

## Nest defence intensity in House Sparrows *Passer domesticus* in relation to parental quality and brood value

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**Abstract.** We investigated whether brood value (laying date, brood size, nestling age and condition) and parental quality (condition, male badge size) affect experimentally provoked nest defence in House Sparrows in the Czech Republic. We included the badge size (a melanin-based throat feather patch) because it serves as a signal of social status, age and condition. We presented a stuffed Black-billed Magpie *Pica pica* to 19 pairs of sparrows. To assess the defence intensity we used the „risk index“, increasing with time spent reacting and riskiness of the reaction (number of approaches and attacks), while declining with increasing distance from the predator. Females did not adjust their nest defence to the brood value and males did so only partially, tending to defend the early broods more intensely, which marginally supports the “value of offspring hypothesis”. The birds did not adjust their nest defence to quality or defence intensity of their partners, thus the “differential allocation hypothesis” was not supported. Male nest defence was more intense than in females and increased with male badge size. As male contribution to nest defence may affect the breeding success, we hypothesize the badge size could be used as a signal of nest defence intensity used by females.

**Key words:** Nest defence, House Sparrow, badge size, brood value, Black-billed Magpie

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### INTRODUCTION

Parental care is a complex behaviour which enhances the offspring survival, in birds including mainly nest building, incubation of eggs and brooding of nestlings, food provisioning and nest defence (Clutton-Brock 1991). While nest predation is the most common cause of breeding failure in birds (Ricklefs 1969), nest defence is an important component of parental investment, because it can significantly reduce the loss of young taken by predators (Andersson et al. 1980, Knight & Temple 1986, Hogstad 2005). However, this behaviour is associated with several costs for parents, including time and energy expenditure (Biermann & Robertson 1983) and risk of injury or death (Poiani & Yorke 1989). Therefore it is crucial for the parents to balance costs and benefits in reaction to the predator to maximise their reproductive success (Montgomerie & Weatherhead 1988). According to the “value of offspring hypothesis” (Andersson et al. 1980, Clutton-Brock 1991) parents should adjust their investment in nest defence to current brood

quality as age and condition, because older nestlings and those in better condition have higher chances for survival and thus are more valuable for parents. Nest defence intensity should also increase with the brood size as the benefits of deterring the predator will be positively correlated with nestling number (Wiklund 1990). Finally, the clutches laid sooner in the breeding season should be defended more intensely than later broods, because the former are usually more successful (Andersson et al. 1980, Clutton-Brock 1991). Parental investment may also be affected by the individual quality of the parent, while birds in better condition may invest more energy in defence (Hogstad 2005) and older individuals may utilize their experience from previous encounters with predators and thus provide more effective defence (Montgomerie & Weatherhead 1988). The intensity of nest defence may also vary according to the sex of the parent resulting from different costs and benefits of males and females due to different size, re-nesting potential or confidence of genetic parentage (Montgomerie & Weatherhead 1988).

In the House Sparrow *Passer domesticus*, a sexually dichromatic and socially monogamous species with biparental care, the nest defence behaviour was rarely studied, although in recent decades this species attracted considerable attention as an ideal model for studies of parental investment. Kopsisch et al. (2005) investigated individual consistency of parental effort and found no relationships between nestling feeding or brood size and nest defence. In a population studied by Reyer et al. (1998) age and number of nestlings also had no effect on nest defence. Their study took into account the melanin-based throat patch of feathers (so called badge) displayed by males and found that frequency of risky approaches to the predator increased with badge size in males and decreased proportionally in their females. Thus females benefited from the higher investment of larger-badged males, because they could reduce their own effort. Therefore the authors discussed the possible function of badge as a signal of parental investment. They supposed that more intense reaction of larger-badged males was due to the fact that their certainty of paternity was higher than that of smaller-badged males. However, the relationship between the badge size and the certainty of paternity has not been supported by subsequent studies on different populations (Veiga & Boto 2000, Whitekiller et al. 2000, Stewart et al. 2006).

In many species with biparental care a signalling system has evolved, where certain male traits correlated with condition or parental care may be used by females to choose high quality partners in sexual selection (Andersson 1994). In birds the plumage characteristics often serve as such traits (e.g. Hill 2002, Jawor & Breitwisch 2003). Many studies have aimed to find correlates of badge size in House Sparrow. The results were reviewed in a meta-analysis by Nakagawa et al. (2007a), who concluded that badge size signals status in social hierarchy, age and possibly reflects body condition, but found little association between the badge size and parental care, certainty of paternity or reproductive success. Therefore Nakagawa et al. (2007a) stated that badge size does not signal parental care. However, they included only studies measuring parental care as time spent incubating and nestling provisioning, while nest defence was not analysed because of the lack of studies on this topic.

Possible function of plumage ornaments as signals of nest defence intensity was studied in two

other passerine species. In Rock Sparrows *Petronia petronia* males increased their nest defence intensity not according to their own carotenoid-based breast patch size, but according to that of their partners, independently of brood value variables (Griggio et al. 2003). This result does not corroborate the ornament as a signal of male nest defence. However, since patch size in female Rock Sparrows predicts their phenotypic quality (Pilaastro et al. 2003), it is in accordance with "differential allocation hypothesis" (Burley 1986). According to this hypothesis individuals can enhance their fitness by increasing their parental investment in offspring sired by a partner of high quality, because such offspring would be more viable (Fisher 1930) or attractive (Møller & Alatalo 1999). Quesada & Senar (2007) investigated the role of melanin- and carotenoid-based coloration in nest defence of Great Tits *Parus major*. Males with larger black breast-stripe defended their nests more vigorously, while the yellow breast coloration had no effect. Taken together, the results of Reyer et al. (1998) and Quesada & Senar (2007) indicate that melanin-based ornaments may signal nest defence intensity. This presumption agrees with the fact that they often correlate with individual's fighting ability and aggression (Jawor & Breitwisch 2003, Senar 2006, Ducrest et al. 2008). Compared to the widespread function of melanin ornaments in intrasexual communication, their role in female choice is less well supported because it is less clear what benefits females could gain by choosing more melanized males (Griffith & Pryke 2006, Hill 2006). Mating with a healthy partner might be such a possible benefit as it was shown, at least in some bird species, that melanin based coloration correlates positively with resistance to stressors, immune response against nonpathogenic antigen (reviewed in Ducrest et al. 2008) and negatively with ectoparasite load (Fitze & Richner 2002).

As parental care is a complex behaviour, its components may be influenced in opposite directions. Such a trade-off could be caused by male sex hormones (e.g. testosterone plasma level on which melanocortins have a positive effect) supporting fighting ability (competition for nest sites: Veiga 1993, Gonzalez et al. 2002, nest defence), while suppressing other aspects of parental care (nestling brooding and feeding: Mazuc et al. 2003). Given this presumption, the lack of evidence of direct benefits for females choosing males with larger melanin ornaments is not

surprising, because the male parental behaviour that was extensively studied (like brooding the nestlings, feeding frequency), is not positively associated with melanin-based coloration on hormonal basis.

