Male barn swallows use different resource allocation rules to produce ornamental tail feathers

Alberto Muñoz, José Miguel Aparicio, and Raúl Bonal

Departamento de Ciencias Ambientales, Facultad de Ciencias del Medio Ambiente, Universidad de Castilla-La Mancha, Avda Carlos III s/n, E-45071 Toledo, Spain, Grupo de Investigación de la Biodiversidad Genética y Cultural, Instituto de Investigación en Recursos Cinegéticos-IREC (CSIC-UCLM-JCCM), Ronda de Toledo s/n, E-13005 Ciudad Real, Spain, and Department of Entomology, Natural History Museum, Cromwell Road, SW7 5BD London, United Kingdom

Sexual ornaments compete for resources with other functional traits. Such resource allocation trade-offs should ensure the honesty of sexual ornaments according to the Zahavi’s handicap principle. However, the existence of costly signals could not be enough to guarantee honesty if different individuals invest different proportions of their limited resources in ornaments. Then, a certain level of sexual signaling would correspond to several levels of individual condition. Here, we explore whether there are different resource allocation rules in tail feather ornaments between males within a barn swallow (Hirundo rustica) population and whether these different rules confer different viability to males. We assessed the proportion of resources invested in ornamental feathers compared with other functional feathers moulted and growing during the same period at expenses of the same resources. We found that 1) different males allocate a different proportion of resources to ornamental feathers in relation to functional feathers and this proportion is repeatable between years and 2) male survival likelihood decreased as the proportion of resources allocated to ornamental feathers increased. Survival costs associated with increased investments in ornaments can maintain the sexual signaling system honest at population level but do not preclude the existence of an array of different allocation rules between males. Thus, males with different viability can produce ornamental feathers of the same length. These results show that the relationship between male viability and ornament expression can be less straightforward than considered previously. Key words: barn swallow, honesty, resource allocation, sexual ornaments, tail feathers, trade-off. [Behav Ecol 19:404–409 (2008)]

More than 3 decades ago Zahavi (1975) suggested the “handicap principle,” which considers secondary sexual traits to be essentially honest signals of male quality because exaggerated ornaments are costly to produce and maintain, and therefore, only high-quality males can afford those costs. It is assumed that the expression of these secondary sexual characters compete for resources with other condition-dependent traits (e.g., Rowe and Houle 1996; Moczek and Nijhout 2004) because the resources are limited and when they are invested in the production or maintenance of ornaments they cannot be allocated in other functions. Thus, investing resources in ornaments may constrain the development of ordinary morphological traits, functions of organs (Blanco and de la Puente 2002), immune system (Folstad and Karter 1992), or parental effort (Siefferman and Hill 2005). Such resource allocation trade-offs should ensure the honesty of secondary sexual signals according to the communication theory based on the principle of handicap. However, the existence of costly signals could not be enough to guarantee honesty if there are different rules of signaling (Aparicio et al. 2003) or multiple optimal rules of resource allocation. When we say different rules of signaling, we mean that a certain signal can be produced using a different amount of resources (see Aparicio et al. 2003). In addition, there can be different ways of allocating optimally the resources between sexual ornaments and other functional traits, that may not be necessarily related to male condition. Under both premises, a signal of a certain level would correspond with several levels of individual condition or quality. It is known that biological signaling systems can be stable with some degree of dishonesty (e.g., Johnstone and Grafen 1993; Smith 1994; Adams and Mesterton-Gibbons 1995), but the proliferation of multiple rules of signaling or allocation could disrupt the signaling system or evolve toward a new and less costly system, depending on the costs associated with the changes in the rules (Aparicio et al. 2003).

