Hard to fly the nest: A study of body condition and plumage quality in house sparrow fledglings

Charlène LELOUTRE, Alice GOUZERH, Frédéric ANGELIER[*]

Centre d'Etudes Biologiques de Chizé, CNRS, F-79360 Villiers en Bois, France

Abstract   Contrary to the nestling phase, the post-fledging phase has been less studied probably because it is challenging to follow the chicks after they fledge. However, this phase is crucial to consider when focusing on the life cycle of individuals because it is associated with new demands: After leaving the nest, individuals have to find their own food and cope with a new set of previously unknown stressors. In this study, we aimed at better understanding how energetically demanding the post-fledging period is in house sparrows *Passer domesticus* by measuring several indices of a fledgling's state (body condition, fat and muscle scores and plumage quality). If the energetic demands of the post-fledging period are greater than those of the adult life, we predicted that fledglings should be in lower condition and should have a plumage of lower quality relative to adults. Supporting this prediction, the condition and the plumage of fledglings differed dramatically from those of adults. Interestingly, this difference disappeared in autumn. Overall, our results suggest that the post-fledging period is probably one of the most energetically demanding of the life cycle in this species. Supporting this idea, the resighting probability of fledglings was lower relative to adults. However, resighting probability depends on many factors (mortality, dispersal, habitat use and behaviours) and future studies are necessary to tease apart their relative importance in determining resighting probability [*Current Zoology* 60 (4): 449–459, 2014].

Keywords   Body condition, Fault bar, Fat score, Muscle score, *Passer domesticus*

In birds, the developmental phase is usually a critical one for individuals because it is associated with a high risk of mortality for the chicks, but it also has important long-term consequences on the phenotype of individuals (reviewed in Lindström, 1999; Metcalfe and Monaghan, 2001) and, thus, on their survival and reproduction later in life (Monaghan, 2008; Harrison et al., 2010). For instance, van de Pol et al. (2006) showed that poor developmental conditions – being reared in a habitat of low quality – were associated with a low survival probability, a low probability of having access to good territories later in life, and, overall, a poor lifetime reproductive success in oystercatchers *Haematopus ostralegus*.

In this context, the chick's developmental phase has received much attention (reviewed in Lindström, 1999; Monaghan, 2008) and many studies have focused on the immediate consequences of developmental conditions on chick growth, morphology and survival (Sheldon et al., 1998; Lummaa and Clutton-Brock, 2002; Searcy et al., 2004). In addition, other studies have investigated the long-term consequences of developmental conditions on physiology (Raberg et al., 2003; Criscuolo et al., 2008; Krause et al., 2009; Honarmand et al., 2010),

morphology (Blount et al., 2003; Soma et al., 2006) and behaviors (Nowicki et al., 2002; Buchanan et al., 2003; Zann and Cash, 2008). For example, developmental stress has been shown to have long-term effects on the ability of individuals to cope with stressors (Lendvai et al., 2009), immune challenges (Raberg et al., 2003) or oxidative stress (Stier et al., 2009).

Although it is known that the post-fledging phase is associated with very high mortality in many bird species (Dhondt, 1979; Magrath, 1991; Naef-Daenzer et al., 2001; Vitz and Rodewald, 2011; Streby and Andersen, 2013), this phase requires further investigation (King et al., 2006; Rivers et al., 2012). Indeed, this phase is crucial because the developmental phase extends to the post-fledging phase in birds and chicks have not reached their adult phenotype (e.g. final size) at the time of fledging (Starck and Ricklefs, 1998; Becker and Wink, 2002; Schauroth and Becker, 2008; Ricklefs, 2008). Moreover, the post-fledging phase is associated with new demands for individuals: they have to find their own food (Wheelwright and Templeton, 2003) and they have to cope with a new set of stressors (e.g., evading predators, locating food; Keedwell, 2003). Therefore, investigating the differences between fled-

---

gling and adult condition will elucidate how fledglings adapt to the specific energetic demands of this phase (King et al., 2006; Vergara et al., 2010; Rivers et al., 2012).

Body condition can be used to assess how energetically demanding the environment is for an individual (Ardia, 2005; Costantini et al., 2009). Indeed, body condition is known to decrease when individuals cannot acquire enough energy to maintain a balanced energetic budget ('the nutritional stress hypothesis', Moe et al., 2002; Trites and Donnelly, 2003). Despite this common pattern, body condition regulation is complex and also depends on other factors (Lima, 1986). Thus, body condition can also be adaptively reduced or increased during specific phases in order to help individuals cope with a specific situation (McNamara et al., 2005). For instance, it has been shown that body condition decreases when predation risk is high in order to decrease wing load and, thus, to improve an individual's flight and escape abilities (Rands and Cuthill, 2001). Alternatively, body condition can be adaptively increased when food abundance becomes unpredictable in order to improve an individual's ability to cope with temporary food shortages (Cuthill et al., 2000). In addition, plumage quality is also important to consider because a plumage of poor quality can result from the occurrence of energetically demanding environmental conditions during the period of feather growth. For instance, fault bars - narrow, translucent bands found in the plumage of many bird species (Riddle, 1908; Machmer et al., 1992) - are thought to be caused by the occurrence of stressors, such as nutritional or handling stress, during feather growth (King and Murphy, 1984; Machmer et al., 1992; Bortolotti et al., 2002; Vágási et al., 2012). Similar to body condition, plumage quality may also be adaptively reduced under specific situations in order to increase resource allocation towards other resource-demanding activities (growth, immunity, etc.). Although such adaptations may occur, a plumage of poor quality should generally be associated with poor environmental conditions.

In addition to the study of fledglings' phenotype, it is also crucial to examine the fitness consequences of phenotypic variation for fledglings. As stated earlier, a high body condition can entail survival costs or benefits depending on the situation (food abundance, food predictability, predation risk, etc. McNamara et al., 2005; Rands and Cuthill, 2001; Cuthill et al., 2000). On the other hand, a plumage of poor quality is likely to have a negative impact on the short-term survival of individuals (Dawson et al., 2000; Vágási et al., 2012). Indeed, plumage quality probably affects the flight ability of fledglings and, therefore, their ability to forage but also to escape from predators.

In this study of house sparrows, we compared the phenotypes of fledglings and adults in summer (i.e. a few weeks after fledgling) and, then, in autumn (i.e. a few months after fledgling) in order to better understand the demands of the post-fledging phase and the phenotypic adjustments to the demands of this phase. We specifically focused on multiple and complementary indices of body condition. We monitored body condition through an index of body mass corrected by body size but we also recorded fat and muscle scores since they can also help interpret the demands of the post-fledging phase (Green, 2001). Plumage quality can be assessed by multiple methods but, in the field, counting the number of fault bars on the flight feathers is the most non-invasive method because it does not require plucking feathers (McDonald and Griffith, 2011). Importantly, these fault bars are often points of feather breakage and can therefore reduce flight or thermoregulation efficiency (Sarasola and Jovani, 2008; Jovani et al., 2010; Vágási et al., 2012).

