The capacity to escape from predators in *Passer domesticus*: an experimental study

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Summary

An experiment was performed simulating the effect of an aerial predator chasing house sparrows (*Passer domesticus*). For this, 82 sparrows were captured in an aviary using a sweep net and assigned a capture order. Morphological measurements were also taken. It was assumed that the capture order of the sparrows correlated positively with their flight ability. Older individuals and those with longer wings were captured later, while birds with longer tails were captured in the first trials. This suggests that predation could be a selective pressure on longer wings and shorter tails. The effect of age is probably due to the greater flight experience acquired by older sparrows. A relationship appeared between male badge size and flight ability, males with larger badge sizes having higher capture orders. Capture order did not correlate with sex, mass or tarsus length.

Key words: flight ability, manoeuvrability, morphology, predation, sexual dimorphism

Zusammenfassung

Das Fluchtvermögen von Haussperlingen gegenüber Räubern (*Passer domesticus*): eine experimentelle Studie

An Haussperlingen (*Passer domesticus*) wurde experimentell geprüft, wie sie sich gegenüber einem Lufträuber verhalten. Dazu wurden 82 Vögel in einer Voliere mit einem Kescher gefangen, ihre Fangreihenfolge notiert und sie wurden vermessen. Es wurde die Annahme geprüft, dass die Reihenfolge beim Fang Ausdruck der Fähigkeit ist, einem Räuber auszuweichen. Ältere Vögel und solche mit längeren Flügeln wurden später gefangen, während solche mit längeren Schwänzen schon zu Beginn gefangen wurden. Daraus wird vermutet, dass der Predationsdruck Vögel mit längeren Flügeln und kürzeren Schwänzen selektioniert. Ältere Vögel sind zudem noch geübter. Männchen mit ausgeprägterem Kehlfleck wurden später gefangen, was wohl ihre bessere Flugfähigkeit ausdrückt. Keine Zusammenhänge gab es zwischen der Reihenfolge beim Fang und dem Geschlecht, der Körpermasse und der Tarsuslänge.

Introduction

Mortality selection is one of the most important processes of natural selection (Endler 1986), as only those individuals that survive to repro-duce will transmit their genes to the next generation. For small passerines such as house sparrows (*Passer domesticus*), mortality through predation may be high (e. g. Møller 1989). For this reason, for example, they forage

in flocks, and adjust their vigilance time according to the predation risk (Barnard 1980b). In this way, they can detect predators at a distance. However, if a predator surprises the sparrows and chases them, flight ability may determine whether or not birds escape (Witter & Cuthill 1993). Flight ability may depend on morphological traits such as wing or tail length. For example, Møller & Nielsen (1997) found that sparrowhawks (*Accipiter nisus*) capture more barn swallow (*Hirundo rustica*) males than females. These authors suggested that this sexual bias is due to the greater tail length of males, which constitutes a handicap. In the same study, individuals (males and females) with greater wing lengths were less depredated by sparrowhawks. In starlings (Sturnus vulgaris), individuals with greater mass had less manoeuvrability and thus were more easily depredated in a chase (Witter et al. 1994). In short, predation in birds may exert a selective pressure on some morphological traits related to flight ability.

Differences in the morphological traits of predated and non-predated animals in the same population may indicate selective patterns in mortality by predation (e.g. Møller & Nielsen 1997). However, the results may be difficult to interpret. For example, subordinate willow tits (*Parus montanus*) are forced to forage in sites more exposed to predators (Koivula et al. 1994). House sparrows with lower foraging rates (i.e. subordinate ones) have shorter flushing distances than those with higher status, and this increases their predation risk (Barnard 1980a). That is, the fact that predated individuals differ morphologically from non-predated ones does not necessarily signify that those morphological differences affect the escape response to predators. Other factors correlated with those morphological differences, such as different foraging behaviours, could influence their higher probability of being predated.