Most theoretical studies assume that there is a single optimal strategy of resource allocation in ornamental versus functional traits, which maximizes fitness performance (see Rolf 1992; Stearns 1992). However, given that resource allocation trade-offs occur at individual level, there may be individual differences in fitness return that, theoretically, could lead to a wide range of potential optimal levels of resource allocation to ornaments in a population (Lindström et al. 2005). Under this scenario, each individual would invest a different proportion of their limited resources in secondary sexual traits, depending on their particular circumstances (see Hunt et al. 2004). For example, Basolo (1998) found that male green swordtails shifted their relative levels of allocation from growth in both body and sword length to growth in sword length alone when they were subjected to an experimental reduction in food availability. Also, studies carried out with fish (Candolin 1999) and beetles (Sad et al. 2006) have shown that individuals increase their allocation of resources to sexual attractiveness when they perceive survivorship threats.
These individuals develop ornaments greater than those expected according to their condition. Furthermore, the optimal rule of resource allocation to sexual ornaments could depend on the expression of sexual ornaments of other conspecifics with which individuals interact (Kokko 1997; Lindström et al. 2005).

Experimental manipulations on the levels of resource allocation to ornaments have generally shown negative consequences on fitness. For example, some studies have evidenced that experimental increases of the level of circulating testosterone may cause an increase of resource allocation to sexual ornaments, reducing the investment in other functions such as the immune system (Folstad and Karter 1992), and those changes may provoke a reduced condition, impaired immune function, and reduced survival (Grosman 1985; Ketterson and Nolan 1992; Salvador et al. 1997; Verhulst et al. 1999; Casto et al. 2001; Peters et al. 2004; Redpath et al. 2006). In addition, other studies have shown that experimental enlargements of ornamental traits frequently reduce individual viability too (Møller and de Lope 1994; Veiga 1995; Grewell 1997). Although these experiments reveal the costs of bearing enlarged ornaments that would penalize a disproportionate resource inversion in such traits, it is still unknown whether different individuals can have different rules of resource allocation and which would be the fitness consequences of the different ways of allocating resources between ornamental and functional traits in wild populations.

In this study, we want to ascertain whether there are different and repeatable allocation rules in tail feather ornaments between individuals within a barn swallow (Hirundo rustica) population and whether these different natural rules of resource allocation confer different viability to males. The barn swallow is a good study model because its outermost tail feathers are a typical example of sexual ornament (Møller and de Lope 1994; Møller et al. 1998). Many studies evidence that these sexually dimorphic feathers, longer in males than in females, are honest signals of male quality because females mate preferentially with long-tailed males, which are more viable than short-tailed ones (Saino and Møller 1994, 1996; Saino, Bolzern, et al. 1997; Saino, Primmer, et al. 1997; Saino et al. 1999, 2002; Møller et al. 1998; but see Bro-Jørgensen et al. 2007). Moreover, we can characterize the allocation rules by assessing the proportion of resources invested in ornamental tail feathers in relation to other functional feathers such as primary wing feathers, which are moulted and then grow during the same period at expenses of the same resources. We considered feather mass as a reliable and comparable currency for resource allocation in feathers, given that all structural components of feathers have a similar origin and composition (King and Murphy 1987; Vincent 1990; Prum 1999). Barn swallows have a single complete annual moult that starts in autumn and continues for 4–6 months. Moult of wing and tail feathers takes place in the same period and lasts several weeks before the feathers are completely grown (Møller 1994). Thus, there is a compromise regarding the investment of their limited resources to ornamental feathers (i.e., outermost tail feathers) or to functional ones (e.g., primary wing feathers) when moultling. In order to assess the relative investment on each type of feathers we calculated the residuals from the regressions of the outermost tail feather mass on primary 7 wing feather mass. Obviously, these residuals could be either simply random deviations or really different resource allocation rules. To confirm the existence of different allocation rules, we assessed the repeatability of those residuals within individuals in the population throughout different moultles. We also analyzed whether the different allocation rules were related to the survival prospects of individuals. Finally, we discuss the implications of our results for the theory of sexual selection and the honesty of sexual signaling. We suggest that the existence of different allocation rules among males could make the relationship between male viability and ornament expression less straightforward than previously considered.

**MATERIALS AND METHODS**

**Study area and field methods**

The study area was located in the Province of Toledo (Central Spain). In this area, barn swallows breed in colonies from May to August in abandoned buildings. During the breeding seasons of 2004 and 2005, we captured adults using mist nets at 10 and 8 colonies, respectively. We could not recapture in 2 of the colonies because the buildings were demolished or re-formed at the beginning of 2005. Barn swallows roost overnight in the abandoned buildings where they breed, and mist nets were set up covering all windows and doors before sunrise. This ensured that very few birds escaped during our capture sessions. Individuals captured in 2004 and not recaptured in 2005 were thus considered not to have survived because barn swallows have a very large breeding philopatry to their breeding colony (Møller 1994; Saino et al. 1999).

