Master degree in Biodiversity and Conservation Biology

Are males choosy?:

Investigating male mate preference in a songbird

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Abstract

Sexual selection has been a key topic of several studies in evolutionary biology, as sexual selection can explain the diversity of conspicuous traits and displays in both males and females. Through the preference for the most conspicuous males, females gain direct or indirect benefits, which drive female choice along the classical models of sexual selection. However, the role of female traits mediating mate choice in males remains unclear. To fill this gap, we tested the association between female identity and female traits with the intensity of male courtship behaviour (reflecting male preference) in a field study of the collared flycatcher (*Ficedula albicollis).* To describe the male's interest toward a particular female, we estimated the time delay that occurred between the detection of female decoy and the initiation of courtship behaviour (latency to display). We predicted a positive relationship between female traits and the intensity of male courtship, if female traits reflect quality and males show preference for them. Contrary to this prediction, our results showed no statistical relationship between latency to display and female traits. However, we detected that the same female elicited similar responses from different males, which may suggest that some females are considerably more attractive for males than others, thus males may also show preference towards particular females to some degree. We also found a relationship between date of the observation and the latency displayed by males indicating that males arriving latter in the season have shorter latencies than early males. This result suggests that males become less choosy as the season progressed suggesting that the cost of delaying breeding is substantially higher than mating with best females. Further research is needed to identify the female traits that mediate male choice, and the benefits that males gain by developing preference for them.

Keywords: *Ficedula albicollis*, male mate choice, conspicuous traits, male preferences, individual quality.

Introduction

Sexual selection has been topic of considerable study in the realm of the evolutionary biology (Majerus 1986; Amundsen 2000; Kokko et al. 2003; Andersson and Simmons 2006; Kraaijeveld et al. 2007). Sexual selection could be defined as a result of interactions between individuals of the same sexes, opposite sexes or both (Kokko et al. 2006). These interactions between individuals could lead the evolution of conspicuous traits via intra- or intersexual mechanisms. Given that reproductive success of males depends on females availability and fecundity of females among other, it may be expected that males are under strong sexual selection (Kokko et al. 2006). Thus, males in nature have developed a range of extravagant ornament or courtship displays to attract the attention of females and/or monopolize them (Kodric-brown and Brown 1984; Iwasa and Pomiankowski 1994). However, conspicuous traits entail costs due to increased visibility to predators (Stuart-Fox et al. 2003; Ercit and Gwynne 2015), decrease of nutrients needed for other physiological functions (Nordeide et al. 2006) or energetic trade-offs (Fitzpatrick et al. 1995). Consequently, only individuals with the highest quality are able to bear these costs and maintain elaborate traits.

Several models have been postulated to explain the evolution of mating preferences, divided in two major groups according to the type of benefits –direct or indirect- to females (Kokko et al. 2003). Females may gain direct benefits such as nuptial gift, better territory quality (Alatalo et al. 1986; South et al. 2012) or/and higher investment on parental care (Møller and Thornhill 1998) by mating with the most ornamented male. In other cases, females may gain indirect, genetic benefits by improving the fitness of their offspring, for example, through higher growth or survival (Petrie 1994). Within the indirect-benefits models, two of the most popular hypotheses predict that selection acts on progeny survival -“good genes” models- or on progeny mating success -“Fisherian” or “sexy son” models-

(Kokko 2001; Kokko et al. 2002). Furthermore, other genetic models have been proposed to explain the evolution of mate choice such as the genetic compatibility (Neff and Pitcher 2005)–female choose males to maximize the genetic compatibility between herself and the male – or the genetic diversity model (Piertney and Oliver 2005)– choice is performed to increase the genetic diversity of the offspring-. Regardless the underlying model explaining the evolution of mate choice, the dominant trend in studies of sexual selection has been to assume a role of competitive males and choosy females (Kirkpatrick 1982; Majerus 1986; Andersson and Simmons 2006).