In the present study, an experiment was performed in captivity on 82 sparrows. Here, I simulated the chase of a predator in an aviary. I assumed that the order in which each bird was captured positively correlated with its flight ability, and that the flight ability was positively correlated with the capacity to escape predators. Various morphological traits of animals, sex and age, were recorded, and related to their escape ability.

Methods

The experiment was performed during November 2001 in a colony of 82 house sparrows breeding in captivity at the Science Faculty of the University of Granada. A total of 13 male and 14 female sparrows were captured in the wild in December 1998, and they have been breeding successfully in the aviary for almost three years (Moreno-Rueda & Soler 2002). Therefore, I assumed that they were completely accustomed to the aviary. The other individuals (23 males and 32 females) were born and raised in the aviary, which was thus the only environment they knew. Of these, 12 individuals (4 males and 8 females) were yearlings that bred successfully that year. The remaining sparrows were juveniles born the same year the study was performed. The volume of the aviary was 20.5 m^3, and it was divided into four units, two longer ones of 8 m^3, and two other smaller ones of 2.25 m^3. The birds were provided *ad libitum* with access to food and water. More details about captivity characteristics may be found in Moreno-Rueda & Soler (2002).

In the experiment, sparrows were placed in one of the larger units (8 m^3; $2 \times 2 \times 2$ m). Then, I simulated being a predator entering the aviary and chasing sparrows with a sweep net of 50 cm in diameter. The sparrows were captured in a random fashion. As I had already had ample experience at capturing sparrows with a sweep net, I did not increase my sparrow-capturing ability in the course of the experiment. Chasing lasted no more than 5 minutes, and each capture was followed by at least 30 minutes pause for the birds to rest. The aviary was visually isolated to reduce stress to birds.

The captured sparrows were sexed and their ages were determined by means of their individual colour rings, applied at the time of their capture in the wild or their fledging in the aviary. Morphological traits were also measured. Both wing and tail length were measured with a ruler (accuracy 1 mm) because both traits may affect flight ability. Tarsus length was measured with a calliper (accuracy 0.02 mm).

Mass was measured with a spring balance (accuracy 0.5 g). In males, both badge width and height were measured with the calliper. Badge size was calculated according to the formula $166.7 + 0.45 \times$ height $\times$ width (Møller 1987b). After being measured, the sparrow was separated from the rest, and another sparrow was captured. I recorded the order in which each sparrow was captured, assuming that flight ability correlated positively with capture order. That is, those with the greatest flying skills would be the last to be captured. As one female was not weighed, and the tail length of another female was not registered, the sample size was lower in some tests than in others.

The repeatability of measurements taken (including badge size) was calculated to determine their reliability (Lessells & Boag 1987, Senar 1999). All measurements had a high repeatability (Table 1), only tail length showing a measurement error higher than 10 %. Accordingly I measured each bird only once, thus avoiding inflicting unnecessary stress on the sparrows. All variables had a parametric distribution according to a Kolmogorov-Smirnov test; thus, parametric statistics were used for analyses under the programme Statistica (Statsoft 1998). Data shown are mean ± standard deviation.

Results

Table 1. Repeatability of morphological traits measured.
Tab. 1. Wiederholbarkeit der morphologischen Messungen.

Variable	Repeatability	n
Mass	> 0.999	11
Tail length	0.842	15
Wing length	0.976	15
Tarsus length	0.978	15
Badge size	0.991	12

Mean capture order in males and females did not differ statistically (males: 45.7 ± 20.92, n = 36; females: 38.2 ± 25.60, n = 45; t-test, $t_{81} = 1.42$, p > 0.15). Males and females had significantly different mass, wing length and tail length (Table 2). In terms of whether these morphological traits affect capture order, differences due exclusively to sex would not be detected. To analyse this, I performed an

Table 2. Morphological differences between males and females. Males: n = 36, females: n = 45 for both mass and tail, n = 46 for both wing and tarsus.
Tab. 2. Morphologische Unterschiede der Geschlechter. Männchen: n = 36; Weibchen: n = 45 für Körpermasse und Schwanz, n = 46 für Flügellänge und Tarsus.