**Bird measurements and feather collection**

When first captured, each adult was individually marked with a numbered aluminum ring. Then, we measured tarsus and head–bill lengths with a digital caliper (to the nearest 0.01 mm), and the bird was weighed with a digital balance (to the nearest 0.1 g). Body mass varied in females with the date of capture ($r = 0.26, n = 63, P < 0.01$) and in males increased along the morning ($r = 0.38, n = 53, P < 0.01$). Thus, we standardized their masses to control for those variables, and the residuals for each sex were used as a measure of body condition. From each individual, we also took a sample of blood in heparinized capillary tubes from the brachial vein. The birds were sexed by inspecting the presence (females) or absence (males) of an incubation patch, and sexes were additionally confirmed with blood analyses.

We collected the right outermost tail feather and the right primary 7 wing feathers from each bird. These feathers were taken to the laboratory, where they were cleaned and inspected to detect and discard those broken or damaged. Feathers were scanned and weighed with a digital high-precision balance (to the nearest 0.1 mg). Feather length was measured over the scanned image (to the nearest 0.1 mm). Both the length and the mass of the feathers were measured on 17 females and 14 males 2 times in nonconsecutive order by different persons showing a high repeatability (for all measures on females: $F_{16} = 1529, r > 0.99, P < 0.00001$; for all measures on males: $F_{13} = 2290, r > 0.99, P < 0.00001$).

**Data analyses**

We regressed the mass of the tail feather against the mass of the wing feather and then calculated the residuals from that regression. These residuals were used as a measure of the resources allocated to tail (ornamental) feathers relative to wing (functional) feathers by each bird. To test whether these residuals are simply random deviations or not, we examined their repeatability within individuals throughout different moultles by regressing the residuals of each surviving individual from the first to the second year. Binary (yes/not) survival data of adult males and females were analyzed by logistic regressions in which the residuals and the morphological measures (tarsus length, bill–head length, body mass, body
condition, and tail length) were entered as parametric explanatory variables. Explanatory variables to be included in the final regression models were selected using a stepwise forward selection procedure.

RESULTS

Sex differences in tail and wing feathers

There were significant sex differences in the length and mass of the tail feathers, and in the mass of the wing feathers (Table 1). Sexual dimorphism (measured as the value of the male trait minus value of female trait) was 3.0% for the mass of primary 7 feathers, 0.9% for its length, 10% for outermost tail feather mass, and 16% for its length. The variance in mass and length of wing feathers was not significantly different between sexes. By contrast, the variance in tail feather mass tended to be larger in males than in females, and, in addition, males showed a much higher variance in tail length than females (Table 1). The length of the outermost tail feather was positively related to feather mass in both sexes (males: $b_3 = 4.546, P < 0.001$; females: $b_3 = 8.807, P < 0.001$; Figure 1).

Individual differences in resource allocation to ornamental and wing feathers

An analysis of covariation including the mass of the primary 7 feather as dependent variable, sex as factor, and body condition as covariate showed that the mass of the primary 7 feather differed between sexes ($F_{1,112} = 5.29, P = 0.02$) and was positively associated with body condition ($F_{1,81} = 6.21, P = 0.015$). The interaction between sex and body mass was not significant ($F_{1,81} = 0.24, P = 0.88$) so that the effect of body condition on the mass of the primary 7 was similar in both sexes.

An analogous analysis performed for the outermost tail feather showed that the mass of this feather also varied between sexes ($F_{1,112} = 52, P < 0.0001$). There was no significant effect of body condition on feather mass ($F_{1,112} = 0.25, P = 0.62$), but the interaction between sex and body condition was significant ($F_{1,112} = 4.43, P = 0.038$) because the association of body condition and feather mass occurred in females, but not in males.