In a number of species, females show ornamental or colourful traits similar, but usually reduced, to those found in males (Andersson and Iwasa 1996; Kraaijeveld et al. 2007; Clutton-Brock 2009). For example, in some species of empidid dance flies, females show abdominal sacs and enlarged pinnates leg scales similar than those in males (LeBas et al. 2003). In the crested auklet (*Aethia cristatella*), a monogamous seabird, females and males have a crest in the forehead, and both sexes show mate preferences for individuals with larger crests (Jones and Hunter 1993). Except sex-role reversed species, female ornamentation has been traditionally assumed to be non-functional, being explained as a genetic by-product of the sexual selection acting on male traits i.e. due the genetic correlation between male and female traits (Smiseth and Amundsen 2000; Kraaijeveld et al. 2007). In the last decades, however, an increasing number of works has shown a functional role of female traits in sexual selection either via female-female competition and/or male preference (Owens et al. 1994; Bernet et al. 1998; Jones and Hunter 1999). A key fact of the underlying hypothesis is that female traits under sexual selection should signal aspects of individual quality. Accordingly, although some works have reported a lack of correlation between sexual selected traits in females and quality (Møller 1993; Cuervo et al. 1996; Rohde et al. 1999; Smiseth and

Amundsen 2000), there is increasing evidence showing a positive correlation between female traits and individual quality. For example, in northern cardinals (*Cardinalis cardinalis*), a dichromatic species in which both sexes are ornamented, female plumage colour was positively associated with their investment in parental care (Linville et al. 1998). In the striped plateau lizard (*Sceloperus virgatus*), the size of female's ornament predicts body quality and sprint speed in offspring (Weiss et al. 2009).

Assuming a functional role of female traits in sexual selection, an important question remains: If certain female traits have a potential to signal individual quality or reflect maternal investment, is male willingness for mating influenced by these females' traits?. If male readiness to mate varies in response to females traits, we could predict that certain female traits expressing individual quality should be eliciting different response from males. Female individual quality could be expressed as better offspring quality and/or higher parental investment. Consequently, male preferences for better quality females would increase male fitness. However, existence of male preferences is expected in a scenario with high availability of fertile females. Thus, empirical evidence is warranted to understand the mechanism underlying the maintenance and variation of male mate preferences.

In this study, we empirically tested the existence of male preference for female traits in the collared flycatchers (*Ficedula albicollis*). The species has a socially monogamous mating system with facultative polygyny (Gelter 2017). Previous work in this species has shown the influence of different male's traits (e.g. wing patch size (WPS): (Gustafsson et al. 1994; Garamszegi et al. 2006); forehead patch size (FPS): (Garamszegi et al. 2006), age: (Garamszegi et al. 2007) in both intra- and inter-sexual contexts. Interestingly, females show certain ornamental traits similar to those found in males such as WPS, but the role of female traits in sexual selection has been scarcely explored. Given that males are visited by several females prior mating (i.e. (Lundberg and Alatalo 2010), and there is variance in the quality of female determining reproductive success, we can hypothesise that males develop preference towards certain traits depending on female quality (e.g. tarsus and mass: (Garamszegi et al. 2004; age: Török et al. 2007; WPS: Hegyi et al. 2008). Here, we examined whether the intensity of the male's courtship –used as a proxy of the male preference by females- was related to the characteristics of the different females used as decoys in a set of behavioural assays. In particular WPS, tarsus, mass and age, are traits that could reflect quality or maternal investment/effort. Thus, we predict that these female traits might affect the intensity of male's display.

Materials and Methods

Study species and area

The study was conducted in a breeding population of collared flycatchers, in the Pilis Mountains, near Budapest (Hungary), that is monitored as a part of a long-term study since 1981. The study population is located in a continuous, unmanaged, oak-dominated woodland, within the protected area of Duna-Ipoly National Park. Nest boxes are about 1.5–2 m above the ground at a mean distance of 12-15 meters (Török and Toth 1988).

The collared flycatcher is a small (13 g), insectivorous passerine that breeds in Central-European broad-leaved forests. After arriving at the breeding sites from their wintering refuges in Africa south of equator, male collared flycatchers establish a small territory around a nest hole (Gelter 2017). Males defend their nest boxes by aggressive interactions against intruding individuals (Garamszegi et al. 2008) and try to attract females by singing and through conspicuous courtship displays based on callings, excited flights around the nest box and repeating landings on its top and entrance hole. Females arrive at the breeding area later than males (about a week later) and usually visit several territories that are occupied by males prior mating (Garamszegi et al. 2007). Clutch size typically ranges between 5-7 eggs and, except rare events (e.g. early desertion/dead of the mate, predation attempt), females lay one clutch per breading season. Only females incubate the eggs, but both sexes provide parental care during the nestling stage. Although the species is primarily monogamous, some males acquire a second female and become polygynous (< 10%). In those cases, polygynous males usually reduce their parental care in the secondary brood (László Zsolt Garamszegi et al. 2004).

