analyse whether female annual survival is related to the expression or not of the forehead patch (two states) and to estimate transition rates within and between states (i.e. the probability of changing from ornamented to nonornamented and *vice versa*) while correcting for recapture rates. The general model was the time- and state-dependent Arnason–Schwarz model (Brownie *et al.*, 1993) besides an age effect with two age classes (first-breeders and older individuals). As both newborn and adult birds were marked in our population, these two groups were distinguished in the models by assuming that survival, recapture and transition parameters were equal for birds marked as adult and for the adult stages of birds marked as fledglings. This general model incorporating time-, age- and state-dependent variations in survival (ϕ), reencounter (p) and transition probabilities (ψ) resulted in a large number of inestimable parameters, so we began with a constrained model in which transition rates varied between states and age classes but were constant over time. This model was denoted $\phi_{(t*a2*m)} \, p_{(t*a2*m)} \, \psi_{(a2*m)}$, subscripts t, a2 and m indicating time-, age- and ornament-specific parameters, respectively. In addition, we parameterized single-state Cormack–Jolly–Seber (CJS) models to investigate whether expressing the ornament at an early age (1 or 2 years old) affected apparent survival

and reencounter probabilities. Our general model was $\phi_{(t*g)}\ p_{(t*g)}$, where t indicates time-constrained parameters and g two groups of individuals (expressing or not the ornament at an early age).

We first assessed goodness-of-fit (GOF) of the Jolly–Move (JMV) and CJS models (for multistate and single-state models, respectively) using software U-CARE (Pradel *et al.*, 2003; Choquet *et al.*, 2009). Then, all models were fitted to the data using program MARK (v. 5.1; White & Burnham, 1999). As no recapture effort was made in 2003, the corresponding reencounter parameter for this occasion was set to 0. Model selection was based on the Akaike information criterion corrected (AICc) for small sample sizes, models within 2 AICc points being considered equal (Burnham & Anderson, 1998). We also calculated the relative plausibility of each model with normalized Akaike weights and used multimodel inference (model averaging) when more than one model had substantial support (Burnham & Anderson, 1998).

Lifetime analyses

Generalized mixed models were also employed to ascertain whether patch expression correlated with lifetime breeding performance, that is, number of eggs, fledglings and recruits produced throughout lifetime. Model structures and selection were similar to those described for annual parameters (Poisson error for lifetime number of eggs and binomial models with previous stage as a denominator for numbers of fledglings and recruits). Cohort identity was fitted as a random term and age at first breeding, longevity and patch expression as fixed terms. As stated above, two sets of models were carried out by considering (i) whether the female expressed the ornament at least once throughout her life and (ii) whether she expressed the ornament or not at 1–2 years of age.

Results

A forehead patch was recorded at least once in 172 of 466 females followed throughout their lifetimes (36.9%). Thus, contrary to males where the forehead patch is expressed by all individuals to a variable degree, only a minority of females express the trait. Summary statistics of components of LRS in ornamented and nonornamented females are given in Table 1.

Age dependency of female ornamentation

Female expression of the ornament was related to age as only 6% of yearling females compared to 40%, on average, of the older females expressed the trait ($n = 846$ records of 466 individuals; $\chi^2_6 = 148.66$, $P < 0.0001$; Fig. 1a). The age when the ornament was first recorded was very variable, ranging from 1 to

8 years (median = 2, mean ± SD = 2.7 ± 1.2 years), with most females (75%) starting to display it in their second or third year (Fig. 1b).