Regarding body condition, we predict that fledglings should be in lower body condition than adult sparrows in summer (i.e. a few weeks after fledging, prediction 1). Such a low condition could result from decreased foraging proficiency (Weathers and Sullivan, 1989; Wheelwright and Templeton, 2003; Yoda et al., 2004). Regarding plumage quality, nestlings and fledglings have to grow all their feathers at a similar time that is energetically demanding because they also have to grow their organs and skeletons. On the other hand, adults moult over a longer period and they usually do so after the breeding period when their energetic resources do not have to be shared between maintenance and reproductive effort (Jovani and Blas, 2004; Vagasi et al., 2012). Therefore, we predict that fledglings should show a higher number of fault bars in comparison to adults (prediction 2). After a few weeks/months, juveniles may have acquired enough experience to forage efficiently. Moreover, they have moulted (post-fledging moult) during a period that may have been less energetically demanding because their growth was almost completed and they may have acquired enough foraging skills to be in better condition. Therefore, we predict that juveniles and adults should not differ in body condition and the number of fault bars in autumn (i.e. a few months after fledging, prediction 3a). Alternatively,

juveniles may still suffer from a lack of experience. In that case, we predict that juveniles would still be in worse condition and have a higher number of fault bars than adults (prediction 3b). Finally, fault bars may reduce the ability of fledglings to fly efficiently and, therefore, to forage and to escape predators (Bortolotti et al., 2002; Sarasola and Jovani, 2008) and body condition could obviously affect resighting probability through an effect on survival or dispersal (McNamara et al., 2005; Cuthill et al., 2000; Rands and Cuthill, 2001; Altwegg et al. 2000). Therefore, we will also examine the relationship between resighting probabilities, body condition and the number of fault bars.

1 Materials and Methods

1.1 Study site, captures and sightings

This study took place at the Centre d'Etudes Biologiques de Chizé (46°08′48″ N, 00°25′32″ O, CEBC-CNRS) in France where a free-living population of house sparrows *Passer domesticus* has been studied since 1996. The study started in June 2011 and ended in February 2012. Sparrows were captured during two specific periods: (i) in summer (from June 23 to August 5 2011) and (ii) in autumn (from October 19 to November 15, 2011). We caught house sparrows by permanently monitored passive netting as detailed in Angelier et al. (2010). Briefly, we set up 3 mist-nets at the study site and we then monitored these mist-nets permanently until a bird hit one of the mist nets (2 twelve meters net and 1 six meters net that were located in areas frequently used by house sparrows). Then, we immediately extracted the bird from the net, ringed it with an aluminum ring and a unique combination of three color rings for identification from a distance. We then weighed, bled and measured the birds before releasing them (see the next paragraph for details). We captured a total of 63 fledglings and 23 adults in summer. In addition, we recaptured 11 of these fledglings as juveniles during the autumn and we also caught 7 adults during the autumn. In summer, fledglings were a few weeks old when captured (age was not precisely known) and they were approximately 4–5 months old in autumn. We also caught 21 unringed birds during the autumn but we could not assign them to an age category (juveniles or adults) and they were therefore not considered in the analyses. In addition to the capture, we also intensively visited the study site during the autumn (from October 19 to November 15, 2011) and then again in winter (from February 14 to March 11, 2012) in order to monitor the resighting of fledglings and juveniles. On this study site, birds are attracted by multiple feeders and sparrows appear to visit these feeders very regularly. We observed these feeders from a distance with binoculars and, thus, were able to monitor the resighting of several additional birds. We respectively spent 50 and 62 hours of observation in autumn and winter to observe these feeders. In addition, we monitored 3 other sites for potential short-distance dispersal of sparrows in autumn and winter (Fleischer et al., 1984; Clarke et al., 1997). These sites are located in the vicinity of the CEBC-CNRS – within 10 km of the study site - and are known for having populations of house Sparrows that are the closest to the study site. Each site is also equipped with bird feeders that are regularly visited by house sparrows. All these sites were monitored through observation with binoculars during 20 hours in autumn and 20 hours in winter. During these observation sessions, we did not see any ringed sparrows outside of the study site (CEBC-CNRS). However, we cannot exclude that long-distance dispersal occurs in our studied house sparrows. Indeed, it is known that young house sparrows can disperse to establish their own territory and to avoid unsuitable conditions in their natal area (Altwegg et al., 2000). In house sparrows, natal dispersal can occur soon after fledging (Fleischer et al. 1984) or later during the autumn/winter (Altwegg et al., 2000). Because of this potential dispersal, we were only able to study the apparent survival or resighting probability of house sparrows in this study.

1.2 Blood sampling, molecular sexing, body condition and fault bars

For all sparrows, we collected a blood sample from the brachial vein using a 27-gauge needle and heparinized microcapillary tubes (50–100 µl). Blood samples were stored at 4°C until later processing. Within 6 hours of capture, blood samples were centrifuged, and plasma was decanted and stored at -20°C for another study. After centrifugation, red cells were kept frozen for molecular sexing. We determined the sex of fledglings by polymerase chain reaction amplification of part of two CHD genes present on the sex chromosomes at the Centre d'Etudes Biologiques de Chizé (CEBC), as detailed in Weimerskirch et al. (2005). We determined the sex of adults by plumage characteristics (Anderson, 2006). In addition, we weighed all birds with a precision scale (± 0.1 g, Scaltec, SBA53), and we measured their tarsus and bill length using a caliper (± 0.1 mm). At the time of capture, fledglings had not totally reached full size but their body size was comparable to adult body size (wing size, Mean ± *SE*, adults: 76.0 ±