In 2004, we examined the relationship between the masses of the tail and wing feathers, performing reduced Mayor axis regressions for each sex separately. We found a relationship between the masses of both feathers in males ($B \pm \text{standard error } [\text{SE}] = 0.512 \pm 0.103, b_6 = 4.981, P < 0.001, R^2 = 0.39$) and females ($B \pm \text{SE} = 0.522 \pm 0.073, t_{43} = 7.172, P < 0.001, R^2 = 0.53$; Figure 2). The variance of the residuals was significantly higher in males than in females (Levene’s statistic: $F_{1,81} = 4.35, P = 0.04$). In the birds recaptured in 2005, we compared the repeatability of the residuals from one year to another. The analyses showed that they were repeatable in males, as the residuals from the regressions of tail feather mass on wing feather mass in 2005 were predicted by those of 2004 ($B \pm \text{SE} = 0.962 \pm 0.200, t_{11} = 4.805, P < 0.001, R^2 = 0.65$; Figure 3), but not in females ($B \pm \text{SE} = 0.237 \pm 0.229, t_{53} = 1.031, P = 0.32, R^2 = 0.004$; Figure 5). We also found a positive relationship between the residual values and tail length ($B \pm \text{SE} = 0.520 \pm 0.210, b_{60} = 2.471, P = 0.018$) so that males increasing their proportional investment in tail feathers produced comparatively longer tails. None of the other morphological variables measured in males were correlated with the resource allocation rules ($P > 0.3$ in all cases).

Allocation rules and survival

For the survival analyses we considered 37 males and 40 females because the rest of the birds were breeding in buildings that had been demolished or reformed at the beginning of 2005. Survival rate in the colonies monitored in both years was 35.1% for males and 37.5% for females (36.4% on average). In the forward stepwise regression model only the residuals of tail mass on wing mass (i.e., the allocation rules) were related to male survival (Table 2). Because none of the male morphological traits correlated with the allocation rules, except the tail length, we did not expect that this result was confounded by problems of collinearity between the explanatory variables. To confirm this, we calculated the partial correlations of all explanatory variables with male survival, and the results showed that the allocation rules still predicted male survival ($B = -0.47, t = -2.86, P = 0.008$) but not the tail length ($B = 0.16, t = 0.85, P = 0.40$) or the remaining variables ($P > 0.30$ in all cases). Male survival likelihood strongly decreased as the relative proportion of resources allocated to the tail feathers increased (Table 3). To test for the robustness of this result, we performed 50 simulations adding up to 3 randomly selected no-surviving males as surviving, which would be still within the natural range of survival in barn swallow populations. After 50 simulations the inverse relationships between male residuals and survival still remained significant ($P$ value averaged from 50 simulations = 0.04). In addition, the mean value of allocation rules was lower in surviving than nonsurviving males ($F_{1,32} = 5.512, P = 0.025$; Figure 4). The probability of female survival did not correlate with those residuals or any other body measurement. The head–bill length was included in the forward stepwise regression model as explanatory variable (Table 2), but its effect was not significant, though (Table 3).

DISCUSSION

Multiple allocation strategies and survival in male barn swallows

We found a positive relationship between the mass of the primary 7 wing feathers and body condition in both males and females. In the case of the mass of the outermost tail feather it was correlated with body condition in females, but not in males. These results suggest that individual condition predicts the allocation of resources in functional feathers, but, surprisingly, it is not correlated with the investment in the

<table>
<thead>
<tr>
<th>Table 1</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Comparisons between males and females in mean and variance of wing and tail feather length (in mm) and mass (in $10^{-4}$ g)</strong></td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>---</td>
</tr>
<tr>
<td>P7 mass</td>
</tr>
<tr>
<td>P7 length</td>
</tr>
<tr>
<td>R6 mass</td>
</tr>
<tr>
<td>R6 length</td>
</tr>
</tbody>
</table>

Data are presented as mean ± standard deviation.
outermost tail feather, which is a secondary sexual trait (Møller et al. 1998) and should thus reflect male individual condition. This finding points to the existence of a certain variability between males in the investment of resources in tail feathers in relation to their body condition (e.g., the mass of the P7 wing feather). In fact, these differences seem rather consistent, as the residuals from the regressions of tail feather mass on wing feather mass were correlated between different moults in males, but not in females. This repeatability between years suggests that, in the population studied, different males allocate a different proportion of their limited resources to ornamental feathers in relation to functional feathers when moulting. This contrasts with the classical view of a single and fixed optimum strategy in resource allocation in sexual versus functional features (Rolf 1992; Stearns 1992), in which the residuals would be considered as random deviations from that single and optimum allocation rule.