General fieldwork procedures are detailed in (Wilson and Hegyi 2010). Briefly, during the breeding season (March-June), nest-boxes were checked daily to ascertain the arrival date of males. Once we locate the newly arrived males, we measured the intensity of male’s courtship by presenting territory owners with a live decoy female, placed in a wire cage (20x15x15 cm) on the top of a nest box. Decoy females were caught at arrival, ringed with numbered aluminium rings, if necessary, measured and supplied with mealworms and drinking water ab libitum while they were in captivity (ranged from 0 to 18 days in captivity). Different females were randomly assigned to different tests, and the same females were used several occasions as decoy individuals for different males. Behavioural tests were conducted in good weather conditions, during the most active period of individuals (between 5 and 12 am). To quantify the intensity of male’s courtship, we measured the latency (in seconds) elapsed between the appearance of the resident male on its territory and the first landing on entrance hole of the nest-box (Garamszegi et al. 2012). Males were recorded for 5 minutes, beyond which, it was assumed that the male’s interest for the female was low. This assumption was based on previous works in the study population, wherein males not responding aggressively to decoy males in the first 5 minutes, did not responded at all.

Therefore, males not responding to decoy females were given a latency of 301 seconds (Garamszegi et al. 2012). The behavioural assays were conducted by the same researchers (Balázs Rosivall, Gábor Markó, Gergely Hegyi) at a distance of 25–30 m from the focal nest-box.

Although morphological traits are typically measured after capture in males and females during feeding the nestlings, for the experimental individuals, traits were measured at arrival (for females, as explained above) and immediately after experimental assays for males. Body mass was measured with a spring balance (to the nearest 0.1 g) and tarsus length (as a proxy of body size) was measured with a calliper (to the nearest 0.1 mm). We used tarsus length and mass as covariate to express body condition. Forehead patch size in males (it was not measured in females as only a small fraction of females in the population express this trait) was estimated as the product of largest width and largest height of the patch (to the nearest 0.1 mm with a calliper). Wing patch size (WPS) was estimated in both sexes as the sum of the length of white bars on the outer vanes of 4th–8th primaries, measured from the tip of the coverts. WPS is condition-dependent, sexually selected and heritable trait. Given that the expression of WPS changes from yearling to adult plumage in males (Török et al. 2003). We standardized WPS across age categories bringing the age classes to a common mean of 0 and standard deviation of 1. The exact age of many individuals was known due to natal philopatry of the species (Hegyi et al. 2008). Unringed birds first captured as adults were aged as first year (yearlings hereafter) or older on the basis of plumage traits (Svensson 2002).

Statistical analyses

To investigate the factors affecting the male's willingness to courtship the females, we fitted a Generalized Linear Mixed Model (GLMM; normal error distribution and Gaussian link function). GLMMs were fitted in the R statistical environment (version 3.1.2, http://www.R-project. org) using the function lmer in the package ‘lme4’ (Bates et al. 2014). As a response variable, we included the latency to land on the hole of the nest box. Although latency was truncated in 301 sec (figure 1) due to individuals non-responding to decoy females, this truncation showed no serious violence effects when investigating the statistical assumptions of the GLMM based on log-transformed latency scores. After transformation, diagnostic plots of model residuals did not indicate obvious deviation from the assumed normality criterion. As fixed effects, we included age of both sexes, the mass and tarsus of males and females, the WPS (standardized by age as explained in field procedures) of both sexes and FPS of males. We also included the date of the experiment as a covariate in the model, since breeding date is a strong determinant of reproductive success in the species (Kokko 1999). Therefore, it is expected that the male willingness to mate varies as the breeding season advances due to the lower number of fertile females is available tater in the season and due to other costs of delayed breeding (Canal et al. 2012). As random effects, we included year (to account by environmental heterogeneity) and female ID (as some females were included several times in the behavioural tests). The inclusion of female ID as a random factor allowed us to investigate the variance in the male’s latency explained by females i.e. to quantify the repeatability in the male’s response of different males caused by the same female, which could suggest the extent of a male preference for certain females.