0.5, fledglings: 72.2 ± 0.4; tarsus size, Mean ± *SE*, adults: 19.14 ± 0.18, fledglings: 19.07 ± 0.08). Therefore, we calculated body size using factor analysis for each individual. Factors were extracted from a principal component analysis performed on the two morphological variables (tarsus and bill length). The first factor accounted for 61.8% of the variance and wing and tarsus length were highly correlated with this factor (correlations, $P < 0.001$ and $r > 0.750$ for all variables), which was therefore assumed to represent overall body size. Then, we calculated an index of body condition by using the residuals from a linear regression of body mass against the body size factor ($P < 0.001$). In addition, we scored all birds for muscle and fat scores in summer as detailed in previous studies (Kaiser, 1993; Brown, 1996; Nyeland et al., 2003). Specifically, the fat score classification ranges from 0 (no visible fat) to 8 (fat deposits covering the flight muscles) and the muscle score classification ranges from 0 (keel very obvious with thin pectoral muscles making each side of the keel concave) to 3 (large pectoral muscles making the chest profile look very bulky and concave). We did not measure fat and muscle in autumn. In our study and contrary to passerine migrants that can accumulate large fat reserves in preparation for migration, sparrows do not have high fat scores (min: 1, max: 4 in our study) but this measure still provides relevant information on the amount of fat reserves available to individuals (Kaiser, 1993; Brown, 1996). In this study, sparrows did not show emaciated pectoral muscles and no bird had a muscle score of 0 (min: 1, max: 3, Nyeland et al., 2003). Before release, we monitored all sparrows for the presence of fault bars according to Bortolotti et al. (2002). Briefly, we inspected the primary and secondary remiges and rectrices of each bird for the presence of fault bars. For each bird, we thus counted a total number of fault bars. The number of fault bars, fat score and muscle score were always monitored by F. Angelier (FA) or C. Leloutre (CL). For 10 birds, each observer counted the number of fault bars three times and all these counts were identical ($n = 10$, Mean ± *SE*: 5.2 ± 1.6 for both field workers). For the same 10 birds, FA and CL assessed fat and muscle scores. All fat and muscle scores were identical ($n = 10$, Mean ± *SE*: 1.9 ± 0.3 for both field workers) and 9 of 10 muscle scores were identical ($n = 10$, Mean ± *SE*: 2.1 ± 0.2 for FA, 2.0 ± 0.2 for CL). Moreover, the discrepancy was limited for the 10th muscle score since FA scored it as a '3' whereas CL scored it as a '2'.

1.3   Statistical analyses

We conducted all analyses with RStudio (R Develo-

pment Core Team, 2008) and we constructed graphics with Sigmaplot 10.0. Significance was set to $P < 0.05$. We first tested whether body condition, fat score, muscle score and the number of fault bars differed between fledglings ($n = 63$) and adults ($n = 23$) during the summer period by using general linear models (GLMs) with a normal or a Poisson (specifically for 'the number of fault bars' variable) distribution and an identity or a log (specifically for 'the number of fault bars' variable) link function (dependent variables: body condition, fat score, muscle score or the number of fault bars, independent variables: sex (male, female), age (fledgling, adult), date of sampling, hour of sampling, and interactions). We included the 'date of sampling' and 'hour of sampling' variables in these GLMs because they are likely to affect body condition in our study species. The same analysis was done in autumn to test whether body condition and the number of fault bars differed between juveniles ($n = 11$) and adults ($n = 7$). To properly test whether body condition and the number of fault bars varied with age (fledglings vs. adults) and the period of sampling (summer vs. autumn), it would have been necessary to run a model with age, sex, period of sampling, hour of sampling and all the interactions. However, that was impossible because of a limited number of captures in autumn (11 juveniles and 7 adults). Instead, we used a paired student's test and a Wilcoxon test to determine whether body condition and the number of fault bars changed from summer to autumn for fledglings that were caught in both seasons ($n = 11$). This analysis was not done for adults because only three adults were caught both in summer and autumn. Note also that fat and muscle scores were not analyzed in autumn because these measures were not available.

Second, we tested whether the probability of resighting a bird – in autumn or winter – varied between fledglings ($n = 63$) and adults ($n = 23$) by using GLMs with a binomial distribution and a logit link function (dependent variable: resighting rate (0 for did not resight, 1 for resighted in fall or winter), independent variables: age (fledgling, adult), sex (male, female) and interaction).

Finally, we tested whether fledglings' resighting probability ($n = 63$) was affected by body condition, fat score, muscle score or the number of fault bars by using multiple GLMs with a binomial distribution and a logit link function (dependent variables: resighting rate (0 for did not return and 1 for returned), independent variables: sex (male, female), number of fault bars, body condition, fat score, muscle score and interactions). We also tested

whether our indices of condition (body condition, fat score, muscle score) and plumage quality were correlated in fledglings ($n = 63$).

2 Results

2.1 Differences between fledglings and adults in body condition and the number of fault bars

In summer, body condition of individual house sparrows was affected by 'age' (GLM, $F_{1,80} = 6.33$, $P = 0.014$), but not by 'sex' (GLM, $F_{1,80} = 0.24$, $P = 0.626$) or the 'sex x age' interaction (GLM, $F_{1,80} = 1.93$, $P = 0.169$). Adults were in better body condition than fledglings during the summer (Fig. 1A). In addition, body condition significantly improved throughout the day (GLM, $F_{1,80} = 22.37$, $P < 0.001$) but did not vary throughout the study period (GLM, $F_{1,80} = 1.94$, $P = 0.167$). Fat and muscle scores were affected by 'age' (GLM, fat: $F_{1,80} = 6.71$, $P = 0.011$; muscle: $F_{1,82} = 4.18$, $P = 0.044$) but not by 'sex' (GLM, fat: $F_{1,80} = 1.71$, $P = 0.194$; muscle: $F_{1,82} = 2.69$, $P = 0.105$) or the 'age x sex' interaction (GLM, fat: $F_{1,80} = 0.18$, $P = 0.675$; muscle:

$F_{1,82} = 1.68$, $P = 0.198$). Fledglings had higher fat scores than adults, whereas adults had higher muscle scores than juveniles (fat score, mean ± SE, fledglings: 1.83 ± 0.10, adults: 1.39 ± 0.10; muscle score, mean ± *SE*, fledglings: 1.63 ± 0.08, adults: 1.96 ± 0.12). Contrary to muscle score, fat score significantly improved throughout the day (GLM, fat: $F_{1,80} = 14.37$, $P < 0.001$, muscle: $F_{1,80} = 1.30$, $P = 0.258$). Fat and muscle scores did not significantly vary throughout the study period (GLM, fat: $F_{1,80} = 1.05$, $P = 0.308$, muscle: $F_{1,80} = 2.46$, $P = 0.121$). The number of fault bars was affected by age ($F_{1,82} = 18.67$, $P < 0.001$) but not by 'sex' ($F_{1,82} = 0.87$, $P = 0.351$). Adults had fewer fault bars than fledglings during the summer (Fig. 1C). There was a significant effect of the 'sex x age' interaction ($F_{1,82} = 7.43$, $P = 0.006$), demonstrating that this difference between adults and fledglings was especially marked for males (males, mean ± *SE*, fledglings: 19.08 ± 2.56, adults: 5.42 ± 1.26; females, mean ± SE, fledglings: 13.69 ± 1.27, adults: 10.72 ± 1.53).