Variable	Male	Female	t-test	P
Mass (g)	24.31 ± 1.86	23.35 ± 1.90	2.29	0.025
Tail length (mm)	59.56 ± 2.24	57.54 ± 2.11	4.18	0.00008
Wing length (mm)	77.72 ± 2.31	75.48 ± 2.26	4.40	0.00003
Tarsus length (mm)	18.00 ± 1.47	17.93 ± 1.41	0.24	0.81

ANCOVA with sexually dimorphic traits as covariates. The analysis of covariance removed any differences between sexes ($F_{1, 75} = 0.00003$, p = 1.00).

The average of capture order varied according to the age of individuals (Figure 1). Older birds were captured later, while juveniles were captured during the first trials. No significant interaction appeared between sex and age (2-ways-ANOVA, $F_{2, 76} = 0.05$, p = 0.95). Nevertheless, sparrows of the different age classes showed morphological dissimilarities in the four traits measured (tarsus, wing and tail length, and mass; Table 3). Thus, differences
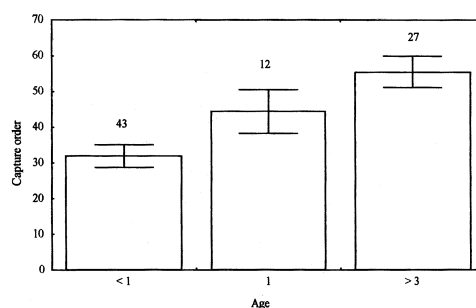
Fig. 1. Differences in capture order according to age. Lines show standard error. Sample size on bars. ANOVA, $F_{2, 79} = 10.14$, p = 0.0001.
Abb. 1. Fangreihenfolge in Abhängigkeit vom Alter. Die Anzahl untersuchter Vögel ist an den Säulen angegeben. Vertikale Linien = Standardfehler. ANOVA, $F_{2, 79} = 10.14$, p = 0.0001.

Table 3. Morphological differences according to age.

Tab. 3. Altersunterschiede in der Morphometrie.

Variable	< 1 year (n = 43, 42 for tail)	1 year (n = 12, 11 for mass)	> 3 years (n = 27)	F	P
Mass (g)	23.38 ± 2.06	22.75 ± 1.28	24.82 ± 1.47	7.45	0.001
Tail (mm)	57.58 ± 2.15	58.65 ± 2.10	59.68 ± 2.33	7.46	0.001
Wing (mm)	75.47 ± 2.41	76.21 ± 2.14	78.14 ± 2.02	11.70	0.000035
Tarsus (mm)	17.28 ± 1.21	17.54 ± 1.32	19.22 ± 0.87	25.60	0.000000

found amongst age classes might be due to these morphological differences. To test this hypothesis, I performed an ANCOVA with the four morphological traits as covariates. Although morphological differences were statistically controlled, significant differences in capture order due to age classes were found ($F_{2, 73} = 4.48$, p = 0.015).

In females (n = 44), capture order correlated positively with both tarsus and wing length (Table 4), but not tail length or mass. I used a forward stepwise multiple regression model with all these morphological variables and age on capture order. The model included only age and wing and tail length as traits that explained the variance in the capture order of females (Table 5), rejecting the other variables. Wing length was the most important variable (Ta-

Table 4. Correlations between morphological traits and capture order for males and females.

Tab. 4. Korrelationen zwischen Reihenfolge beim Fang und morphologischen Merkmalen.

Variables	Females (n = 44)		Males (n = 36)	
	r	P	r	P
Mass (g)	0.16	0.3	0.21	0.21
Tail length (mm)	0.04	0.8	0.31	0.07
Wing length (mm)	0.40	0.008	0.41	0.01
Tarsus length (mm)	0.32	0.04	0.37	0.03
Badge size (mm^2)	–	–	0.63	0.000

Table 5. Forward stepwise multiple regression of morphological traits and age on female capture order. $F_{3, 40} = 5.09$, R = 0.53, $R^2 = 0.28$, P = 0.004.