We performed model diagnostics statistics during prior interpreting the final model to avoid conclusions based on statistical artefacts. To check GLMM assumptions of normality in the distribution of residuals, we used diagnostics plots (e.g. Q-Q plots, histograms). These analyses did not show any obvious deviation from GLMM assumptions. Further, to assess collinearity among fixed factors, we calculated the Variance Inflation factors using the function vif of the R-package ‘car’ (Fox and Weisberg 2011). An average VIF for pairs of variables that is substantially higher than 2 indicates a problem. Further, to determine the existence of influential observations, we performed DFFit and DFBeta tests (Quinn and Keough 2003). We did not detect collinearity among the predictors (largest Variance Inflation Factor=1.25) and leverage values as well as DFBeta values indicated no obviously influential cases (Quinn and Keough 2003). Selection of the final model (containing only statistically significant terms) was carried out by dropping non-significant terms from a fully saturated model (containing all main effects and interactions) in a hierarchical way, starting with the least significant terms. Once we got final model containing only significant variables we re-introduced non-significant variables one by one to determine their significance (Table 1).

Results

We conducted 364 observations in 9 non-consecutive years of monitoring. Females were used as decoy individuals, on average, in 6 occasions (range 1-34) in the trials. Latency of males to enter the nest box was, on average, 104.69 sec (median=51.50, standard deviation=114.10).

Latency to enter the nest box was not significantly associated with any of the measured traits in males or females (see table 1). By contrast, male willingness to mate increased as the season progressed, as latency to land decreased along the date of the experiment. Female identity explained 2.6 % of the total variance in the model, suggesting that behaviour of males was somewhat consistent for the same decoy females after controlling for the characteristics of the male and other co-founders considered in the statistical models.

Discussion

Here, we have shown in a field study of a wild passerine bird that the intensity of male's courtship is influenced by the identity of females. However, we failed to identify the female traits that influence the male behaviour suggesting that other non-measured variables of females mediate the variation in male courtship. Date of experiment was negatively related to latency (Figure 2) suggesting that males become less choosy as the season advances.

Our results suggest that males adjust the intensity of their courtship according to the identity of decoy females, suggesting that male mate preferences in the species may be in effect at some degree. Several works have shown a relationship between reproductive success, female age (Angelier et al. 2007; Mauck et al. 2017) and female ornamentation (Morales et al. 2007). Given that in this species, males are usually visited by several females in a single breeding season, males might benefit by modifying their courtship according to the quality of the females. Hence, if males show differences in the display of courtship depending on female ID, we could speculate that some differences in females quality that translates into differences in breeding success or other fitness benefits may exist that further encourage males to show preferences towards females with superior quality. In the rock sparrow (*Petronia petronia*), a monomorphic passerine in which both sexes show a yellow breast patch, patch size in females is related to body mass and fecundity, and females with reduced breast patch were courted less intensely than control females (Griggio et al. 2005). Further, females with reduced ornaments were less likely to mate and paired at a significantly later date than controls (females with non-reduced patches) (Griggio et al. 2005). Moreover, in dark-eyed juncos (*Junco hyemalis*) males and females bear white tail feathers. Males showed individual preferences but neither preferences for trait that indicate age/experience nor preferences for less male-like females' tails (Wolf et al. 2004). This results give us evidence to elucidate that non-measured female variables could be underlying the effects of female identity on courtship latency.

All traits that we measured in females were unrelated to the latency of males to land on nest-box. This was an unexpected result because if male adjust their courtship according to the quality of female and the expected reproductive success, one would predict that female traits signalling quality (tarsus, mass, age, and WPS expression) would influence the intensity of courtship in males. Nevertheless our results don’t show any obvious relation of these traits to male preferences, but given the existence of male responsiveness to female identity, a plausible explanation is that we did not measure the variable affecting the preferences of males. For example, other studies have shown an influence of UV reflection of males feathers in the mating patterns and female male choice in the similar species *Ficedula hypoleuca* (Siitari et al. 2002) and it has been proven that plenty of birds species are sensitive to near UV light (Bennett and Cuthill 1994). Further, behavioural traits such as aggression or activity rate could be underlying males preferences. Thus, more behavioural variables should be measured to elucidate a possible relation between them and the intensity of male courtship. Ultimately, experiments of artificially modification of ornamental traits have been shown in males as a proper approach to discriminate with more certainty the existence or lack of effects of ornamental traits on behavioural assays (Griggio et al. 2005).

None of the measured traits of males influenced their latency to land on the nestbox during courtship. We included these male traits (WPS, FPS, mass, tarsus and age) in models to control the possible influence of males traits in their own behaviour. Besides, since males are visited by several females, we could speculate that better males (e.g. individuals with larger WPS) could adjust properly their display based on perceived female quality. Likewise, worse males should show less preferences as they are less likely to mate with better females, assuming the influence of both mate choice.