In autumn, body condition of individual house spar-
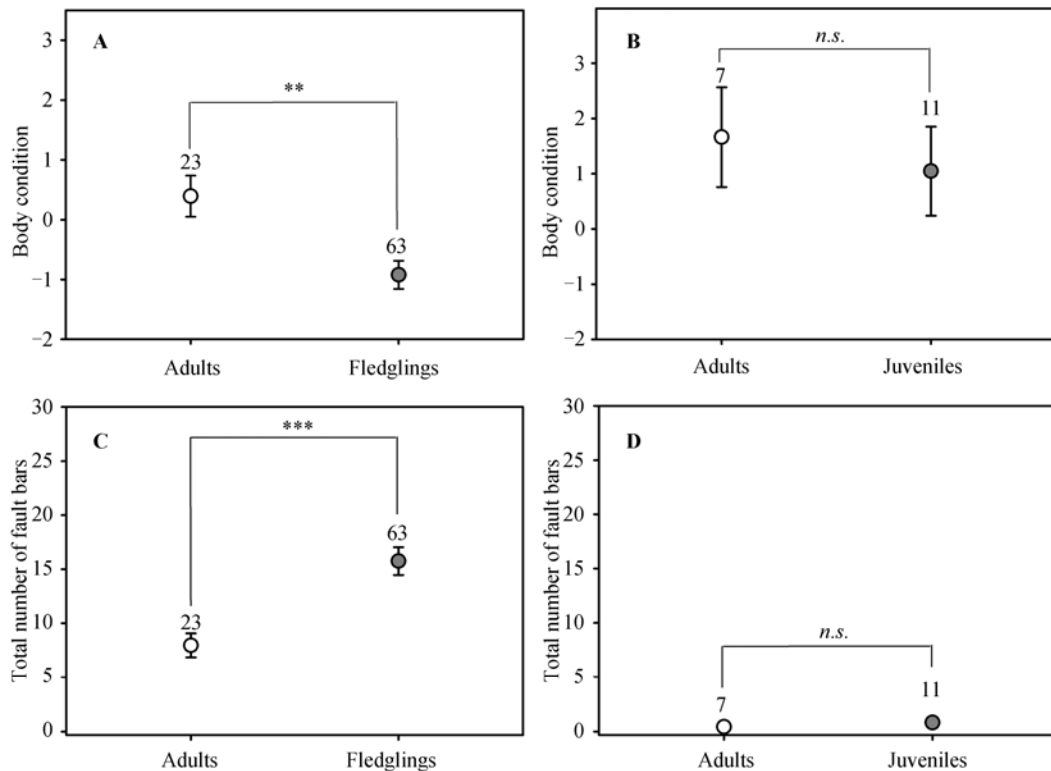
Fig. 1 Differences in body condition (mean ± *SE*) between adult and fledgling or juvenile house sparrows in summer (A) and autumn (B), and differences in the number of fault bars between adult and fledgling or juvenile house sparrows in summer (C) and autumn (D)

Body condition refers to the residuals of the regression between body mass and body size. The number of fault bars was counted on rectrices and primary and secondary remiges. Numbers above bars denote sample sizes. Asterisks indicate significant differences between groups (**: $P < 0.01$; ***: $P < 0.001$); n.s. indicates no significant differences between groups. For each figure, the variance in body condition or the number of fault bars did not differ between fledglings and adults (Levene's tests, $P > 0.05$).

rows was not affected by 'age' ($F_{1,12} = 1.06$, $P = 0.323$, Fig. 1B), sex ($F_{1,12} = 1.90$, $P = 0.193$) or the 'sex x age' interaction ($F_{1,12} < 0.01$, $P = 0.956$). Body condition significantly improved throughout the day (GLM, $F_{1,12} = 22.21$, $P < 0.001$) but did not change throughout the study period (GLM, $F_{1,12} = 1.37$, $P = 0.264$). In autumn, the number of fault bars was not affected by 'age' ($F_{1,14} = 2.52$, $P = 0.135$, Fig. 1D), 'sex' ($F_{1,14} = 1.93$, $P = 0.187$) or the 'sex x age' interaction ($F_{1,14} = 1.15$, $P = 0.302$). In addition, body condition significantly improved from summer to autumn for the fledglings that were caught in both seasons (paired student's test, $df = 10$, $t = 3.41$, $P = 0.007$, Fig. 2A). Moreover, the number of fault bars significantly decreased from summer to autumn for the fledglings that were caught in both seasons (Wilcoxon test, $n = 11$, $Z = 2.936$, $P = 0.003$, Fig. 2B).

2.2 Differences between fledglings and adults in resighting probability

Among the 63 fledglings captured in summer (39 females and 24 males), 21 were recaptured or resighted in autumn and/or in winter (30.7% of females and 37.5% of males). Among the 23 adults captured in summer (11 females and 12 males), 15 were recaptured or resighted in autumn and/or in winter (41.7% of females and 81.8% of males). This resighting probability was affected by 'age' ($F_{1,82} = 5.97$, $P = 0.017$) but not by 'sex' ($F_{1,82} = 3.46$, $P = 0.067$) nor the 'age x sex' interaction ($F_{1,82} = 1.76$, $P = 0.188$). Adults were more likely to be resighted than fledglings (65.2% and 33.3% respectively).
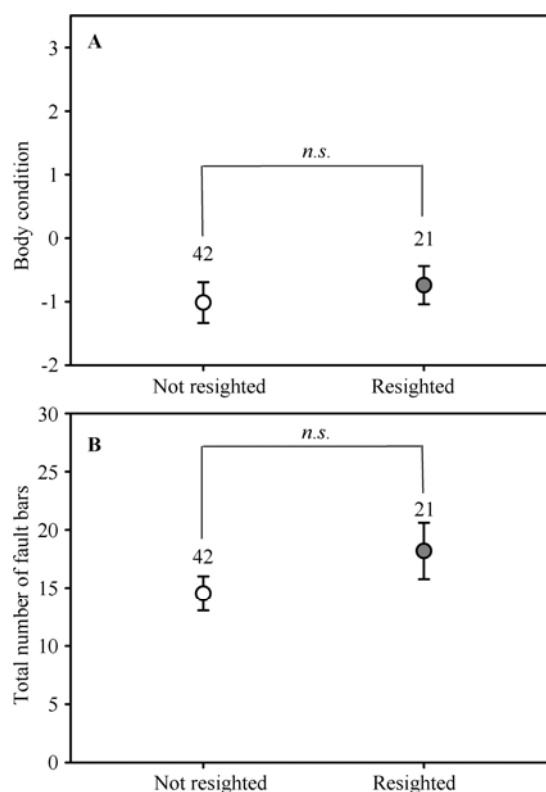
2.3 Body condition, fault bars and resighting probability in fledglings