In the present study we aimed to analyze the variation in the nest defence in House Sparrows, taking into account several features of parents (sex, condition, male badge size, partner's nest defence behaviour) and offspring (laying date, brood size, nestling age and condition) that may affect the breeding success, and thus influence the intensity of nest defence behaviour.

## MATERIALS AND METHODS

### Study area and population

Our study was conducted in the cow-shed in Veselí nad Lužnicí, Czech Republic (49°11'N, 14°41'E), during the breeding seasons 2005 and 2006. In autumn 2004 we erected 50 nest boxes (25 x 15 x 15 cm) and monitored them every other day for signs of nesting activity since April 2005. Once egg laying had begun, we checked the nests to determine the date of hatching. When the nestlings reached the age of 10 days, they were ringed with aluminium rings and marked with unique combination of plastic colour rings. Each nestling was weighed using spring scale to the nearest 0.1 g and morphological measurements were taken (tarsus and wing length). We caught the adults using mist nets and nest-box traps during feeding the nestlings (May–June). The adults were ringed, weighed and measured in the same way as the nestlings. To estimate the condition of the birds we used the scaled mass index (Peig & Green 2009) computed separately for the males, females and nestlings (mean condition per brood calculated from averaged nestlings' measurements). This index is based on mass and tarsus length and recognizes the scaling relationship between different measures of body size. We gathered data on 19 broods of individual pairs. However, we had information on condition only of 16 females and 16 males, because we did not succeed to catch all individuals and some of them escaped during manipulation before taking all the measurements needed.

### Experimental procedures and behavioural observations

Prior to each trial we watched the colony for 15 min to make sure that both parents were present

and feeding the nestlings and that no disturbing event had happened. All trials were conducted at an average of  $9.21 \pm 0.76$  (3–14) days of age of the nestlings from the first broods, between 12 and 30 June 2005 (7 nests) and between 12 May and 10 June 2006 (12 nests) during morning (6:00–11:00 GMT) or afternoon (15:00–19:00 GMT) when the birds were most active. There was no effect of time of the day on the defence behaviour of the birds (T-test:  $df = 36$ ,  $t = 0.158$ ,  $p = 0.875$ ) measured as „risk index“ (for explanation see below).

To induce defence behaviour we used a stuffed Black-billed Magpie *Pica pica*, a predator of eggs and fledglings, which does not threaten the adult birds. We chose this predator species to test parental investment and eliminate the probability of self-defence. Predator was fixed directly on the roof of each nest box. All trials were recorded for 20 min from the arrival of the first bird (after Reyer et al. 1998) to the vicinity of the nest (< 5 m from the nest box) with a digital video camera JVC from a hiding place that was at least 10 m distant from the nest boxes. To minimize the possible effect of habituation the next trial with neighbouring nest box followed after at least 3 days interval. After exposition of the predator model one or both parents of the nestlings from the nest box arrived and started to perform the reaction. The male was the first one in 5 trials as well as was the female, while in remaining 9 trials both parents arrived together. The reaction was defined as the presence of the bird in the view, less than 5 m from the predator model. The birds moved to and from the model alternately, uttering alarm calls, and sometimes also flew over the model. During a 20 min trial each bird arrived to the vicinity of the model and flew out of the view several times, which means that each bird performed several reactions during one trial. When the parents did not detect the predator together, the second bird arrived on average  $93 \pm 43$  s after the first one. Although there was less than 20 minutes left for the reaction of the second bird, time spent reacting within the trial did not differ between the first and second bird (Wilcoxon matched-pairs test:  $N = 10$ ,  $T = 19$ ,  $Z = 0.866$ ,  $p = 0.386$ ). The most risky reaction of the second birds was performed on average  $80 \pm 37$  s after their arrival, which was never later than 10 minutes after the arrival of the first bird.

We recorded the following variables of the reaction for each parent observed during the trial: (i) Number of approaches — we distinguished approach to the predator model (< 5 m from the model) with and without alarm calls; (ii) Number

of attacks — as an attack flight directly over the predator model was considered; (iii) Time reacting — time (in s) the bird spent in view (< 5 m from the model) performing approach or attack; (iv) Distance — The mean distance (in m) between the bird and the predator model. We estimated the distance from 1 to 5 m (to the nearest 1 m) each 10 s of the bird's reaction. From these distances (1–5) we calculated mean distance during performance of each type of behaviour (approach or attack) for each bird.

To assess the risk-taking of individual mobbing reaction we used the „risk index“ (RI) (modified after Windt & Curio 1986; see also Brunton 1990):  $RI = R (tr/dr)$ , where  $R$  is the rank value of defence behaviour  $r$ ,  $tr$  is time spent in behaviour  $r$ , and  $d_r$  is the mean distance from the predator during  $t_r$  (calculated from 10 s intervals of  $t_r$ ). The rank values of defence behaviour were assigned according to its increasing degree of risk: 1 — approaches without alarm calls, 2 — approaches with alarm calls, and 3 — attacks. The risk index assumes that risk increases with time spent reacting ( $t_r$ ) and rank value of the reaction ( $R$ ), while it declines with the distance from the predator ( $d_r$ ). In presented analysis the sum of risk indices of all reactions performed by each individual during 20 min of a trial was considered. Latency was not analysed for the same reason as in Reyer et al. (1998), because it was influenced rather by the foraging pattern than the nest defence, as the parents noted the predator when returning to the nest with food.

### Badge measurements

Badge size was estimated from detailed digital photographs. Males were photographed in standard conditions laying on their backs when holding the bill perpendicular to the body axis. Badge size increases with time because of the abrasion of white feather tips concealing the badge (Møller 1987). Therefore we measured badge size from May onwards when it should be almost fully developed (Møller & Eritzoe 1992). We measured the area (mm<sup>2</sup>) of the “black” and “total” badge in UTHSCSA Image Tool 3.0 program (University of Texas, Houston, TX, USA, <http://ddsdx.uthscsa.edu/dig/itdesc.html>) (e.g. Quesada & Senar 2007). The black badge is covered by completely black feathers, whereas the total badge involves feathers with black bases and white tips, which gradually wear off (Møller & Eritzoe 1992). The area of the total badge and the area of the black badge were highly correlated ( $r^2 = 0.866$ ,  $p < 0.001$ ,  $n = 19$ )

(see also Griffith et al. 1999; Gonzalez et al. 2001). Griffith et al. (1999) found that the measure of the total badge was more repeatable than the black badge. Therefore we used area of the total badge (further on reported as badge size) in statistical analyses. Average total badge area ( $\pm$  SE) of 19 males was  $483.84 \pm 15.14$  mm<sup>2</sup> (range 350–628 mm<sup>2</sup>). All the measurements were done by the same person (A.K.).