We found that the date of the observation was negatively associated with the latency of male displays (Figure 2). This result suggests that the male's interest to mate changes as the season advances. A plethora of studies has shown that an early reproduction is one of the main determinants of breeding success in seasonally breeding taxa (e.g. mosquitoes, (Kleckner et al. 1995); butterflies, (Carvalho et al. 1998); flycatchers, (Canal et al. 2012, Garamszegi et al. 2004)). Accordingly, males are expected to increase their investment in courtship displays regardless to the quality or identity of females due to the increased costs of delayed breeding or the higher risk of missing a breeding opportunity. These seasonal changes in the reproductive outcomes are expected because, for example, later in the season the number of fertile females decreases in the population or conditions for successful breeding deteriorates (sub-optimal food supply, less time for moult before winter migraton (Wilson and Hegyi 2010; Canal et al. 2012)). Consequently, later arriving males should not discriminate between females of different quality, because the costs of late paring are higher than costs of pairing with less ideal female (best-of-a-bad-job).

Overall, our results suggest that male preference for females in the collared flycatcher may occur, since the intensity of male courtship behaviour was consistently differed among females, to which males were exposed: some females elicited systematically higher interest among males than other females. However, we failed to identify a female trait that may mediate male preference implying that an unobserved property of females may be important in this regard. Furthermore, we observed that males were less choosy as the season progressed, as later males started their courtship with lower latency shown. A possible explanation to this phenomenon is that the cost of delayed breeding and/or the reduced number of fertile females available mediate a generally high interests for any female in late arriving males. Future studies with broader focus on female traits (i.e. with the inclusion of coloration or behaviour, see (Siitari et al. 2002) in the combination with experimental approach are needed to identify the most important female signals of quality that determines the intensity of male courtship.

Compliance with ethical standards

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Permissions for the fieldwork have been provided by the Middle-Danube-Valley Inspectorate for Environmental Protection, Nature Conservation and Water Management, ref. no's: KTVF 16360-2/2007, KTVF 30871-1/2008, KTVF 43355-1/2008, KTVF 45116-2/2011, KTVF 21664-3/2011, KTVF 12677-4/2012, KTVF 10949-8/2013) and was approved by the ethical committee of the Eötvös Loránd University (ref. no. TTK/2203/3).

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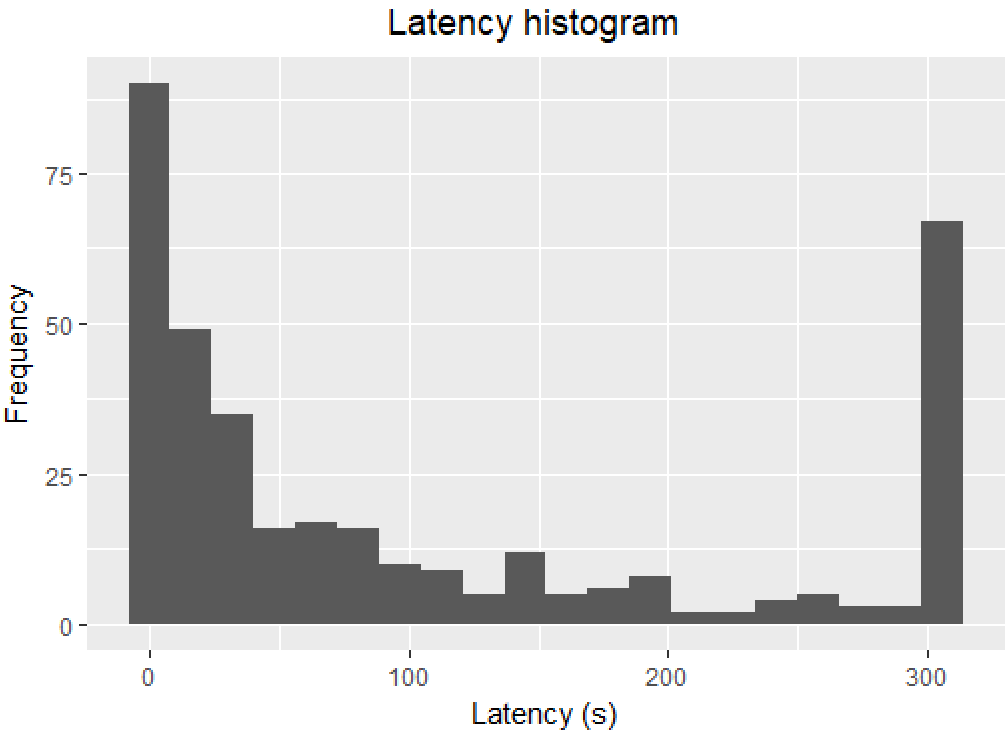

Figure 1. The distribution of the latency to land on the nest-box hole (initiation of courthisp) in the collared flycatcher (N=364).