The likelihood of expressing the ornament increased with age (Fig. 1c) and was due to within-individual variation, not to the selective appearance or disappearance of ornament-related expression of phenotypes in the
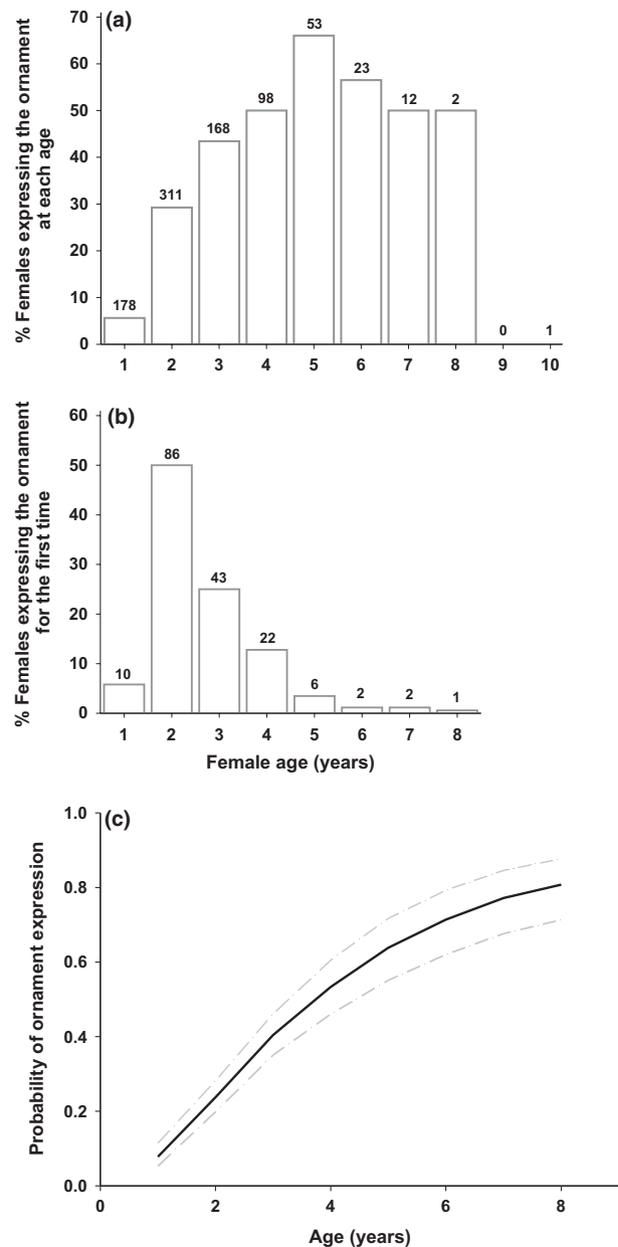

Fig. 1 Percentages of females expressing the ornament in relation to their age (a) and their age at first expression (b); the probability of expressing the ornament (mean estimate ± 95% CI) as derived from model parameters is shown in (c). Numbers above bars are sample sizes.

population (binomial mixed model; estimate LogAge (SE) 0.0459 (0.0066), $F_{1,379} = 48.22$, $P < 0.0001$; estimate (SE) age at first measurement -0.01342 (0.1502), $F_{1,379} = 0.01$, $P = 0.9577$; estimate (SE) age at last measurement -0.0509 (0.0916), $F_{1,379} = 0.39$, $P = 0.5337$).

Annual reproductive success and female ornament expression

Clutch size
Females expressing the forehead patch in a given year laid significantly larger clutches than those not expressing it. As shown by the slope of the final model, ornamented females lay, on average, 0.129 more eggs per clutch than nonornamented individuals (Table 2, Fig. 2). Similarly to ornament expression, the increase in clutch size with increasing age was due to within-individual changes, not to selective effects in the population (Table 2).

Fledging success
The yearly numbers of fledged young, after taking clutch size into account, were affected by an interaction between age and female ornament expression status (Table 3, Fig. 2). Nonornamented females tended to rear larger broods with increasing age, following the pattern due to corresponding increases in clutch size, whereas ornamented females started strongly but their fledging production tended to decline as they aged (Fig. 2). As a result, the older ornamented females reared, on average, as few nestlings as nonornamented yearling females even though they laid larger clutches.