The existence of different strategies of resource allocation in sexual ornaments between males implies that a single level of sexual signaling can be reached by individuals of different condition or quality (see Basolo 1998; Candolin 1999; Hunt et al. 2004; Sadd et al. 2006). That is, a certain tail feather length can be achieved either by males with more resources that invest a lower proportion in the ornament or by males with modest resources that invest a large proportion in such feathers. This fact may disrupt, to some extent, the relationships between male condition and sexual advertisement, depending on the costs associated with different strategies of allocation.

We found that different resource allocation rules had different costs in terms of survival. Our results evidenced a negative relationship between the proportion of resources invested in ornamental feathers and male survival. This result is consistent with the handicap principle (Zahavi 1975), which states that sexual ornaments are costly signals that require an allocation of resources that cannot be used in other functional life-history traits (see Blanco and de la Puente 2002; Siefferman and Hill 2005). Thus, males allocating a relatively large amount of resources to tail feathers are probably constraining other vital functions that finally decrease their survival prospects. For example, a large number of experimental studies have evidenced a trade-off between resource allocation in ornaments and in the immune system (Folstad and Karter 1992; Verhulst et al. 1999; Casto et al. 2001; Peters et al. 2004; Munoz et al. • Resource allocation strategies in the barn swallow 407

![Figure 1](#) Relationship between the length and mass of the outermost tail feather in male (open circles) and female (filled circles) barn swallows.

![Figure 2](#) Relationship between the mass of the outermost tail feather and the primary 7 wing feathers in male (open circles) and female (filled circles) barn swallows.

![Figure 3](#) Relationship between the residuals from the regression of tail feather mass on wing feather mass in males (open squares) and females (filled squares) from the second year to the third year.
for barn swallows see Saino and Möller 1994, 1996; Saino, Bolzern, et al. 1997; Saino et al. 2002). Thus, there is probably a relationship between the resource allocation strategies and the immune function, although this subject still needs to be specifically addressed.

Möller and de Lope (1994) found an increased survival for male barn swallows with artificially shortened tails and a reduction in survival for males with artificially elongated tails. This experiment evidenced the costs of holding a sexual ornament but did not provide evidences on the natural variation in resource allocation to those feathers in wild populations. Thus, whereas their results point to the costs of holding the tail feathers, ours show the costs of producing them in nonmanipulated birds. Nevertheless, our study puts forward an interesting question: Why such variability is maintained even if it implies survival costs?

**Implications for honesty and the theory of sexual selection**

We found that different males can invest a different proportion of their limited resources in a sexual ornament and that male survival likelihood decreases as its relative investment in the ornament increases. Such survival costs probably preclude the allocation of an exaggerated proportion of resources in the tail feathers, ensuring honesty in this sexual ornament at population level, as suggested by other studies which have found a relationship between male performance and tail length (Saino and Möller 1994, 1996; Saino, Primmer, et al. 1997; Saino et al. 1999, 2002). However, those survival costs do not preclude the existence of an array of different allocation rules between males, differences that hold and are repeatable at the intraindividual level between breeding seasons. This fact could make the relationship between male viability and ornament expression less straightforward than considered previously because a single level of sexual advertisement (i.e., tail length) can correspond with several levels of individual viability (i.e., survival likelihood).