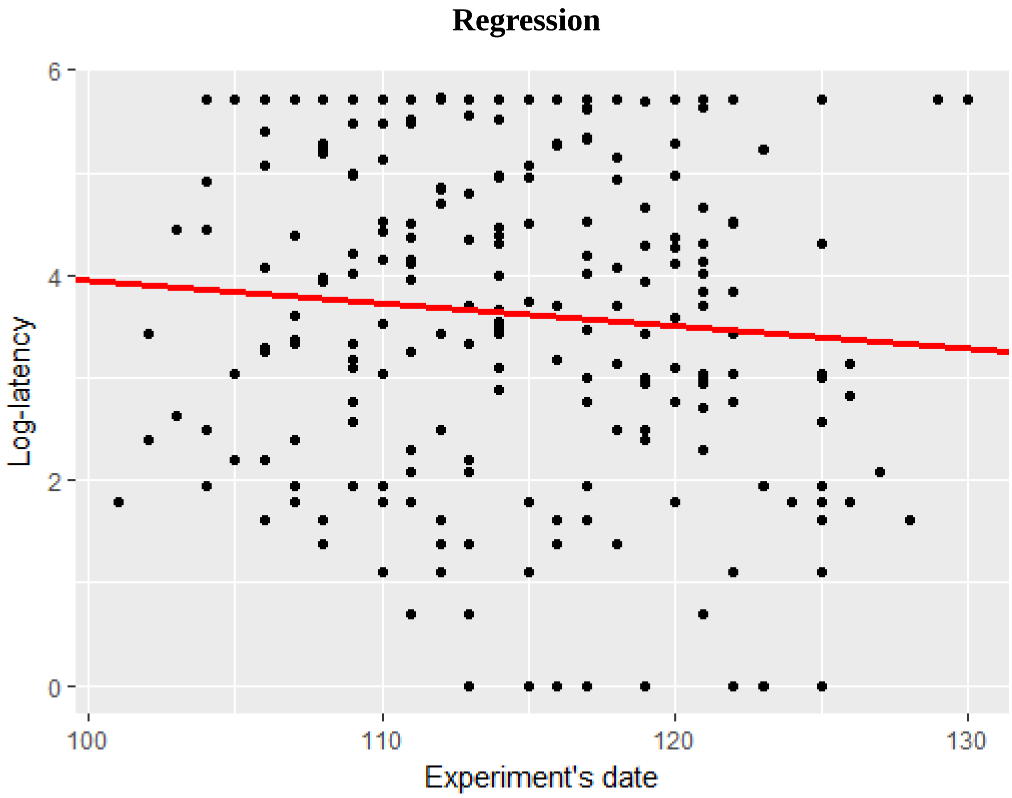

Figure 2. The relationship between the latency to start displaying and the date of observation. The line is the regression line, which has the equation of Y = -0.022X+6.123.

Table 1. Results of a mixed testing for the relationship between the latency to land on the hole of the nest-box and female and male traits. Male and female traits were included as fixed factors in the model, while female ID and year were random factors. Values for non-significant effects are derived from the selected final model (based on backward stepwise model selection procedure), to which the given variable was re-introduced. The significant variable retained in the final model typed in bold.

Variables	Estimate	Std. Error	df	t value	Pr(>|t|)
Random effects					
Decoy female identity	0.082	0.286			
Fixed effects					
Male WPS	0.121	0.102	269.290	1.118	0.121
Male mass	-0.213	0.177	246.200	-1.204	0.230
Males tarsus lenght	0.160	0.206	262.410	0.776	0.439
Male age (yearling/adult)	-0.165	0.213	224.560	-0.773	0.440
Male FPS	0.000	0.000	258.600	0.154	0.878
Female WPS	-0.001	0.002	33.040	-0.476	0.637
Female mass	-0.014	0.140	38.030	-0.103	0.919
Female tarsus	-0.082	0.251	31.490	-0.326	0.747
Female age	0.068	0.079	22.640	0.860	0.399
Date of experiment	**-0.034**	**0.018**	**75.750**	**-1.954**	**0.054**

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