Recruitment success
After controlling for female age and number of young fledged, there was no effect of expressing the forehead patch in a given breeding season on the number that recruited as breeders in later years. However, there were effects of both the age at which the individual was recorded in the population for the first and the last
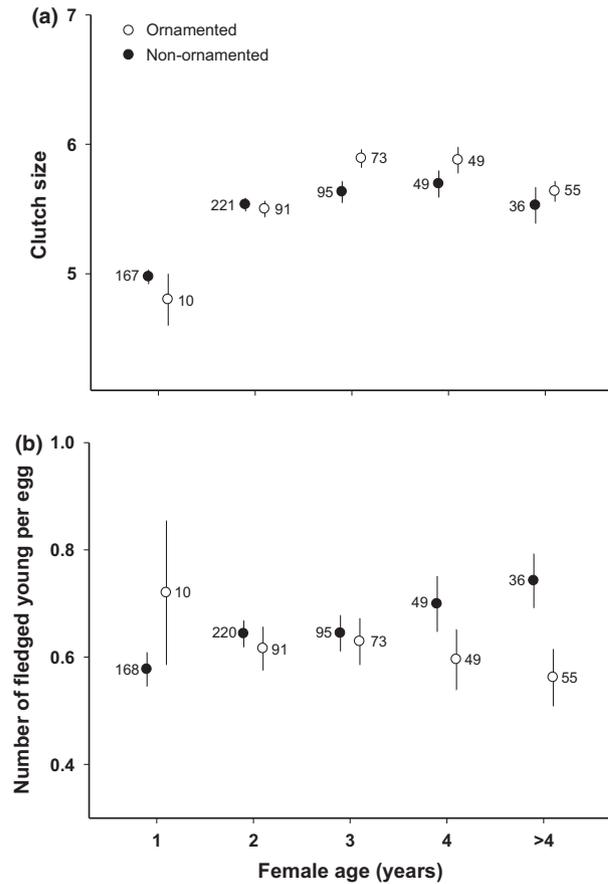

Fig. 2 Variation (mean ± SE) in clutch size (a) and fledged young (b) in relation to female age and the concurrent expression (or lack thereof) of the forehead patch by female pied flycatchers; open and filled dots denote ornamented and nonornamented females, respectively; numbers besides bars are numbers of females.

Table 2 GLMM showing the effect of female age and forehead patch expression on clutch size in female pied flycatchers. LogAge indicates within-individual age effects on a logarithmic scale. Models were fitted with Poisson distribution of errors and log link function.

	Estimate	SE	F	P
Intercept	6.0906	0.1245		
FP expression			5.18	0.0234
Yes	0			
No	−0.1294	0.0568		
LogAge	0.6124	0.1203	25.92	< 0.0001
Laying date	−0.03368	0.0039	76.59	< 0.0001
d.f.	1360			

GLMM, generalized mixed models.

Table 3 GLMM showing the effect of female age and forehead patch expression on numbers of young fledged by female pied flycatchers after controlling for clutch size (binomial error, number of eggs as a binomial denominator and logit link function). LogAge indicates within-individual age effects on a logarithmic scale. See Table S1 for equivalent analyses of absolute numbers of fledglings.

	Estimate	SE	F	P
Intercept	2.6630	0.4432		
FP expression			2.75	0.0980
Yes	0			
No	−0.4855	0.2926		
LogAge	−1.2804	0.5501	1.59	0.2086
Fp expression × LogAge			8.35	0.0041
Yes	0			
No	1.6702	0.5781		
Laying date	−0.05470	0.009793	31.20	< 0.0001
d.f.	1341			

GLMM, generalized mixed models.

time across lifetime, so that the number of recruits was larger for females breeding at early ages and for those captured for the last time at older ages (Table 4).

Annual survival and transition probabilities

The GOF tests indicated that both JMV and CJS models fitted the data well (JMV: $\chi^2_{87} = 50.93$, $P = 0.99$; CJS: $\chi^2_{44} = 10.29$, $P = 1.00$). Multistate analyses were little informative as to differences in yearly survival rates in relation to expression of the forehead patch in females, as revealed by the four highest-ranked candidate models (those with ΔAICc < 2; Table 5). Model averaging of these top-ranked models pointed to a very small difference (< 2%) in female survival between females expressing or not the forehead patch. Models including different transition probabilities for each state had, however, overwhelming support (Table 6; $w_i = 0.999$). The between-year probability of remaining ornamented was 0.86 ± 0.03 (SE), indicating that once expressed most females displayed the ornament in subsequent breeding seasons. Nonornamented females had a smaller probability (0.74 ± 0.03) of remaining within the nonornamented state in the subsequent year. Consequently, the probability of changing from nonornamented to ornamented state was almost twice as large as the opposite (0.26 ± 0.03 vs. 0.14 ± 0.03).