### Statistical analyses

We compared nest defence behaviour (time spent reacting, number of approaches with alarm calls, mean distance from the predator, and risk index values) of males and females within the breeding pairs by Wilcoxon matched-pairs tests. Number of approaches without alarm calls and number of attacks were not compared because these were rather rare. To limit the overall error in the set of tests to 5% we used the Bonferroni correction ( $\alpha = 0.0125$  in individual tests). We analyzed the factors influencing the defence behaviour separately for males and females. The intensity of nest defence was expressed as risk index value (RI). To find out whether RI values were influenced by brood value and/or the quality and behaviour of the parents and their partners we conducted analyses of covariance (ANCOVAs) with year as categorical factor and laying date, brood size, nestling age, mean nestling condition per brood, parent condition, partner's risk index and badge size (only in case of males) as continuous predictors. The laying dates were expressed as a number of days from 1<sup>st</sup> April till the laying of the first egg. To control for annual differences in timing, we set the median laying date of the population for each year to zero and calculated the relative laying date for each brood as the deviation from “time zero” (after Rossmann et al. 2007). We used forward stepwise variable selection based on Mallows  $C_p$  statistics to find a minimal adequate model which best explained the variation in RI values without incorporating unnecessary non-significant variables. Due to missing data about condition of several individuals, we cannot include the partner's condition into full model and its effect on RI values was tested separately using simple regression.

All dependent variables were normally distributed, except for the female risk index, which had gamma distribution and was analysed in corresponding GLM with log-link function. All statistical tests were performed using S-PLUS 4.0 software (MathSoft 1997).

## RESULTS

Mean laying date ( $\pm$  SE) at the 19 nests was 39.05 ( $\pm$  4.74) days and average brood size was 3.32 ( $\pm$  0.23) nestlings. Average weight of 10 days old nestlings in the nest was 23.37 g ( $\pm$  0.87) and average tarsus length was 20.3 mm ( $\pm$  0.3). Average condition of nestlings was not affected by laying date (simple regression:  $F = 0.54$ ,  $df = 1, 17$ ,  $p = 0.473$ ).

Males spent longer time reacting than females, which resulted in higher risk index of males, while the mean distance from the predator did not differ between the sexes (Table 1). The number of males' and females' approaches with alarm calls did not differ after the application of Bonferroni correction (Table 1).

Females' risk indices did not relate neither to their condition nor the value of their broods (Table 2). Males' risk indices increased significantly with their badge size (Pearson's  $r = 0.537$ ; Table 2, Fig. 1) and decreased marginally with laying date (Pearson's  $r = -0.395$ ; Table 2).

The risk index was not related to the partner's risk index in either sex (Table 2) and females' risk indices were not affected by the badge size of their partners (Table 2, Fig. 1). Partner's condition had no effect on risk index in males (simple regression:  $F = 0.005$ ,  $df = 1, 14$ ,  $p = 0.946$ ) or in females (simple regression:  $F = 1.856$ ,  $df = 1, 14$ ,  $p = 0.195$ ).

## DISCUSSION

In this study we investigated nest defence behaviour of House Sparrows in respect to parental quality (condition, male badge size) and the current value of their broods. In females neither parameters of brood quality nor their own condition predicted their nest defence intensity. In males the laying date was the only brood value variable, which tended to affect their nest defence intensity, but this effect was only marginally significant. The broods laid later in the breeding season tended to be defended less intensely than the sooner broods. Thus the "value

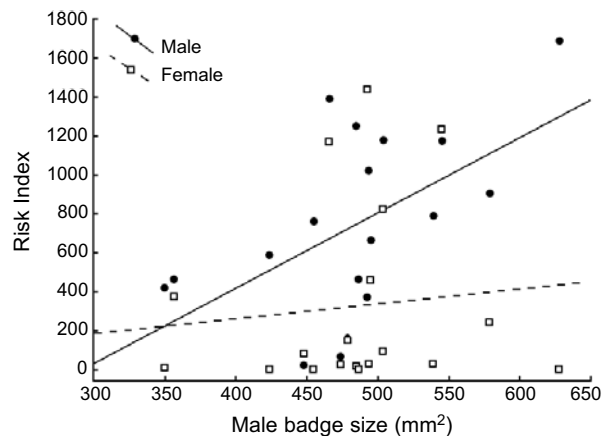


Fig. 1. Risk index of reactions to a stuffed Black-billed Magpie of 19 House Sparrow males (black dots, solid line) and 19 females (open squares, dashed line) in relation to the total area of male badge.

of offspring hypothesis" (Andersson et al. 1980, Clutton-Brock 1991) was only partially supported. Our results could further partially support the "relative offspring survival probability hypothesis" (Curio et al. 1984), which predicts that earlier broods have a higher probability to survive than later broods and, consequently, are of greater value for the parents. It is in contrast with "re-nesting potential hypothesis" (Montgomerie & Weatherhead 1988), according to which the parents should increase their investment with the progress of the breeding season, because their re-nesting potential decreases. As also both previous studies of House Sparrow nest defence (Reyer et al. 1998, Kopisch et al. 2005) failed to reveal a relationship between brood value and nest defence, we can only speculate that parents base their estimates of brood value on other aspects, which were not investigated so far.

Concerning male quality parameters tested, there was no effect of condition on nest defence, but the risk index increased with badge size. More intense reaction of larger-badged males agrees with the finding of Reyer et al. (1998). They reported that risky approach to the predator increased from small- through medium- to large-badged males. They explained this relationship by

Table 1. Comparison of male and female nest defence variables. Descriptive statistics (mean  $\pm$  SE) and Wilcoxon matched-pairs test results are given ( $n = 19$ ). Bonferroni correction was applied, \* —  $p \leq 0.0125$ .

	Males	Females	Z	p
Time spent reacting (s)	456.95 $\pm$ 65.70	224.63 $\pm$ 66.26	2.576	0.010*
Number of approaches with alarm calls	5.47 $\pm$ 0.82	3.42 $\pm$ 0.95	2.249	0.025
Mean distance (m)	2.59 $\pm$ 0.18	2.97 $\pm$ 0.3	0.776	0.438
Risk index	744.34 $\pm$ 105.37	324.54 $\pm$ 108.91	2.857	0.004*

Table 2. Factors affecting risk index of male and female House Sparrows — results of analyses of covariance (ANCOVAs,  $N = 16$ ). Significant results ( $\alpha = 0.05$ ) are indicated by asterisks. Full model includes all response variables, minimal adequate model is a result of forward variable selection.

	Risk index of					
	F	male df	p	F	female df	p
Full model						
Year	0.033	1, 14	0.861	1.522	1, 14	0.257
Laying date	3.471	1, 13	0.105	0.386	1, 13	0.554
Brood size	0.005	1, 12	0.945	0.078	1, 12	0.788
Nestling age	0.755	1, 11	0.414	0.409	1, 11	0.543
Nestling condition	0.524	1, 10	0.493	0.308	1, 10	0.596
Parent condition	0.953	1, 9	0.362	0.604	1, 9	0.463
Partner's risk index	2.591	1, 8	0.152	4.245	1, 8	0.078
Male badge size	6.462	1, 7	0.039*	0.906	1, 7	0.373
Minimal adequate model						
Male badge size	6.060	1, 14	0.029*			
Laying date	3.991	1, 13	0.067			

higher possible confidence of paternity of larger-badged males, which could contribute to their motivation to defend the nest more intensely. However, the recent meta-analysis (Nakagawa et al. 2007a) did not support the relationship between badge size and cuckoldry. Moreover, studies of other passerines, where the genetic fathers of the nestlings were known, found no effect of paternity on male nest defence (Lubjuhn et al. 1993, Griggio et al. 2003, Rytönen et al. 2007).