Tab. 5. Ergebnisse einer Multiplen Regression zur Abhängigkeit der Fangreihenfolge von morphologischen Merkmalen bei Weibchen. $F_{3, 40} = 5.09$, R = 0.53, $R^2 = 0.28$, P = 0.004.

Independent variables in final model	Partial correlation	Probability
Wing length	0.36	0.018
Age	0.29	0.065
Tail length	–0.28	0.068
Independent variables not in final model		
Tarsus length	0.06	0.71
Mass	–0.01	0.96

ble 4), while tail length had a negative correlation with capture order when it was controlled by the other variables included in the model. A multiple regression model including all variables explained no more variance in female capture order ($R^2 = 0.28$).

For males (n = 36), I found a positive and significant correlation between capture order and tail, wing, and tarsus length (Table 4). Badge size, a sexual status signal (Møller 1987a, b, 1988, 1989, Veiga 1993) had the strongest correlation with capture order (Table 4). The forward stepwise multiple regression model with all these variables and age as independent variables, and with capture order as dependent variable, included only badge size and age, but the partial correlation between age and capture order was not significant (Table 6). The remaining morphological traits were rejected by the model. A multiple regression model that included all variables explained only 5 % more variance in male capture order ($R^2 = 0.48$). A model without badge size reduced by 12 % the explained variance as against a model that included this trait. The forward stepwise model without badge size included only age (data not shown).

Lastly, I performed a forward stepwise multiple regression model using the four morphological traits, age and sex as independent variables, with capture order as the dependent

Table 6. Forward stepwise multiple regression of morphological traits and age on male capture order. $F_{2, 33} = 12.30$, R = 0.65, $R^2 = 0.43$, P = 0.0001.
Tab. 6. Ergebnisse einer Multiplen Regression zur Abhängigkeit der Fangreihenfolge von morphologischen Merkmalen bei Männchen. $F_{2, 33} = 12.30$, R = 0.65, $R^2 = 0.43$, P = 0.0001.

Independent variables in final model	Partial correlation	Probability
Badge size	0.41	0.015
Age	0.24	0.17
Independent variables not in final model		
Tail length	–0.12	0.49
Wing length	0.09	0.63
Tarsus length	–0.07	0.70
Mass	0.02	0.92

variable. Badge size was not included because it appears only in males. Sex was introduced as a dummy variable with the value 0 to females and 1 to males. In this model, only age (the most important variable), wing length and tail length significantly explained the variance of capture order. The last variable correlated negatively with capture order (Table 7). When all variables (including one rejected by the stepwise model) were introduced into the standard

Table 7. Forward stepwise multiple regression of morphological traits (badge size not included), age and sex, on capture order. $F_{3, 76} = 10.72$, R = 0.55, $R^2 = 0.30$, P = 0.000006.
Tab. 7. Ergebnisse einer Multiplen Regression zur Abhängigkeit der Fangreihenfolge von morphologischen Merkmalen in Abhängigkeit von Alter und Geschlecht. $F_{3, 76} = 10.72$, R = 0.55, $R^2 = 0.30$, P = 0.000006.

Independent variables in final model	Partial correlation	Probability
Age	0.35	0.002
Wing length	0.33	0.003
Tail length	–0.20	0.072
Independent variables not in final model		
Sex	0.10	0.39
Mass	–0.08	0.46
Tarsus length	–0.06	0.58

multiple regression model, the explained variance in capture order increases by only 1 %.

Discussion

Results show no sexual differences in capture order, although sexual dimorphism exists for different morphological traits that affect flight ability. This suggests that, although males are lager and heavier than females, different parts of body, especially tail and wing, are optimised for similar manoeuvrability in both sexes. In contrast, barn swallows are dimorphic for tail length, and this dimorphism seems to give rise to a higher predation risk to males (Møller & Nielsen 1997).