In fledglings, the resighting probability was not affected by body condition (GLM, condition: $F_{1,59} = 0.689$, $P = 0.315$, sex: $F_{1,59} = 0.16$, $P = 0.694$, interaction: $F_{1,59} < 0.01$, $P = 0.960$, Fig. 3A), fat score (GLM, fat score: $F_{1,59} = 0.37$, $P = 0.544$, sex: $F_{1,59} = 0.25$, $P = 0.622$, interaction: $F_{1,59} = 0.56$, $P = 0.458$), muscle score (GLM, muscle score: $F_{1,59} = 2.07$, $P = 0.156$, sex: $F_{1,59} = 0.29$, $P = 0.595$, interaction: $F_{1,59} = 0.12$, $P = 0.734$) nor the number of fault bars (GLM, fault bars: $F_{1,59} = 1.44$, $P = 0.235$, sex: $F_{1,59} = 0.02$, $P = 0.899$, interaction: $F_{1,59} < 0.01$, $P = 0.978$; Fig. 3B). In summer,
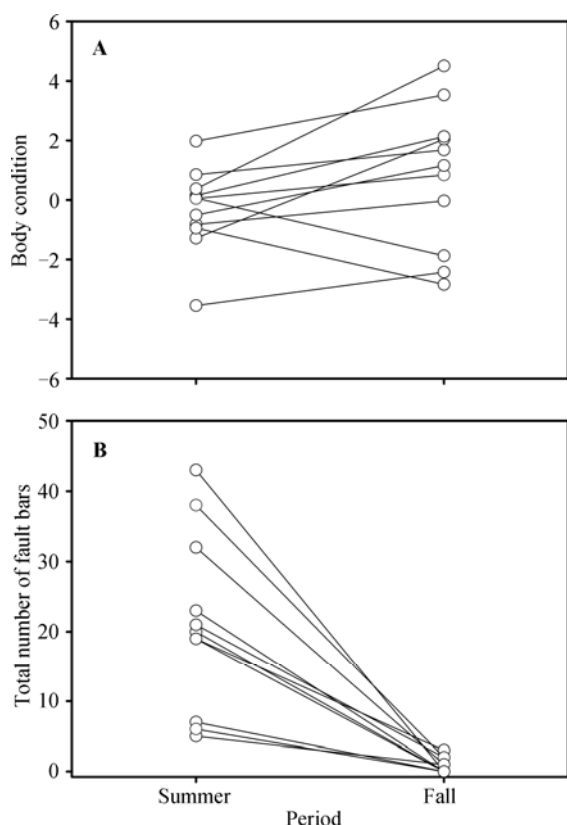
Fig. 2   Individual changes in (A) body condition ($P < 0.01$) and (B) the number of fault bars from summer to autumn for fledglings ($P < 0.01$)

Body condition refers to the residuals of the regression between body mass and body size. The number of fault bars was counted on rectrices and primary and secondary remiges.

Fig. 3   Resighting probability of fledgling house sparrows in autumn in relation to (A) body condition (mean ± *SE*) and (B) the number of fault bars (mean ± *SE*)

Body condition refers to the residuals of the regression between body mass and body size. The number of fault bars was counted on rectrices and primary and secondary remiges. Numbers above bars denote sample sizes. n.s. indicates no significant differences between groups.

the number of fault bars was not correlated with any condition indices (correlations, $n = 63$, body condition, fat score or muscle score, $P > 0.250$). However, body condition was significantly and positively correlated with muscle score (correlation, $n = 63$, $P = 0.030$, $r = 0.274$) and slightly and positively correlated with fat score (correlation, $n = 63$, $P = 0.076$, $r = 0.225$). However, fat and muscle score were not significantly correlated (correlation, $n = 63$, $P = 0.130$).

3 Discussion

3.1 Energetic demands of the post-fledging period

Our first prediction that fledglings would have a lower body condition than adult sparrows in summer was supported by the results. In addition, we found that fledglings improved their body condition from the summer to the autumn and, as a result, adults and juveniles did not differ anymore in body condition during the autumn (prediction 3a). Therefore, our results suggest that the post-fledging period is energetically demanding relative to other periods of the life cycle (Naef-Daenzer et al., 2001; Berkeley et al., 2007; Grüebler and Naef-Daenzer, 2008). Indeed, fledglings have no experience with their environment (e.g. predation, resources, etc.) when they fledge and they have low flight ability relative to adults (Anders et al., 1997; McFadzen and Marzluff, 1996; Naef-Daenzer et al., 2001; Cohen and Lindell, 2004). Although young house sparrows can be fed by their parents after fledging, it only lasts for 2–3 weeks and this parental provisioning may not be sufficient to fulfill their energetic needs (Anderson, 2006). Therefore, their reduced foraging skills and their lack of experience could explain their lower body condition relative to adults (Wheelwright and Templeton, 2003). Although there are no data available on intraspecific competition in this species, fledgling house sparrows might also have a low dominance rank in comparison with adults and, thus, may be less likely to have access to food (Nilsson and Smith, 1985, 1988; Sandell and Smith, 1991; Marra, 2000). Finally, fledglings have elevated energetic needs because they have not reached their adult size at the time of fledging (Starck and Ricklefs, 1998; Becker and Wink, 2002; Schauroth and Becker, 2008). Consequently, most of their energy intake may be allocated to growth – organs, skeleton, feathers etc. – and they may not have sufficient energy intake to maintain a high body condition.

Interestingly, we found that the muscle and fat scores of fledglings were respectively lower and higher than those of adults in summer. Although the low muscle scores of fledglings might suggest that they are in lower condition than adults, this difference may rather result from minimal flight experience of fledglings (Weathers and Sullivan, 1989; Anders et al., 1997; McFadzen and Marzluff, 1996; Naef-Deanzer et al., 2001; Cohen and Lindell, 2004; Wheelwright and Templeton, 2003; Yoda et al., 2004). The flight muscles are likely to develop and become larger when individuals have had a lot of flight practice (Ricklefs and Weremiuk, 1977; Ricklefs, 2008), and contrary to adults, fledglings have had only a limited period of time – a few days to a few weeks – to practice flight. Contrary to our first prediction, we reported that fledglings had overall higher fat scores than adults. This result is surprising and appears contradictory to our other findings since high fat score should be a sign of good condition. However, chicks accumulate fat reserves before fledging, probably in order to sustain their energetic needs during the period of time when they cannot efficiently fly and forage (Veiga, 1990; Both et al., 1999; Perrins and McCleery, 2001; Monros et al., 2003; Garant et al., 2004). Contrary to fledglings, adults may not need to accumulate fat reserves to improve their survival because of an easier access to food that makes food availability more predictable for adults than fledglings (Lima, 1986). This means that the differences we observed in fat, muscle scores and body condition may also result from a different allocation of energy between adults and fledglings.

Importantly, fledglings significantly improved their body condition from summer to autumn (at least for the juveniles that were recaptured and, thus, stayed on the study site), suggesting that house sparrows are able to fulfill the energetic demands of the post-fledging period after a few weeks (prediction 3a).