Cormack–Jolly–Seber candidate models analysing survival and recapture probabilities as functions of ornament expression at early ages (1–2 year old) are shown in Table 6. The top-ranked model was 2.9 times better supported than the next best model, suggesting that females expressing the forehead patch at an early age had a probability of survival about 10% greater than those that did not (0.60 ± 0.04 vs. 0.49 ± 0.02; Fig. 3). This translates to a higher mean life expectancy (Seber, 1982) of 1.93 (95% CI: 1.55–2.43) years for individuals expressing the ornament at early ages, as opposed to 1.40 (1.25–1.59) years for those expressing the forehead patch at older ages or not expressing it at all.

Table 4 GLMM showing the effect of female age and forehead patch expression on numbers of recruits of female pied flycatchers after correcting for the number of fledged young (binomial error, fledglings as a binomial denominator and logit link function). Age at first and last measurements indicates the selective appearance and disappearance of phenotypes, respectively. See Table S1 for equivalent analyses of absolute numbers of recruits.

	Estimate	SE	F	P
Intercept	−1.3357	0.3625		
Age at first measurement	−0.2251	0.0955	5.56	0.0193
Age at last measurement	0.1304	0.0470	7.70	0.0061
Laying date	−0.0346	0.0117	8.75	0.0035
d.f.	1198			

GLMM, generalized mixed models.

Table 5 Candidate multistate capture–recapture models. Shown are AICc, difference in AICc with the highest-ranked model (ΔAICc), model weight, number of identifiable parameters (K) and deviance for survival (ϕ), reencounter (p) and transition (ψ) probabilities of female pied flycatchers.

Model	AICc	ΔAICc	AICc Weight	K	Deviance
$\phi_{(a2)}\, p_{\ (t*m)}\, \psi_{\ (m)}$	1767.714	0	0.3161	22	517.30
$\phi_{(.)}\, p_{\ (t*m)}\, \psi_{\ (m)}$	1768.392	0.6779	0.2252	21	520.08
$\phi_{(a2+m)}\, p_{\ (t*m)}\, \psi_{\ (m)}$	1769.296	1.5821	0.1433	23	516.76
$\phi_{(a2[1\ yr*m,\ ad])}\, p_{\ (t*m)}\, \psi_{\ (m)}$	1769.689	1.975	0.1177	23	517.16
$\phi_{(m)}\, p_{\ (t*m)}\, \psi_{\ (m)}$	1770.456	2.7426	0.0802	22	520.04
$\phi_{(a2)}\, p_{\ (t*m)}\, \psi_{\ (a2*m)}$	1770.878	3.1643	0.0649	24	516.23
$\phi_{(a2*m)}\, p_{\ (t*m)}\, \psi_{\ (m)}$	1771.371	3.6575	0.0507	24	516.72
$\phi_{(a2)}\, p_{\ (t*m)}\, \psi_{\ (.)}$	1779.589	11.8752	0.0008	24	524.94
$\phi_{(t)}\, p_{\ (t*m)}\, \psi_{\ (m)}$	1780.664	12.9501	0.0004	36	500.17
$\phi_{(t\ +m)}\, p_{\ (t*m)}\, \psi_{\ (m)}$	1782.417	14.7036	0.0002	37	499.74
$\phi_{(t\ *m)}\, p_{\ (t*m)}\, \psi_{\ (m)}$	1792.891	25.1775	0	46	490.27
$\phi_{(a2)}\, p_{\ (t)}\, \psi_{\ (m)}$	1795.672	27.9582	0	18	553.66
$\phi_{(a2)}\, p_{\ (t+m)}\, \psi_{\ (m)}$	1796.954	29.2401	0	19	552.85
$\phi_{(t\ *m)}\, p_{\ (t*m)}\, \psi_{\ (.)}$	1799.433	31.7194	0	45	499.05
$\phi_{(t\ *m)}\, p_{\ (t)}\, \psi_{\ (m)}$	1816.579	48.8648	0	42	522.87

AICc, akaike information criterion corrected.
Subscripts denote age (a2), time (t) and ornament (m) effects. Symbol '*' denotes interaction, and symbol '+' additive effects. a2 [1 year*m, ad] indicates age dependency with an ornament effect in yearlings, but not in adults. Only the 15 top-ranked models are shown.