Younger individuals are captured before older ones. This may in part be due to morphological differences among age classes. Nevertheless, although morphological differences were statistically controlled, differences in capture order according to age are found. This suggests that experience, directly proportional to age, is an important asset in avoiding predators during a chase. Experience apparently improves manoeuvrability and knowledge of the environment. In fact, older individuals had been captured other times in previous years. Other unmeasured variables may also account for this result.

Mass does not appear to be important in the escape ability of sparrows, as opposed to other birds, in which greater body mass affects flight manoeuvrability and increases depredation risk (Witter & Cuthill 1993). Witter et al. (1994) showed that starlings with artificially added mass had decreased flight manoeuvrability. Robins (*Erithacus rubecula*) have reduced take-off ability when they have larger fuel loads (Lind et al. 1999). Thus, a relationship would be expected between mass and capture order in house sparrows. It has been suggested that birds can regulate their body mass according to their predation risk (e.g. Lima 1986), a hypothesis corroborated by some empirical studies (Gosler et al. 1995, Lilliendahl 1997, Carrascal & Polo 1999). Predation risk of an

individual depends on habitat and individual features. Habitat was the same for all sparrows in this study, and therefore differences in predation risk felt by birds were due to individual characteristics such as age or wing and tail length. House sparrows might regulate their body mass according to their individual characteristics, in which case differences according to body mass in capture order would not be detectable. Although the birds had free access to food they did not use feeders for long periods during the day (personal observations). This indicates that differences in body mass among these birds can not be attributed to different foraging habits. Kullberg (1998), similarly, found that diurnal variations in fat loads in the willow tits (*Parus montanus*) do not affect the take-off ability of birds.

Tarsus length, as an indicator of structural body size, is not an important indicator of escape ability which is controlled by other variables. Wing length is the most important morphological trait indicating escape ability (Table 7). Longer wings favour greater flight ability. In barn swallows, individuals with longer wings are less predated by sparrowhawks than those with shorter wings (Møller & Nielsen 1997). However, individuals with longer tails seem to lose escape ability, although it would be expected that tail length is optimised to improve flight ability. A possible explanation is that tail length is optimised to other sorts of flight for example, to fly great distances between food patches, or to maximise flight speed in a straight line when feeding chicks. Likewise, other traits may be modelled by other selective pressures and they in turn may be optimised in a secondary fashion to better enable the bird to avoid predators during a chase.

Male badge size was the most important variable to explain capture order variance. Evidently, badge size has no function during flight, but it has been suggested as an indicator of male quality (Møller 1987b, 1988). On the other hand, Møller (1989) found that males with larger badge sizes were more predated by sparrowhawks, perhaps because a badge, being conspicuous, may attract more predators the bigger it is (Møller 1989, but see Veiga 1995). Moreover, males with larger badge sizes may behave in a more perilous fashion against predators, for example, while defending the nest (Reyer et al. 1998). Thus, these males may undergo greater predation. In summary, males with larger badge sizes may be predated at a high rate despite their greater ability to escape predators.

In general, flight ability may determine whether or not birds escape from predators (Witter & Cuthill 1993). In my experiment, the capture order of sparrows may be correlated with flight ability, and thus with the ability to escape from predators during a chase. According to results in this study, in the house sparrow, age and wing length appear to be the most important factors determining a successful escape response to predators during a chase. Badge size seems to be an indicator of flight ability, capture order increasing with badge size. The tail appears to be under selective pressures favouring a tail that is suboptimal in escaping from predators during a chase. Sex, mass, and tarsus length did not importantly affect capture order. These results would relate to predators that hunt by chasing sparrows, even for very short chases (e.g. some raptors), but would not account for predators that hunt through surprise attacks and that usually do not chase birds (e.g. cats).

Acknowledgements

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