The explanation for male nest defence intensity increasing with badge size can reside in the fact that birds with larger badges are in better physical condition (Veiga & Puerta 1996) and can afford higher energy expenditure as well as better avoid the risk of injury. The same conclusion was reached by Hogstad (2005) who found that Fieldfares *Turdus pilaris* in better condition were more aggressive towards the predator exposed near the nest. However, in House Sparrow the condition was found to correlate with the badge size only weakly (Nakagawa et al. 2007a) and its effect on nest defence intensity was not found in our population.

Larger-badged sparrows also are older (Nakagawa et al. 2007a, b). Owing to this finding our result may just represent a relationship originating from the fact that older birds respond more strongly than young birds due to their experience with a predator (Smith et al. 1984). In our study the predator species was resident and often observed in the vicinity of the nest boxes providing the opportunity for young sparrows to learn to recognise it as a threat early in their life via social learning from their parents (Curio et al. 1978). Although we did not know the age of the

parents, most other studies of passerines have not found relationship between age and nest defence (e.g. Winkler 1992, Hatch 1997).

Males with larger badges possess higher testosterone plasma levels mediating increased aggressiveness, fighting ability and dominance status (Jawor & Breitwisch 2003, Senar 2006, Ducrest et al. 2008, Buchanan et al. 2010). Higher circulating levels of testosterone arise from pleiotropic effects of the genes regulating melanogenesis (Ducrest et al. 2008), further including higher sexual activity, lesser sensitivity to stress, better antibody response and higher metabolic rate (reviewed by Ducrest et al. 2008). These aspects might be also associated with higher nest defence intensity. While for other males the melanin ornament is a useful signal for decisions whether or not to engage in antagonistic interactions, the females could rather use the information on ability of the male to behave aggressively also towards the nest predators. In our study males defended the nest more vigorously than their females, which is in opposite with the results of Reyer et al. (1998). The usually mentioned explanations for sex differences in defence as different body size, ability to raise offspring alone, re-nesting potential or mortality (Montgomerie & Weatherhead 1988, Westneat & Sargent 1996) do not seem to be plausible in House Sparrow (discussed in Reyer et al. 1998). However females of this species usually spent more time incubating (Hoi et al. 2003, Bartlett et al. 2005, Hořáková, unpubl. data) and achieve higher feeding frequency than males (VOLTURA et al. 2002, Hoi et al. 2003, Hořáková, unpubl. data). Thus it could be possible that there is a division of labor, when females and males

contribute disproportionately in different components of care, resulting in equal shares of both sexes in general level of care as predicted in species with biparental care.

However, females mated to larger-badged males did not lower their investment, as was the case in study of Reyer et al. (1998). Their study was carried out in the university campus, where the predation pressure could be lower than at our rural study site. Further the authors used mustelid predators, which threaten also the adult birds unlike the Black-billed Magpie, which predaes only the eggs and nestlings. We suppose these different conditions might affect the nest defence behaviour of females.

In our experiments the females of larger-badged males did not invest more in nest defence as predicted by the "differential allocation hypothesis" (Burley 1986). So in our population the benefit for these females was above-average intensity of nest defence performed by their partners and thus better protection of their nests. The value of nest defence to female is the protection of her offspring. Even though we did not observe different predation rates of nests in respect to badge size, studies of other passerine species confirmed that successful nests were defended more aggressively than nests that failed (Knight & Temple 1988, Weatherhead 1990).

Since nest defence can affect the breeding success (Knight & Temple 1986), we hypothesize that the badge size may be a valuable signal of investment in this component of parental care used by females in mate choice, especially in areas under high predation risk, where the benefits from increased nest defence may exceed the benefits from increased food-provisioning. To corroborate this assumption it would be necessary in the future to conduct nest defence experiments on birds with manipulated badge sizes while controlling for other possible effects as brood value or testosterone level.

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## STRESZCZENIE

### [Intensywność obrony gniazda u wróbla]

W pracy analizowano dwa czynniki, które mogą wpływać na intensywność obrony gniazda u wróbla: jakość rodziców (określoną jako ich kondycja oraz wielkość czarnego krawata samca) oraz „potencjał” lęgu (określony jako liczba piskląt, ich kondycja i data złożenia jaj). W eksperymencie na dachu skrzynki lęgowej 19 par wróbli umieszczano wypchaną srokę (symulacja ataku drapieżnika na lęg) i przez 20 min określano ich reakcję. Aby ocenić intensywność obrony gniazda do analiz wykorzystano obliczony „wskaźnik ryzyka”, który bierze pod uwagę m. in. długość reakcji oraz agresywność ptaków.

Samce broniły lęgów intensywniej niż samice (Tab. 1), przy czym intensywność obrony zwiększała się wraz z wielkością krawata samca (Fig. 1). Stwierdzono, że samice nie zwiększały swej obrony w związku z „potencjałem” lęgu, zaś samce nieznacznie silniej broniły lęgów wczesnych (Tab. 2).



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### The condition of nestling House Sparrows *Passer domesticus* in relation to diet composition and the total amount of food consumed

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# The condition of nestling House Sparrows *Passer domesticus* in relation to diet composition and the total amount of food consumed

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**Capsule** A higher animal component in the diet and a greater amount of food result in better condition.

**Aims** To investigate the relative importance of different food types to nestling House Sparrows.

**Methods** Faecal sac samples ( $n = 206$ ) from 106 nestlings of 31 broods were analyzed in 2 breeding seasons (2008, 2009). The nests were in a nestbox colony on a farm in south Bohemia, Czech Republic.

**Results** Faecal sacs contained 362 identifiable animal food objects belonging to 5 arthropod orders. The nestlings were fed primarily on beetles (mainly Scarabeidae) and Diptera (mainly muscids and tipulids). The total amount of food found in the faecal samples increased with nestling age. This increase was because of an increase in the total mass of plant material; the total mass of animal component did not change with nestling age. The total amount of food, and the mass of animal component in the diet of older nestlings were all positively related to nestling body condition.

**Conclusions** To compensate for the increasing demands of older nestlings, the parents increased the mass of plant material in the nestlings' diet. This might have been caused by an upper limit to their ability to catch invertebrate prey, or by the growing nestlings' preference for plant material. The effect of food amount and animal component in nestling diet on their condition stressed the importance of arthropods for the breeding success of House Sparrows.