LRS and female ornament expression

Similarly to the analyses of yearly reproductive success, analyses of fitness components across lifetime showed that ornamented females were more fecund, that is, they laid more eggs during their reproductive careers, than nonornamented ones even after taking longevity into account (Table 7a). Expressing the ornament at early ages did not influence lifetime number of eggs (Table 7a), but that effect became apparent when longevity was removed from the model (estimate for nonornamented females at early ages = -0.2227 ± 0.04335, $F_{1,276} = 8.87$, $P = 0.0032$), indicating that the differences were mainly due to differential lifespans between both groups of individuals, in accordance with analyses of survival probabilities (see above). Lifetime fledging success (number of fledglings/number of eggs) was slightly associated with ornament expression (Table 7b). The relationship between expressing the ornament at early ages and lifetime fledging production was marginally nonsignificant when longevity was maintained in the model (Table 7b), but again the effect was stronger when this variable was removed (estimate for nonornamented females at early ages = -0.2345 ± 0.09282, $F_{1,284} = 6.38$, $P = 0.0121$). In contrast, lifetime recruit production was unrelated to female trait expression both throughout lifetime and at early ages (Table 7c), and this result persisted when longevity was removed from analyses.

Table 6 Candidate CJS capture–recapture models. Shown are AICc, difference in AICc with the highest-ranked model (ΔAICc), model weight, number of identifiable parameters (K) and deviance for survival (ϕ) and reencounter (p) probabilities of female pied flycatchers.

Model	AICc	ΔAICc	AICc Weight	K	Deviance
$\phi_{(g)}\, p_{(g*t)}$	1172.233	0	0.70554	22	198.2186
$\phi_{(.)}\, p_{(g*t)}$	1174.391	2.1574	0.23991	20	204.623
$\phi_{(g)}\, p_{(t)}$	1178.008	5.7745	0.03932	17	214.5657
$\phi_{(.)}\, p_{(t)}$	1180.041	7.8075	0.01423	15	220.7862
$\phi_{(t)}\, p_{(g*t)}$	1185.687	13.4537	0.00085	33	187.8769
$\phi_{(t)}\, p_{(t)}$	1190.431	18.1977	0.00008	28	203.5297
$\phi_{(g*t)}\, p_{(t)}$	1191.063	18.8302	0.00006	39	179.9539
$\phi_{(g*t)}\, p_{(g*t)}$	1193.012	20.7793	0.00002	44	170.6418
$\phi_{(t)}\, p_{(.)}$	1223.601	51.3681	0	17	260.1593
$\phi_{(t)}\, p_{(g)}$	1225.672	53.4384	0	18	260.127
$\phi_{(g*t)}\, p_{(.)}$	1226.379	54.1455	0	29	237.3082
$\phi_{(g*t)}\, p_{(g)}$	1228.324	56.091	0	30	237.0782
$\phi_{(g)}\, p_{(.)}$	1255.008	82.7752	0	3	320.3941
$\phi_{(g)}\, p_{(g)}$	1256.689	84.4556	0	4	320.0523
$\phi_{(.)}\, p_{(.)}$	1258.68	86.4469	0	2	326.0824

AICc, akaike information criterion corrected; CJS, Cormack–Jolly–Seber.