3.2 Plumage quality during the post-fledging period

Our second prediction that fledglings would have a more fault bars than adult sparrows in summer was supported by the results. Interestingly, the difference in the number of fault bars between fledglings and adults was large (mean $\pm$ *SE*, fledglings: 15.75 ± 0.52, adults: 7.96 ± 1.11). Contrary to adults that moult over several weeks, chicks have to grow all their feathers at a similar time in order to be ready for fledging (Anderson, 2006) and accelerated moult is known to induce a high frequency of fault bars (Vágási et al., 2012). In addition, this developmental period is also energetically demanding because the chicks have to grow their organs, tissues and skeletons (Starck and Ricklefs, 1998; Ricklefs, 2008). In contrast, adults are not engaged in any other

energetically demanding activity at the time of moult since the breeding period is over (Anderson, 2006). Therefore, chicks are probably more energetically constrained than adults while growing their feathers and this could explain their higher number of fault bars since nutritional stress is thought to be one cause of fault bar formation (King and Murphy, 1984; Machmer et al., 1992; Bortolotti et al., 2002; Vágási et al., 2012). Ultimately, this large number of fault bars in fledglings could be induced by a low investment of fledglings towards their plumage. This may result from the constraints of the post-fledging period but also from the potential minor fitness costs of low plumage quality in fledglings (fledglings only have to pay the costs of this low-quality plumage for a few weeks since the post-fledging molt occurs quickly after fledging).

We also found that the number of fault bars decreased from summer to autumn for fledglings that were recaptured and adults and juveniles did not differ anymore in their number of fault bars (prediction 3a). After the post-fledging phase (July–August), fledglings moult and probably do so once they have started to acquire enough experience to cope appropriately with their environment. Moreover, this post-fledging moult extends over a long period and is asynchronized with some feathers moulting before others (Anderson, 2006). Therefore, this post-fledging moult certainly occurs when individuals face lower energetic demands than while they were forming their first plumage at the nest (prediction 3a). This may explain the limited number of fault bars that was found in juveniles in the autumn. Importantly, the number of fault bars was not correlated with any index of condition in fledglings, suggesting that plumage quality may not dramatically affect the ability of fledglings to fly and forage in house sparrows. However, previous studies found that a low quality diet and a low body condition are correlated with a poor plumage quality (Bortolotti et al., 2002; Pap et al., 2008).

3.3 Determinants of fledgling's resighting probability

We reported that fledglings were less likely to be resighted in autumn than adults. Although fledglings could have survived without having been seen or captured, this result suggests that the post-fledging period may be associated with a high risk of mortality for individuals (Ringsby et al., 1998, 1999; Cohen and Lindell, 2004, Keedwell, 2003, Naef-Deanzer et al., 2001; Powell et al., 2003; Vitz and Rodewald, 2011; Streby and Andersen, 2013). Alternatively, natal dispersal may also partly explain this difference since fledglings may have dispersed to other areas. Indeed, we caught unringed birds

in autumn that were probably birds coming from other sites. We do not have any indication of the dispersal distance at our study site but previous studies have reported that young house sparrows can disperse soon after fledging over several km to establish their new territories (Fleischer et al., 1984; Altwegg et al., 2000). Moreover, there may be behavioural differences between adults and young sparrows that make young birds less likely to be resighted than adults. For instance, juveniles could be more cryptic than adults in autumn and winter. Similarly, young and adult birds may not use the same habitat to forage (Anders et al., 1998): fledglings could have been living in the same environment as adults in the summer when they were still dependent on their parents whereas they could have switched to another habitat in the autumn to avoid competition with the adults.

We did not find any correlation between body condition, fat and muscle scores and resighting probability in fledgling house sparrows. The absence of a correlation could result from the fact that body condition and fat and muscle scores show much day to day variation. For instance, one fledgling could have been in a poor body condition at the time of sampling without necessarily meaning that it has been in poor condition during the whole post-fledging period. For example, it has been shown that body condition of American redstarts can vary quickly from one week to another (Angelier et al., 2011). Indeed, the condition of a fledgling probably depends on daily environmental conditions (e.g. weather) and on its ability to forage and to have access to food during this specific day. Moreover, dispersal behaviour may also be affected by body condition or plumage characteristics (Altwegg et al., 2000). If so, some individuals may have disappeared from our study site but may still be alive, precluding us from finding any significant relationship between the resighting probability and the phenotype of individuals.

Finally, we did not find any correlations between the number of fault bars and fledglings' resighting probability, suggesting that fault bars did not result in elevated survival cost in fledgling house sparrows. However, Bortolotti et al. (2002) reported that adult female American kestrels *Falco sparverius* with many fault bars had lower survival rates. It is possible that other factors play a larger role than body condition or plumage quality in determining fledgling survival in house sparrows. Sparrow fledglings are very susceptible to predation because of their limited experience with predators and poor flight ability (Anderson, 2006). Preda-

tion of house sparrows by feral cats and eurasian sparrowhawks *Accipiter nisus* has frequently been observed at our study site and we believe that the effect of predation on survival outweighs and masks potential effects of condition or plumage quality on fledgling survival. Varying predation pressure among years or sites could also explain why previous studies reported that body condition was correlated with fledgling survival in some circumstances but not others (Ringsby et al., 1998). Therefore, future studies should examine the difference in body condition and plumage quality between adults and fledglings over different years and environmental situations. Again, all these patterns may also result from an effect of body condition, fat and muscle scores and the number of fault bars on dispersal behaviour or resighting/recapture probabilities in house sparrows. The sample size in this study did not allow us to use appropriate capture-mark-recapture models, and therefore, further studies should be conducted to test these questions in fledgling house sparrows.

To conclude, we used several indices to obtain an integrated picture of the constraints that the post-fledging period can impose to fledgling house sparrows. We showed that the condition and the plumage of fledglings differ dramatically from those of adults and our results suggest that the post-fledging period is an energetically demanding period of the life cycle. In addition, varying environmental conditions among years (predation, food availability and weather) could impose contrasted energetic constraints on fledglings and this could possibly attenuate or exacerbate the findings we reported in this study on body condition, plumage quality or resighting probability. Because our sample size was limited in autumn, further studies should also examine these questions in autumn when fledglings have moulted and acquired more foraging experience. Such investigation would allow accurately assessing the constraints of the post-fledging period in house sparrows.

References

Altwegg R, Ringsby TH, Saether BE, 2000. Phenotypic correlates and consequences of dispersal in a metapopulation of house sparrows *Passer domesticus*. J. Anim. Ecol. 69: 762–770.

Anders AD, Dearborn DC, Faaborg J, Thompson FR, 1997. Juvenile survival in a population of neotropical migrant birds. Cons. Biol. 11: 698–707.

Anders AD, Faaborg J, Thompson FR, 1998. Postfledging dispersal, habitat use and home range size of juvenile wood thrushes. The Auk 115: 349–358.

Anderson TR, 2006. Biology of the ubiquitous house sparrow: From genes to populations. Oxford: Oxford University Press.

Angelier F, Tonra CM, Holberton RL, Marra PP, 2010. How to capture wild passerine species to study baseline corticosterone levels. J. Ornithol. 151: 415–422.

Angelier F, Tonra CM, Holberton RL, Marra PP, 2011. Short-term changes in body condition in relation to habitat and rainfall abundance in American redstarts *Setophaga ruticilla* during the non-breeding season. J. Avian Biol. 42: 335–341.