Under this scenario, a female selecting a male with an enlarged tail that is achieved by investing a relative high proportion of resources may be cheated, as that female would mate with a male with low survival prospects. Indeed, the fact that males can unbalance their strategies of allocation has been usually discussed in terms of dishonest sexual signaling (Candolin 1999; Sadd et al. 2006). In principle, this can be true under the perspective of “good genes” models in which enlarged ornaments only evolve through improvement of male quality (Hamilton and Zuk 1982). However, this topic becomes more complicated if both “good genes” and “runaway” models are considered within the same evolutionary process, as have suggested recent approaches (Kokko 2001; Radwan 2002). In that case, females could benefit from mating with males which increase proportionally their investment in tail feathers, but with low survival prospects, because their offspring would inherit genes increasing their attractiveness (Fisher 1915) rather than their viability (Hamilton and Zuk 1982). In other words, besides having lower survival chances, offspring will have the ability of producing a more attractive sexual ornament than other males with the same amount of resources.

Increasing sexual attractiveness at expenses of future survival may have evolved due to the fitness returns of investment coming from current versus future mating success (Kokko 1998, 2001; Lindström et al. 2005). This could be taking place in the barn swallow, a bird with short reproductive lifespan and large mortality rate (Saino et al. 1999, 2002). Our survival rates show that only 36.4% of breeding individuals survive to the next season, which is within the range of 35–40% observed in other barn swallow populations (Möller 1994; Saino et al. 1999). This implies that a considerable proportion of adult barn swallows reproduce only once in their life, what may favor the strategy of investing more resources to the tail feathers to achieve a higher current mating success given the uncertain probabilities for future reproduction (see Sadd et al. 2006).

In summary, we document that different male barn swallows can invest a different proportion of their limited resources to ornamental feathers and that male survival likelihood decreased as the relative proportion of resources allocated to the ornament increased. These survival costs can make the

**Table 2**

<table>
<thead>
<tr>
<th>Step 1</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$F$ to enter</td>
<td>$P$ to enter</td>
</tr>
<tr>
<td>Tarsus length</td>
<td>0.346</td>
<td>0.561</td>
</tr>
<tr>
<td>Bill–head length</td>
<td>2.095</td>
<td>0.139</td>
</tr>
<tr>
<td>Body mass</td>
<td>0.002</td>
<td>0.968</td>
</tr>
<tr>
<td>Body condition</td>
<td>0.033</td>
<td>0.857</td>
</tr>
<tr>
<td>Tail length</td>
<td>0.127</td>
<td>0.724</td>
</tr>
<tr>
<td>Allocation rule</td>
<td>8.160</td>
<td>0.007</td>
</tr>
</tbody>
</table>

For a female, $P$ to enter was settled at 0.05.

**Table 3**

<table>
<thead>
<tr>
<th></th>
<th>$B$</th>
<th>SE</th>
<th>Wald</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Allocation rule</td>
<td>−0.048</td>
<td>0.018</td>
<td>6.657</td>
<td>0.009</td>
</tr>
<tr>
<td>Intercept</td>
<td>−1.020</td>
<td>0.230</td>
<td>19.556</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Females</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bill–head length</td>
<td>0.512</td>
<td>0.304</td>
<td>2.825</td>
<td>0.093</td>
</tr>
<tr>
<td>Intercept</td>
<td>−15.917</td>
<td>9.077</td>
<td>3.075</td>
<td>0.079</td>
</tr>
</tbody>
</table>

Figure 4

Comparisons of residuals (mean ± SE) from the regression of tail feather mass on wing feather mass (i.e., allocation rules) of males surviving and not surviving from 2004 to 2005.
sexual signaling system honest on average, but there is still an array of different allocation rules between males, which make the relationship between viability and ornament expression less straightforward than considered previously. Different allocation strategies could have evolved in a scenario in which both Fisherian and good genes models would be part of the same evolutionary process. However, this hypothesis needs further research, and future studies could focus on the heritability of the resource allocation strategies and their life-history consequences.

FUNDING

CGL 2005-05611-C02-02/BOS from the Ministerio de Educación y Ciencia; Junta de Comunidades de Castilla-La Mancha, grants to A.M. (FPI 2002), and to R.B. (FPI 2001).

Joaquin Ortego and Gustavo Calabuig helped us with the field and laboratory work. Ben Sheldon and 3 anonymous reviewers provided helpful comments on a previous version of the manuscript. Barn swallows were captured under a license from the Junta de Comunidades de Castilla-La Mancha.

REFERENCES