Subscripts denote time (t) and ornament expression early in life (g) effects. Symbol '*' denotes interaction, and symbol '+' additive effects. Only the 15 top-ranked models are shown.
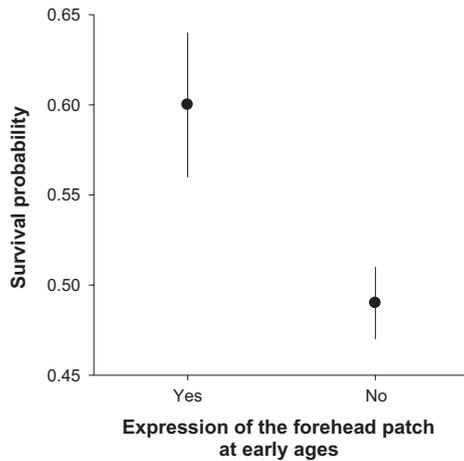

Fig. 3 Differences in survival probability (± SE) between females expressing or not the ornament at early ages (1–2 years old).

Discussion

We have presented long-term evidence on the covariation among the expression of a 'male' secondary sex trait displayed by a fraction of females with their yearly and lifetime fitness in the pied flycatcher, a model species in sexual selection studies. This study thus adds to the scant, long-term evidence on the ecological and evolutionary significance of ornament displaying by

Table 7 Results of GLMM analyses of components of lifetime reproductive success (total number of eggs laid, young fledged and recruits) of female pied flycatchers in relation to the expression (yes/no) of the forehead patch (FP) both throughout lifetime and at early ages (1–2 years). The lifetime number of eggs laid was modelled with a Poisson distribution of errors and a log link function. Lifetime fledglings and recruits were modelled with binomial errors and logit link functions using the number of eggs and the number of fledglings as binomial denominator, respectively. See Table S2 for equivalent analyses of absolute numbers of fledglings and recruits.

	Estimate	SE	F	P
(a) Total number of eggs laid				
FP expressed throughout lifetime				
Intercept	1.3896	0.07664		
FP expression			7.94	0.0051
Yes	0			
No	−0.1007	0.03574		
Age of first breeding	−0.2986	0.02802	113.56	< 0.0001
Longevity	0.3857	0.01398	761.53	< 0.0001
d.f.	1322			
FP expressed at early ages				
Intercept	1.2756	0.05426		
Age of first breeding	−0.3150	0.02499	158.96	< 0.0001
Longevity	0.4055	0.01109	1337.92	< 0.0001
d.f.	1451			
(b) Total number of fledged young				
FP expressed throughout lifetime				
Intercept	0.7780	0.08590		
FP expression			4.14	0.0428
Yes	0			
No	−0.1449	0.07124		
d.f.	1331			
FP expressed at early ages				
Intercept	0.5714	0.1951		
FP expression			3.70	0.0553
Yes	0			
No	−0.1816	0.09435		
Longevity	0.1032	0.03285	9.87	0.0019
d.f.	1283			
c) Total number of recruits				
FP expressed throughout lifetime				
Intercept	−2.4431	0.1826		
Longevity	0.1221	0.04031	9.17	0.0026
d.f.	1411			
FP expressed at early age				
Intercept	−2.4431	0.1826		
Longevity	0.1221	0.04031	9.17	0.0026
d.f.	1411			

GLMM, generalized mixed models.

both sexes in wild vertebrates (Roulin et al., 2010). Ornamented female pied flycatchers had increased (yearly and lifetime) fecundity and fledging success, suggesting that, regardless of the association between trait expression and age, expressing the trait on its own may signal an added age-independent (Hegyi et al., 2006) component to female quality. Interestingly, lon-

gitudinal analyses showed that ornamented females had a lower fledging success late in life than nonornamented females at advanced ages. Taken together, these results point to different 'strategies' of female ornament expression leading to similar payoffs in the long-term, with no differences in final fitness (as measured by recruitment rates) but on the life-history trajectories followed to attain it. On the one hand, females expressing the ornament seem to invest more in reproduction at early ages than nonexpressing females. Although ornamented females did not suffer apparent costs in survival (with the group of females expressing the ornament at early ages constituting in fact the most longeve group), they appear to pay those costs in terms of decreased fledging success at the older ages, in what seems a symptom of accelerated senescence that, unlike in most comprehensive studies performed to date, is paid in lowered fledging output, not in decreased clutch size (Gustafsson & Pärt, 1990) or in diminished survival prospects at older ages (Orrell & Belda, 2002). Females not expressing the forehead patch, on the other hand, seem to follow a slower pace of life, with a trajectory of gradual improvement in reproductive performance with increasing age without incurring in late-life declines in breeding output.