Ardia D,R 2005. Super size me: An experimental test of the factors affecting lipid content and the ability of residual body mass to predict lipid stores in nestling European Starlings. Funct. Ecol. 19: 414–420.

Becker PH, Wink M, 2002. Geschlechtsabhängige Größenunterschiede von Flügglingen der Flussseeschwalbe *Sterna hirundo*. J. Ornithol. 143: 51–56.

Berkeley LI, McCarty JP, Wolfenbarger LL, 2007. Postfledging survival and movement in dickcissels *Spiza americana*: Implications for habitat management and conservation. The Auk 124: 396–409.

Blount JD, Metcalfe NB, Arnold KE, Surai PF, Devevey GL et al., 2003. Neonatal nutrition, adult antioxidant defences and sexual attractiveness in the zebra finch. Proc. R. Soc. B 270: 1691–1696.

Bortolotti GR, Dawson RD, Murza GL, 2002. Stress during feather development predicts fitness potential. J. Anim. Ecol. 71: 333–342.

Both C, Visser ME, Verboven N, 1999. Density-dependent recruitment rates in great tits: The importance of being heavier. Proc. R. Soc. B 266: 465–469.

Brown ME, 1996. Assessing body condition in birds. In: Nolan V, Ketterson ED ed. Current Ornithology, Vol. 13. New York: Plenum Press, 67–735.

Buchanan KL, Spencer KA, Goldsmith AR, Catchpole CK, 2003. Song as an honest signal of past developmental stress in the European starling *Sturnus vulgaris*. Proc. R. Soc. B 270: 1149–1156.

Clarke AL, Saether BE, Røskaft E, 1997. Sex biases in avian dispersal: A reappraisal. Oikos 79: 429–438.

Cohen EB, Lindell CA, 2004. Survival, habitat use, and movements of fledgling white-throated robins *Turdus assimilis* in a Costa Rican agricultural landscape. The Auk 121: 404–414.

Costantini D, Casagrande S, Carello L, Dell'Omo G, 2009. Body condition variation in kestrel *Falco tinnunculus* nestlings in relation to breeding conditions. Ecol. Res. 24: 1213–1221.

Criscuolo F, Monaghan P, Nasir L, Metcalfe NB, 2008. Early nutrition and phenotypic development:"catch-up" growth leads to elevated metabolic rate in adulthood. Proc. R. Soc. B 275: 1565–1570.

Cuthill IC, Maddocks SA, Weall CV, Jones EKM, 2000. Body mass regulation in responses to changes in feeding predictability and overnight energy expenditures. Behav. Ecol. 11: 189–195.

Dawson A, Hinsley SA, Ferns PN, Bonser RHC, Eccleston L, 2000. Rate of moult affects feather quality: A mechanism linking current reproductive effort to future survival. Proc. R.

Soc. B 22: 2093–2098.

Dhondt AA, 1979. Summer dispersal and survival of juvenile great tits in southern Sweden. Oecologia 42: 139–157.

Fleischer RC, Lowther PE, Johnston RF, 1984. Natal dispersal in house sparrows *Passer domesticus*: Possible causes and consequences. J. Field Ornithol. 55: 444–456.

Garant D, Kruuk LE, McCleery RH, Sheldon BC, 2004. Evolution in a changing environment: A case study with great tit fledging mass. Am. Nat. 164: 115–129.

Green AJ, 2001. Mass/length residuals: Measures of body condition or generators of spurious results. Ecology 85: 1473–1483.

Grüebler MU, Naef-Daenzer B, 2008. Fitness consequences of pre-and post-fledging timing decisions in a double-brooded passerine. Ecology 89: 2736–2745.

Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S, 2010. Carry-over effects as drivers of fitness differences in animals. J. Anim. Ecol. 80: 1–15.

Honarmand M, Goymann W, Naguib M, 2010. Stressful dieting: Autritional conditions but not compensatory growth elevate corticosterone levels in Zebra finch nestlings and fledgings. Plos One 5: 1–7.

Jovani R, Blas J, 2004. Adaptive allocation of stress-induced deformities on bird feathers. J. Evol. Biol. 17: 294–301.

Jovani R, Blas J, Stoffel MJ, Bortolotti LE, Bortolotti GR, 2010. Fault bars and the risk of feather damage in cranes. J. Zool. 281: 94–98.

Kaiser A, 1993. A new multi-category classification of subcutaneous fat deposits of songbirds. J. Field Ornithol. 64: 246–255.

Keedweel RJ, 2003. Does fledging equal success? Post-fledging mortality in the black-fronted tern. J. Field Ornithol. 74: 217–221.

King JR, Murphy ME, 1984. Fault bars in the feathers of white-crowned sparrows: Dietary deficiency or stress of captivity and handling? The Auk 101: 168–169.

King DI, DeGraaf RM, Smith ML, Buonaccorsi JP, 2006. Habitat selection and habitat-specific survival of fledgling ovenbirds *Seiurus aurocapilla*. J. Zool. 269: 414–421.

Krause ET, Honarmand M, Wetzel J, Naguib M, 2009. Early fasting is long lasting: differences in early nutritional conditions reappear under stressful conditions in adult female zebra finches. Plos One 4: 1–6.

Lendvai AZ, Loiseau C, Sorci G, Chastel O, 2009. Early developmental conditions affect stress response in juvenile but not in adult house sparrow *Passer domesticus*. Gen. Comp. Endocrinol. 160: 30–35.

Lima SL, 1986. Predation risk and unpredictable feeding conditions: Determinants of body mass in birds. Ecology 67: 377–385.

Lindström J, 1999. Early development and fitness in birds and mammals. Tr. Ecol. Evol. 14: 343–348.

Lummaa V, Clutton-Brock T, 2002. Early development, survival and reproduction in humans. Tr. Ecol. Evol. 17: 141–147.

Machmer MM, Esselink H, Steeger C, Ydenberg RC, 1992. The occurrence of fault bars in the plumage of nestling ospreys. Ardea 80: 261–272.

Magrath RD, 1991. Nestling weight and juvenile survival in the blackbird *Turdus merula*. J. Anim. Ecol. 60: 335–351.

Marra PP, 2000. The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. Behav. Ecol. 11: 299–308.

McDonald PG, Griffith SC, 2011. To pluck or not to pluck: The hidden ethical and scientific costs of relying on feathers as a primary source of DNA. J. Avian Biol. 42: 197–203.

McFadzen ME, Marzluff JM, 1996. Mortality of prairie falcons during the fledging-dependence period. Condor 98: 791–800.

McNamara JM, Barta Z, Houston AI, Race P, 2005. A theoretical investigation of the effects of predators on foraging behaviour and energy reserves. Proc. R. Soc. B 272: 929–934.

Metcalfe NB, Monaghan P, 2001. Compensation for a bad start: Grow now, pay later? Tr. Ecol. Evol. 16: 254 – 260.

Moe B, Langseth I, Fyhn M, Gabrielsen GW, Bech C, 2002. Changes in body condition in breeding kittiwakes *Rissa tridactyla*. J. Avian Biol. 33: 225–234.