Two common factors which influence breeding success in birds are resource availability and weather conditions (Lack 1954). Food supply during the breeding season is a particularly important determinant of fledgling condition and survival (Anderson 1977, Hochachka & Smith 1991, Naef-Daenzer & Keller 1999, Rossmanith *et al.* 2007). Nutrition at the nestling stage may affect fitness later in the life of the birds (Metcalf & Monaghan 2001). A low-quality diet poor in nutrients may reduce growth rates in the nestlings of passerines (Johnston 1993, Birkhead *et al.* 1999). Variable proportions of different prey types (Wright *et al.* 1998) or the presence of particular key prey in the nestling diet is likely to affect reproductive performance. Thus, caterpillars are important components in the nestling diet of Lesser Spotted Woodpeckers *Dendrocopos minor*, as their presence positively affects nestling body mass (Rossmanith *et al.* 2007), insect larvae improve the

condition of young Skylarks *Alauda arvensis* (Donald *et al.* 2001) and lipid-rich fish are needed for successful recruitment in young Red-legged Kittiwakes *Rissa brevirostris* (Kitaysky *et al.* 2006). Finally, the presence of spiders in the diet of nestling Blue Tits *Cyanistes caeruleus* influences risk-taking behaviour and performance in spatial learning tasks, owing to high levels of the amino acid taurine (Arnold *et al.* 2007).

Because breeding success determines population stability (Haig *et al.* 1993), its reduction may cause the decline of a population (Vincent 2005, Baillie *et al.* 2007, Peach *et al.* 2008). In House Sparrows *Passer domesticus*, reduced breeding success may be caused by chick starvation owing to a lower availability of invertebrate food resulting in their poor condition (Mitschke *et al.* 1999, Vincent 2005). Peach *et al.* (2008) showed that low reproductive output in a British population was associated with high proportions of vegetable material in the nestling diet and low aphid (Aphidoidea) densities within the home ranges of their nests. In this way the lack

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of appropriate nestling food might be a contributory factor in the large decline of House Sparrow populations experienced in the last few decades in many European countries (Pan-European Common Bird Monitoring Scheme 2010). The factors determining this negative population trend have been widely discussed (Siriwardena *et al.* 2002, Anderson 2006) and include agriculture intensification (Hole *et al.* 2002), predation risk (MacLeod *et al.* 2006), air pollution (Peach *et al.* 2008) and general habitat changes (Summers-Smith 1999).

During the first three days of life the food of nestling House Sparrows comprises only invertebrates (Summers-Smith 1963). From then on the proportion of animal component decreases gradually and after fledging the diet becomes almost entirely vegetarian (Mueller 1986). Studies of food composition (reviewed in Anderson [2006]), based mainly on analyses of faeces or neck collar samples, showed that the animal material consists mainly of insects and, in a lower quantity, spiders. The most common insect groups are beetles, grasshoppers and crickets, caterpillars and flies, sometimes accompanied by aphids and ants. The plant material consists mostly of various grains and seeds. The composition of nestling food changes geographically and seasonally with the availability of particular prey species (Encke 1965, Anderson 1984).

Published studies on the composition of the diet of nestling House Sparrows in Europe come from Bulgaria (Simeonov 1964), Germany (Encke 1965, Mitschke *et al.* 1999), the UK (Seel 1969, Vincent 2005), Romania (Ion 1971) and Poland (Wieloch 1975). In the Czech Republic the food of nestlings had not been studied and other diet analyses from central and eastern Europe were undertaken several decades before the population started to decline. In the present article we describe the foods that are fed to nestlings in a contemporary central European rural environment. We investigated the influence of food amount and diet composition on nestling pre-fledging condition in order to gauge whether these factors might affect breeding success in this region.

## MATERIALS AND METHODS

### Study area and population

Our study was conducted on a farmstead in Veselí nad Lužnicí, Czech Republic (49°11'N, 14°41'E). The farmstead area of 1430 ha is primarily devoted to arable crops (cereal grains and Rape *Brassica napus*), although some livestock (dairy, pigs and poultry) are also present.

The management is rather intensive, which is typical of the local area. On the farm approximately 100 breeding pairs of House Sparrows occur, several other smaller populations inhabit suitable habitats in the villages nearby. Formerly a very common species in the area House Sparrows have experienced an apparent decrease in the 1980s and the early 1990s, most probably because of the changes in agricultural practice in this region as well as in the whole Czech Republic. The population of the species nationally is in moderate decline (<http://jpsp.birds.cz>).

In 2004, 50 nestboxes (25 × 15 × 15 cm) were erected on the farm buildings, 4–5 m above ground level. Habitat composition was mapped within a 200-m radius of the buildings. This distance was chosen because adults usually forage within this range from their nests (Summers-Smith 1963; pers. obs. at study site). Almost half of the surrounding area was composed of grassland (47%), over one-fifth was built-up or covered in concrete (22%) or a dunghill (11%). Another 10% consisted of broad-leaved trees. Shrubs and arable farmland each took up 4% of the radius, although fields constituted a much larger area beyond the 200-m radius. The remaining 3% consisted of coniferous trees. Human habitation was situated at a minimum distance of 300 m from the study nestboxes.

Data on 31 broods were gathered during the 2008 and 2009 breeding seasons (15 and 16 broods per year, respectively). The nestboxes were monitored every other day for signs of nesting. Once egg-laying began the nests were checked to determine the date of hatching. To control for annual differences in timing, we set the median laying date of the population for each year to zero and calculated the relative laying date for each pair as the deviation from this (Rossmann *et al.* 2007). When the nestlings reached Day 10, they were ringed with aluminium rings and marked with a unique combination of plastic colour-rings. Each nestling was weighed using a spring scale to the nearest 0.1 g and its left tarsus and wing length were measured to the nearest 1 mm. To estimate body condition of nestlings we used the scaled mass index (mean condition per brood calculated from averaged nestlings' measurements) (Peig & Green 2009). This index is based on mass and tarsus length and recognizes the scaling relationship between different measures of body size.

### Diet analysis

Faecal samples were used to evaluate nestling diet (Moreby & Stoate 2000). We were aware that there are problems associated with this method, particularly with

respect to certain items which cannot be detected in the sample because of their high digestibility (Ralph *et al.* 1985). This can result in invertebrates with few hard body parts, such as aphids or ants, being underestimated. However, this bias is not always significant (Poulsen & Aebischer 1995, Moreby & Stoate 2000) and this method is almost without stress for the nestlings (Brickle & Harper 1999). Our aim was to test the effect of nestling food on body condition rather than to describe diet composition in detail. We took food samples from all nestlings twice during the breeding attempt: at the nestling age of 4–6 days (which we refer to as the younger age) and 9–11 days (which we refer to as the older age). Nestlings commonly produced faecal sacs when handled. We analyzed 206 faecal sacs (112 from 58 nestlings in 2008 and 94 from 48 nestlings in 2009). In this sample, 362 food objects were identified. Any arthropod body part was considered a food object.

After collection, fresh faecal sacs were conserved in vials of 70% ethylalcohol. Data were pooled within broods for analysis to avoid pseudo-replication. The contents of each faecal sample were deposited into a Petri dish. The underside of the dish was scored with radial lines at 10° intervals giving 36 equal segments. The contents of each faecal sample were placed on the dish with a small amount of ethanol, spread evenly across the 36 segments and inspected at 30× magnification using a binocular microscope. By rotating the dish through 360° it was possible to search the entire contents and the food objects found in each section were recorded (Green & Tyler 1989, Vincent 2005).