The female ornament as a quality indicator

When ornaments signal female quality, ornament expression should be related to different components of fitness. In birds, including the pied flycatcher (Morales *et al.*, 2007), there was previous support for positive associations between female ornaments and annual reproductive success (Velando *et al.*, 2001; Massaro *et al.*, 2003; Siefferman & Hill, 2005; Dey *et al.*, 2012), and other studies are also consistent with a role of female ornaments as likely indicators of quality (Roulin *et al.*, 2000; Griggio *et al.*, 2005; Kraaijeveld *et al.*, 2007; Vergara *et al.*, 2009; Martínez-Padilla *et al.*, 2011; but see Tella *et al.*, 1997). In contrast, studies examining the association between female ornamentation and LRS, an essential step to assess the adaptiveness of female ornamentation, are much scarcer (Roulin *et al.*, 2010; Dey *et al.*, 2012), and even the predicted relationship with an important fitness components (survival prospects; Andersson, 1994) was far from evident in the review of Amundsen and Pärn (2006). Combined with patterns of expression with age (Fig. 1), the increased lifetime fecundity (in terms of eggs laid and fledglings reared) of females displaying the forehead patch, the enhanced survival of those expressing it at early ages and the diminished fledging production of females that remain ornamented late in life suggest that displaying the forehead patch may be a costly indicator of quality in female pied flycatchers, even if the number of young they recruited did not differ significantly from that of nonornamented females. However, the caveat should be made that recruitment rates are subjected to large stochastic variation, implying a progressively vanishing influence of maternal quality over long timescales (e.g. after independence from parental care and later in adult life; Price, 1998) what would explain the lack of association between ornamentation and recruitment rates. Under this viewpoint, therefore, our results would suggest that ornamented females are indeed of higher quality than nonornamented ones.

Models of evolution of female ornamentation through resource (food, territories, nests, mates) competition state that some ornaments may function in females as agonistic signals in conflict resolution or either signal dominance, as it is common in males (Andersson, 1994; Owens *et al.*, 1994; Swaddle & Witter, 1995; LeBas, 2006; Murphy *et al.*, 2009; Griggio *et al.*, 2010; Midamegbe *et al.*, 2011; Rosvall, 2011; Tobias *et al.*, 2012). For instance, in the related collared flycatcher (Pärt & Qvärnstrom, 1997), the wing patch (another achromatic sex dimorphic signal) functions as a male sexual signal (Sheldon & Ellegren, 1999; Hegyi *et al.*, 2008; de Heij *et al.*, 2011) and is also involved in female agonistic behaviour against territorial intruders. Pryke (2007) has speculated that behavioural differences in dominance, maybe mediated by androgen levels, could result from linkage and/or pleiotropic interactions between genes controlling levels of dominance, aggression and expression of ornaments. Some important components of this scenario, as additive genetic variance and between-sex genetic correlation in ornament size, as well as significant female offspring–female parent resemblance in ornament expression, are present in at least some pied flycatcher populations (Potti & Canal, 2011). Thus, this might be an example that genetic correlations may act as a 'preadaptation' for functional female decoration (Amundsen, 2000b).

As its determination has a heritable basis of both size (both sexes; $h^2 = 0.5$) and expression (females only; $h^2 = 0.3$; Potti & Canal, 2011), it may appear intriguing why the ornament is not displayed by all females, suggesting that its mere expression in this sex may be environmentally induced, epigenetically modified (Badyaev, 2004) and ultimately maintained through a balance between evolutionary benefits and costs. Under the theory of honest signalling, only high-quality individuals can afford the more costly expressions of ornaments (Zahavi, 1975; Grafen, 1990; Dale, 2006). Likely proximate (physiological or behavioural) costs to trait expression could be, for instance, increased predation risk due to enhanced detectability by predators (Götmark *et al.*, 1997), escalated costs of immunological defence against parasites in ornamented females (Folstad & Karter, 1992) or increased rates of aggression by other individuals (Berglund *et al.*, 2008; Cain *et al.*, 2011). Further detailed, preferably experimental studies (Blount *et al.*, 2002; McGraw *et al.*, 2005; Doutrelant *et al.*, 2008; Gasparini *et al.*, 2009; Kekäläinen *et al.*, 2010; Martínez-Padilla *et al.*, 2011) as the recent one of