Monaghan P, 2008. Early growth conditions, phenotypic development and environmental change. Phil. Trans. R. Soc. B 363: 1635–1645.

Monros JS, Belda EJ, Barba E, 2003. Post-fledging survival of individual Great tits: The effect of hatching date and fledging mass. Oikos 99: 481–488.

Naef-Daenzer B, Widmer F, Nuber M, 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. J. Anim. Ecol. 70: 730–738.

Nilsson JÅ, Smith HG, 1985. Early fledgling mortality and the timing of juvenile dispersal in the marsh tit *Parus palustris*. Ornis Scandinavica 16: 293–298.

Nilsson JÅ, Smith HG, 1988. Incubation feeding as a male tactic for early hatching. Anim. Behav. 36: 641–647.

Nowicki S, Searcy W, Peters S, 2002. Brain development, song learning and mate choice in birds: A review and experimental test of the "nutritional stress hypothesis". J. Comp. Physiol. A 188: 1003–1014.

Nyeland J, Fox AD, Kahlert J, Therkildsen OR, 2003. Field methods to assess pectoral muscle mass in moulting geese. Wildlife Biol. 9: 155–159.

Pap PL, Vàgàsi CI, Czirjàk GA, Barta Z, 2008. Diet quality affects postnuptial molting and feather quality of the house sparrow *Passer domesticus*: Interaction with humoral immune function? Can. J. Zool. 86: 834–842.

Perrins CM, McCleery RH, 2001. The effect of fledging mass on the lives of great tits *Parus major*. Ardea 89: 135–142.

Powell LA, Scott LJ, Hass JT, 2003. Nesting success and juvenile survival for wood thrushes in an eastern Iowa forest fragment. Iowa Bird Life 73: 121–129.

Raberg L, Stjernman M, Hasselquist D, 2003. Immune responsiveness in adult blue tits: Heritability and effects of nutritional status during ontogeny. Oecologia 136: 360–364.

Rands SA, Cuthill IC, 2001. Separating the effects of predation risk and interrupted foraging upon mass changes in the blue tit *Parus caeruleus*. Proc. R. Soc. B 268: 1783–1790.

Ricklefs RE, 2008. Patterns of growth in birds. Ibis 110: 419–451.

Ricklefs RE, Weremiuk S, 1977. Dynamics of muscle growth in the starling and Japanese quail: A preliminary study. Comp. Biochem. Physiol. A 56: 419–423.

Riddle O, 1908. The genesis of fault-bars in feathers and the cause of alternation of light and dark fundamental bars. Biol. Bull. 14: 328–371.

Ringsby TH, Saether BE, Altwegg R, Solberg EJ, 1999. Temporal and spatial variation in survival rates of a house sparrow *Pas-

ser domesticus metapopulation. Oikos 85: 419–425.

Ringsby TH, Sæther BE, Solberg EJ, 1998. Factors affecting juvenile survival in house sparrow *Passer domesticus*. J. Avian Biol. 29: 241–247.

Rivers JW, Liebl AL, Owen JC, Martin LB, Betts MG, 2012. Baseline corticosterone is positively related to juvenile survival in a migrant passerine bird. Funct. Ecol. 26: 1127–1134.

Sandell M, Smith HG, 1991. Dominance, prior occupancy, and winter residency in the great tit *Parus major*. Behav. Ecol. Sociobiol. 29: 147–152.

Sarasola JH, Jovani R, 2008. Risk of feather damage explains fault bar occurrence in a migrant hawk, the Swainson's hawk *Buteo swainsoni*. J. Avian Biol. 37: 29–35.

Schauroth C, Becker PH, 2008. Post-fledging body mass increase in common terns *Sterna hirundo*: Influence of age, sex and year. Ibis 150: 50–58.

Searcy WA, Peters S, Nowicki S, 2004. Effects of early nutrition on growth rate and adult size in song sparrows *Melospiza melodia*. J. Avian Biol. 35: 269–279.

Sheldon BC, Merilä J, Lindgren G, Ellegren H, 1998. Gender and environmental sensitivity in nestling collared flycatchers. Ecology 79: 1939–1948.

Soma M, Takahasi M, Ikebuchi M, Yamada H, Suzuki M et al., 2006. Early rearing conditions affect the development of body size and song in Bengalese finches. Ethology 112: 1071–1078.

Starck JM, Ricklefs RE, 1998. Avian Growth and Development: Evolution within the Altricial - Precocial Spectrum. Oxford: Oxford Ornithology Series.

Stier KS, Almasi B, Gasparini J, Piault R, Roulin A et al., 2009. Effects of corticosterone on innate and humoral immune functions and oxidative stress in barn owl nestlings. J. Exp. Biol. 212: 2085–2091.

Streby HM, Andersen DE, 2013. Survival of fledgling ovenbirds: Influences of habitat characteristics at multiple spatial scales.

The condor 115: 403–410.

Trites AW, Donnelly CP, 2003. The decline of Steller sea lions *Eumotopias jubatus* in Alaska: A review of the nutritional stress hypothesis. Mammal. Rev. 33: 3–28.

Vágási CI, Pap PL, Vincze O, Benkő Z, Marton A et al., 2012. Haste makes waste but condition matters: Molt rate-feather quality trade-off in a sedentary songbird. Plos One 7: e40651.

Van de Pol M, Bruinzeel LW, Heg D, Van der Jeudg HP, Verhulst S, 2006. A silver spoon for a golden future: Long-term effects of natal origin on fitness prospects of oystercatchers *Haematopus ostralegus*. J. Anim. Ecol. 75: 616–626.

Veiga JP, 1990. A comparative study of reproductive adaptations in house and tree sparrows. The Auk 107: 45–59.

Vergara P, Fargallo JA, Martinez-Padilla J, 2010. Reaching independence: Food supply, parent quality, and offspring phenotypic characters in kestrels. Behav. Ecol. 21: 507–512.

Vitz AC, Rodewald AD, 2011. Influence of condition and habitat use on survival of post-fledging songbirds. The Condor 113: 400–411.

Weathers WW, Sullivan KA, 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. Ecol. Mono. 59: 223–246.

Weimerskirch H, Lallemand J, Martin J, 2005. Population sex ratio variation in a monogamous long-lived bird, the wandering albatros. J. Anim. Ecol.74: 285–291.

Wheelwright NT, Templeton JJ, 2003. Development of foraging skills and the transition to independence in juvenile savannah sparrows. The Condor 105: 279–287.

Yoda K, Kohno H, Naito Y, 2004. Development of flight performance in the brown booby. Proc. R. Soc. B 271: 240–242.

Zann R, Cash E, 2008. Developmental stress impairs song complexity but not learning accuracy in non-domesticated zebra finches *Taeniopygia guttata*. Behav. Ecol. Sociobiol. 62: 391–400.