First we separated the animal and plant fractions. For identification of the arthropods we followed Calver and Wooller (1982) and Ralph *et al.* (1985). The number and type of food objects, such as legs or mandibles were recorded. For each of the main arthropod groups encountered the following body parts were counted (Vincent 2005): Coleoptera – head, mandibles, legs, elytrae; Diptera – heads, wings, legs; Heteroptera – head, wings, legs; Cicadomorpha – head, wings, legs; larvae – head; Araneae – head, chelicerae, leg tips.

Identifiable parts were then matched to approximate the number of individuals occurring in each sample (e.g. two mandibles and/or up to six legs represented one beetle). As the majority of arthropod pieces were too fragmented to be counted and identified, we calculated the percentage composition of the contents from the identifiable material only. These percentages are not true representations of the diet composition of House Sparrows nestlings but are proportions of the identified material that remained intact throughout the

digestive process. We identified arthropods to the lowest taxonomic level possible. To assess the relative abundance of individual taxa we followed Calver and Wooller (1982). The most abundant arthropods were placed into three categories for statistical analyses. These were Coleoptera adults, Diptera adults, and Larvae (Scarabeidae and Diptera). We measured the frequency (%) with which each taxon occurred in each faecal sample, and calculated the abundance of individual taxa relative to the other taxa detected (%).

In contrast to animal remains, abundance of plant parts in samples could not be accurately estimated because of digestion, which did not allow quantifiable comparison with arthropod remains. Therefore, we weighed the dry animal and plant parts of each sample using an analytical balance and considered only their weight when comparing these two components.

To evaluate the total amount of food consumed by nestlings we weighed the whole dried faecal samples (plant and animal component together). The total amount of food in the sample is not a true representation of the food provided by parents to a particular nestling but is the mass of the proportion of the food that remained in the faeces after digestion.

### Statistical analyses

We employed common statistical procedures such as ANOVA and linear regression, and their non-parametric alternatives where appropriate (Kruskal–Wallis test, Spearman's rank correlation), to test our hypotheses. The effect of nestling age on food composition was tested using Friedman tests to account for repeated measures (young within one nest). A simple mixed-effect model with year as a random factor was used to test the effect of the mass of the two food components (plant and animal part) on body condition of young. We log-transformed the animal component of the diet before the analyses to control for non-linearity in the data. Group data are presented as mean  $\pm$  se. First we tested the relationship between the age categories of the nestlings and the mass of the two components in their faecal samples. Next we looked for differences in the abundance of the three major categories of animal diet (i.e. Coleoptera adults, Diptera adults, and Larvae) within the two age categories of nestlings. For each animal diet category we calculated the average number of individual arthropods per nestling. At the older age, body mass estimates were taken for each nestling. Therefore, we were able to test whether food composition and the total amount of food during nestling

development influenced their pre-fledging body condition. The relationship between food composition and condition was tested separately for younger and older nestlings. All statistical tests were performed using R 2.12.0 (R Development Core Team 2010).

## RESULTS

Diet composition and its effect on nestling condition were investigated during two breeding seasons, 2008 and 2009. In these two years relative timing of breeding did not significantly differ (main effects ANOVA:  $F_{1,29} = 0.148$ ,  $P = 0.704$ ). In both years the beginning of egg-laying in the first breeding attempt ranged from 19 April to 31 May with the median date 29 April; the second breeding started between 16 May and 15 June with the median date 3 June.

Data were gathered on 11 first broods each year, 4 second broods in 2008 and 5 second broods in 2009. The mean nestling body condition did not differ between the breeding attempts ( $F_{1,29} = 0.102$ ,  $P = 0.752$ ), nor did it differ between the years ( $F_{1,29} = 2.730$ ,  $P = 0.110$ ). Consequently, data were pooled from both years and breeding attempts for analysis of nestling condition.

Successful nests produced on average  $3.45 \pm 0.19$  fledglings (range = 1–5,  $n = 31$ ). The relative egg-laying date influenced neither the number of fledglings ( $r^2 = 0.029$ ,  $P = 0.363$ ,  $n = 31$ ), nor the mean nestling body condition per brood ( $r^2 = 0.069$ ,  $P = 0.152$ ,  $n = 31$ ).

### Nestling diet

Nestling diet consisted of both animal and plant components. Samples containing exclusively plant material were gathered only from nestlings older than nine days (21 samples in 2008, 8 in 2009). Plants comprised 56.3% of the mean sample weight. Identifiable plant remains were mostly represented by Poaceae (approximately 90%) in the form of seeds, fragments of stalks and spikelets of Millet *Panicum miliaceum* and wheat *Triticum* spp. The remaining 10% comprised seeds of Poppy *Papaver somniferum* (Papaveraceae), Flixweed *Descurainia sophia* (Brassicaceae), Stinging Nettle *Urtica dioica* (Urticaceae) and an unclassified species of Fabaceae. Inorganic material (sand) was regularly present in the samples and in one case we also found a piece of gastropod shell.

Faecal sacs contained items belonging to five arthropod orders – Coleoptera; Diptera; Heteroptera; Cicadomorpha; and Araneae (see Table 1). Faeces composition calculated per nest was dominated by adult beetles,

mainly of Scarabeidae. Adult Diptera, mainly muscids and tipulids, were the second most abundant prey and Larvae of the scarabeids and dipterans were the third most abundant prey type. Other arthropod taxa accounted for less than 5% of all identifiable animal food objects and, therefore, were listed under the category ‘other arthropods’.

### Effect of nestling age on diet

Because we found no differences between study years in any component of diet (Kruskal–Wallis test: all  $P_s > 0.179$ ), we pooled data for further calculations. The total amount of food in the sample of a particular nestling varied significantly between age categories, being higher in older nestlings (Friedman test:  $\chi^2 = 10.67$ ,  $df = 1$ ,  $P < 0.01$ ). This was mostly because of an increase in the total mass of the plant component (Friedman test:  $\chi^2 = 20.17$ ,  $df = 1$ ,  $P < 0.01$ ), as the total mass of the animal component did not differ between age categories (Friedman test:  $\chi^2 = 0.17$ ,  $df = 1$ ,  $P = 0.683$ ). The mean sample weight at the younger age was 43.35 mg and the animal component comprised 68.12% (Fig. 1). The mean sample weight at the older age was 84.16 mg and the animal component comprised 40.65% (Fig. 1). We also looked for differences in the abundance of the three major categories of animal diet (i.e. Coleoptera adults, Diptera adults and Larvae) in the two age categories of the nestlings. For each animal diet category we calculated the average number of individuals of a given group of arthropods per nestling in the nest. We found no significant differences in abundance of any animal diet category (Coleoptera adults, Friedman test:  $\chi^2 = 0.39$ ,  $df = 1$ ,  $P = 0.532$ ; Diptera adults, Friedman test:  $\chi^2 = 0.00$ ,  $df = 1$ ,  $P = 1$ ; Larvae, Friedman test:  $\chi^2 = 0.07$ ,  $df = 1$ ,  $P = 0.782$ ).