Moreno *et al.* (2012) are needed. By experimentally manipulating forehead patches of female pied flycatchers in a nearby Iberian population, that study has shown that female Iberian pied flycatchers pay costs, in terms of oxidative damage, when expressing the ornament. These authors suggest that the female forehead patch may function as a badge of status under socially mediated control, with females lacking the ornament incurring in less physiological costs while breeding but maybe suffering competitive exclusion from breeding resources (Moreno *et al.*, 2012). From results presented herein, we suggest that fitness advantages are compensating the costs of ornament expression in at least a fraction of females, thus ultimately being involved in the maintenance of the within-sex dimorphism of lifetime ornament expression in female pied flycatchers.

Trait coevolution between the sexes

The evidence here reported suggests that ornament expression in female pied flycatchers is a target of selection and also that sexually antagonistic coevolution is not strong at the stage of the dynamic (Lande, 1980; Bondurianksy & Chenoweth, 2009) coevolutionary race between the sexes in which the population seems to be presently immersed (Potti & Canal, 2011). For genetic sexual conflict to occur, there should be some degree of sexually antagonistic selection, but signs of directional selection in both sexes (on trait expression in females, on trait size in males) have been observed instead. Why forehead patch expression is positively associated with some fitness components could then be due to two alternative processes. On the one hand, the patch may represent a direct target of selection. On the other hand, ornament expression could have no 'true' functional significance in females, but still remain correlated with fitness by virtue of its association with heritable quality in males and due to a genetic correlation between the sexes (which is near unity for ornament size; Potti & Canal, 2011) that should be reinforced by the pattern of assortative mating regarding ornament size (Lande, 1980; Kraaijeveld *et al.*, 2007; Kekäläinen *et al.*, 2010). However, in the first case, the same trait would be under positive selection in both sexes, whereas in the latter case females carrying 'good genes' would be those expressing the male-like ornament (again suggesting that sexual genetic conflict might be weak or absent). Our analyses cannot fully discriminate between both explanations as we still do not know whether females expressing the ornament are those with 'good genes', inheriting male quality. To quantify the relative importance of each type of explanation, a full assessment of selection on ornament in males will be needed as well (Kraaijeveld *et al.*, 2007; Bondurianksy & Chenoweth, 2009; Roulin *et al.*, 2010, 2011). However, a major drawback to that approach is that a joint selection assessment in males and females can

only be performed on ornament size, as ornament expression is universal in males (at least in Iberian populations), making uncertain predictions merely involving its rather limited expression in females (cf. Roulin *et al.*, 2010).

In conclusion, we have presented evidence on variation in a secondary sex trait that is differentially expressed in both sexes being related to lifetime-based benefits and costs of its expression in females. Future work on ornaments shared by males and females should ideally combine molecular (Nadeau *et al.*, 2007; Wright *et al.*, 2007; Williams & Carroll, 2009; Khila *et al.*, 2012; Lehtonen *et al.*, 2012), observational and manipulative studies in both sexes to reveal the intricacies of proximate, including genetic, epigenetic and environmental, influences underlying their phenotypic expression.

Conflict of interest

None declared.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1 GLMMs (final models) showing the effects of female age and forehead patch expression on (a) yearly numbers of young fledged (Poisson distribution); (b) yearly numbers of recruits (negbin distribution).

Table S2 GLMMs (final models) showing the effects of female age and forehead patch expression on (a) total (lifetime) numbers of young fledged (Poisson distribution); (b) total (lifetime) numbers of recruits (negbin distribution) after controlling for longevity and age of first reproduction.