### Body condition and diet composition in younger-age nestlings

No significant relationship between pre-fledging condition and the total amount of food in the samples at the younger age ( $t_{1,21} = 1.466$ ,  $P = 0.158$ ) was found. Neither the mass of plant nor animal diet component influenced condition estimates ( $t_{1,21} = 0.581$ ,  $P = 0.567$  and  $t_{1,21} = 1.006$ ,  $P = 0.326$ , respectively). The abundance of three major categories of animal diet at the younger age had no significant effect on pre-fledging condition (Coleoptera adults,  $t_{1,21} = -0.730$ ,  $P = 0.473$ ; Diptera adults,  $t_{1,21} = 0.217$ ,  $P = 0.830$ ; Larvae,  $t_{1,21} = 0.629$ ,  $P = 0.536$ ).

**Table 1.** Animal food in the diet of House Sparrow *Passer domesticus* nestlings assessed using faecal analysis; based on 206 faecal sacs containing 362 identifiable animal food objects from 106 nestlings from 31 nests.

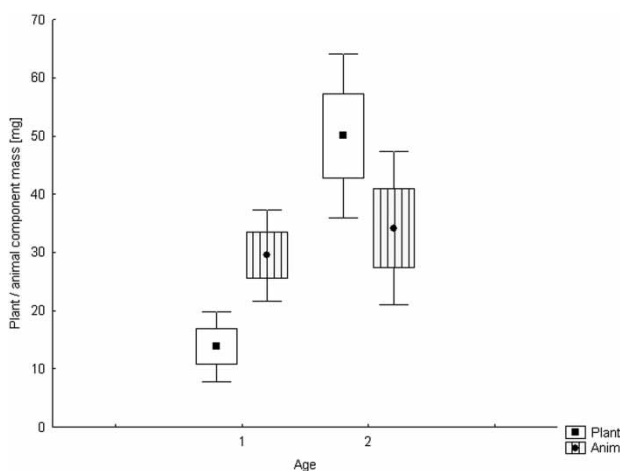
Taxon	Abundance (%)	Frequency (%)	Mean abundance/nest (%)	SD
<b>Adult Coleoptera</b>				
Total	61.05	94.30	61.97	26.40
Total Scarabeidae	34.25	75.76	35.36	27.36
<i>Aphodius</i>	15.19	58.62	14.44	16.18
<i>Ontophagus</i>	0.83	5.17	0.80	3.81
Other Scarabeidae <sup>a</sup>	18.23	70.42	20.12	21.31
Carabidae	11.33	48.28	11.96	15.30
Cerambycidae	4.70	24.14	3.68	7.14
Other Coleoptera <sup>b</sup>	10.77	48.28	10.96	16.73
<b>Adult Diptera</b>				
Total	21.54	74.10	21.73	19.41
Tipulidae	9.39	48.28	10.00	12.76
Muscidae	7.73	31.03	7.90	16.83
Other Diptera <sup>c</sup>	4.42	24.14	3.83	7.62
<b>Larvae</b>				
Total	8.57	39.70	8.64	13.60
Larvae of Scarabeidae	6.91	32.76	6.48	11.75
Larvae of Diptera	1.66	6.90	2.15	8.68
<b>Other arthropods</b>				
Total	8.83	38.00	7.67	11.74
Heteroptera	3.31	18.97	3.24	7.67
Cicadomorpha	1.38	6.90	0.94	3.55
Araneae <sup>d</sup>	4.14	24.14	3.49	7.23

<sup>a</sup>The group 'other Scarabeidae' comprised *Phyllopertha* and other unidentified genera; <sup>b</sup>the group 'other Coleoptera' comprised Oedemeridae, Geotrupidae (*Geotrupes* spp.) and other unidentified families; <sup>c</sup>the group 'other Diptera' comprised Faniidae, Culicidae and other unidentified families; <sup>d</sup>the group 'Araneae' comprised *Pardosa* spp. (Lycosidae), *Tetragnatha* spp. (Tetragnathidae) and other unidentified genera

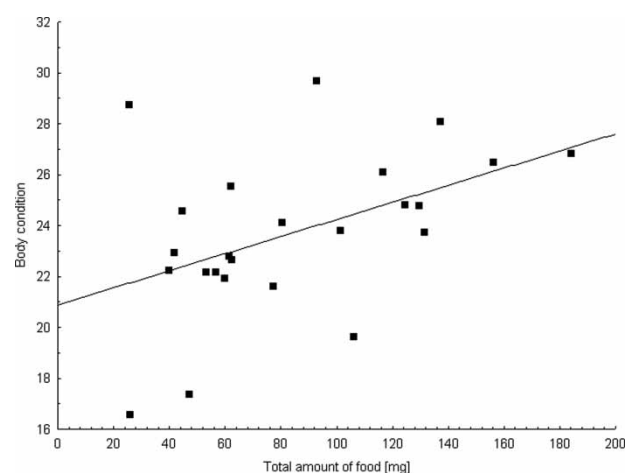
### Body condition and diet composition in older-age nestlings

A significant relationship between pre-fledging condition and the total amount of food in the sample of a particular

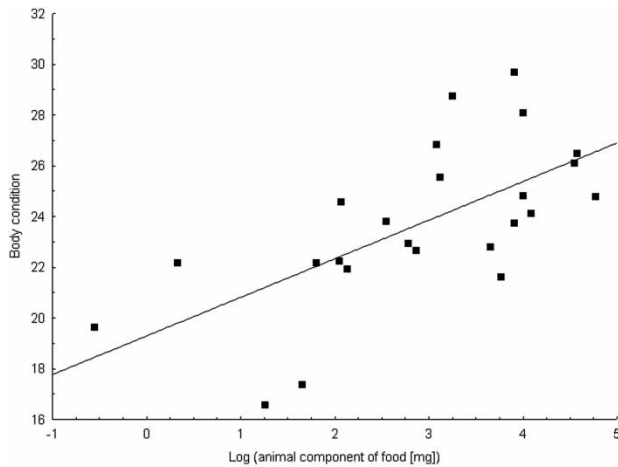
nestling was found ( $t_{1,21} = 2.402$ ,  $P = 0.026$ ) (Fig. 2). We found no evidence that the mass of plant component affected condition ( $t_{1,21} = 0.286$ ,  $P = 0.778$ ). However, the mass of animal component in the diet was positively



**Figure 1.** Average *per capita* mass of plant (open box) and animal (dashed box) components in the faecal samples of 4–6-day-old (age category 1) and 9–11-day-old nestlings (age category 2) of House Sparrow *Passer domesticus*.



**Figure 2.** The relationship between average body condition estimate of 9–11-day-old nestlings in nests of House Sparrow *Passer domesticus* and average *per capita* amount of food in the faecal samples;  $P = 0.026$ ;  $y = 20.88 + 0.03 \times x$ .



**Figure 3.** The relationship between average body condition estimate of 9–11-day-old nestlings in nests of House Sparrow *Passer domesticus* and average *per capita* mass of animal component in the faecal samples;  $P = 0.001$ ;  $y = 19.29 + 3.50 \times x$ .

and significantly related to condition ( $t_{1,21} = 3.926$ ,  $P < 0.001$ ) (Fig. 3). The abundance of three major categories of animal diet at the older age had no significant effect on condition (Coleoptera adults,  $t_{1,21} = 0.381$ ,  $P = 0.707$ ; Diptera adults,  $t_{1,21} = -1.151$ ,  $P = 0.263$ ; Larvae,  $t_{1,21} = 0.245$ ,  $P = 0.809$ ).

## DISCUSSION

The present study indicates the importance of food amount and diet composition for the body condition of nestling House Sparrows. Nestlings were fed with a variety of animal and plant material. The principal nestling diet composition, based on faecal analysis, was similar to those reported in studies conducted in other parts of Europe. Nestlings consumed mainly beetles and dipterans, which accounted for almost 83% of animal food. Coleoptera were the most abundant nestling food type in Poland (Anderson 1984) and Bulgaria (Ivanov 1990). Likewise, in the UK beetles were the most important prey species (Vincent 2005). However, the beetle families most often encountered in the diet of nestlings in previous studies were usually Carabidae and Curculionidae, on both rural and urban sites (Vincent 2005, Anderson 2006). In our study the beetles were represented mainly by scarabeids (*Onthophagus* spp., *Aphodius* spp.) which live in dung and are, therefore, abundant on farmsteads. The locality is probably also especially suitable for muscids and tipulids, which were the most abundant dipterans, while elsewhere the most frequent dipterans were hoverflies

(Syrphidae) (Anderson 2006). Vincent (2005) mentioned also aphids, spiders and ants among the most common prey species in rural habitats (Encke 1965, Mitschke *et al.* 1999). In our study we found spiders only in a quarter of all samples and ants and aphids were not detected at all. The lack of these soft-bodied taxa in the faeces might be caused by their geographically variable seasonal occurrence and their high digestibility; however, Vincent (2005) used the same method for diet analysis.

The abundance of three major categories of animal diet – i.e., adults of Coleoptera, adults of Diptera, and Larvae – did not differ during the course of nestlings' development. This result might arise from the fact that we did not analyze the diet of the nestlings during the very first days of their life, when the difference in diet composition may have been more pronounced. A larger sample size would also allow for finer-scale comparison without combining several taxa into conjunctive categories. Further, because of methodological limitations we cannot exclude that other components, which are hardly detectable in faeces, differed with the age of nestlings. For instance, in some passerines a peak in spider abundance in nestling diet has been reported during the early stages of their development (Cowie & Hinsley 1988, Grundel & Dahlsten 1991, Naef-Daenzer *et al.* 2000). It was shown that parents select spiders because of the high content of taurine – an amino acid that affects the behavioural characteristics of nestlings that can impact on fitness (Arnold *et al.* 2007). However, because of the relatively low abundance of spiders in the diet of nestlings in our study, we could not test the age-dependence of the presence of spiders in House Sparrow nestling diet. Finally, it is possible that for the development of House Sparrow nestlings the presence of animal protein in general is essential, rather than the presence of some specific invertebrate species. This assumption is in accordance with the general opportunistic foraging nature of sparrows (Anderson 2006). The parents usually feed their young with the locally and temporarily most abundant prey – e.g. coprophagous beetles on the farmstead in this study or aphids and ants in cities (Mitschke *et al.* 1999, Vincent 2005). Brodmann and Reyer (1999) previously showed that in Water Pipits *Anthus spinoletta*, parents searching for nestling food select prey by its size and catchability rather than nutritional value.

The older nestlings received more food than the younger ones. The increase in food amount was caused by the higher mass of plant component in the older nestlings' diet, while the mass of the animal component

remained stable across the two stages of development. Thus, the proportion of the animal component decreased with age. The increased amount of food delivered to older nestlings is common in birds and reflects the higher nutritional demands of growing offspring (Pinowski 1967, Conrad & Robertson 1993). The increased proportion of vegetable material in the diet of House Sparrow nestlings has also been reported from other localities (Wieloch 1975, Summers-Smith 1988, Anderson 2006). During the first days of their life the nestling House Sparrows are fed almost solely on an animal diet (Summers-Smith 1963) and this is probably because they need essential amino acids from animal proteins for their development (Ricklefs 1983, Arnold *et al.* 2007). At the age of 16–17 days the nestlings' preferences switch from insects to seeds and the diet gradually becomes almost entirely vegetarian (Mueller 1986). Before fledging, the nestlings need to gain fat stores, for which seeds and grain are a suitable resource. House Sparrow parents supply the higher nutritional demands of growing chicks by providing them with vegetable material, mainly seeds, which was the most abundant food at the study site. The stable amount of animal component fed to the nestlings suggests that there is probably some upper limit of animal prey that the parents are able to catch. Thus, they offset the increasing food demands of young with plant material for several reasons: it is abundant, easy to acquire and it corresponds with the nestlings' increasing preferences for plant food.

The total amount of food and the mass of animal component in the diet that was fed to nestlings in the pre-fledging period, but not at the younger age, were shown to affect their condition positively. The positive effect of the amount of food on the body mass of nestlings and on greater fledging success in House Sparrows was previously shown by Anderson (1977) during the local emergence of 13-year periodical cicadas, which constituted a super-abundant food. The effect of body mass on fledging success was shown by Cleasby *et al.* (2010), who found that House Sparrow nestlings of greater mass on day 11 were more likely to recruit. The importance of the animal component of nestling diet was stressed by Vincent (2005), who found more plant material within the diet of nestlings that subsequently died than in the diet of those that fledged. A shortage of animal prey causes consumption of unsuitable food and/or starvation, which leads to lower breeding success (Seel 1969, Vincent 2005).

None of the three major components of animal diet influenced nestling quality. In the UK, the abundance

of beetles in nestlings' diet has been shown to increase their condition (Vincent 2005). In the same locality the abundance of ants had the opposite effect (Vincent 2005) and reduced nestling body mass was associated with low aphid densities in the vicinity of the nests (Peach *et al.* 2008). Although ants occurred at our study site, we did not detect any in the faecal samples. Therefore, it seems apparent that sparrows select ants as food for their nestlings only in areas where more suitable prey is scarce. Finally, the lack of aphids in our samples shows that their absence does not always lead to malnutrition because sparrows can replace them with alternative prey.

Our study is the first analysis of House Sparrow nestling diet in the Czech Republic, where a single previous study focussed on adult sparrows (Ašmera 1962). The description of the diet of sparrows breeding on a farmstead helped to assess contemporary suitability of rural habitats as sources of nestlings' food and revealed geographic variation in the proportions of different diet components. Our results corroborate the importance of animal prey during the whole nesting period for the quality of nestlings. Hence, we assume that even if the probable decline of arthropods was not the main cause of the negative population trend of House Sparrows, it might contribute to low reproductive success and weaken population productivity.

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