Behavioural responses during feather replacement in house sparrows

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Birds lose feathers, whether during molt or by accident, and replace them by processes that are energetically demanding. We hypothesized that house sparrows *Passer domesticus biblicus* use behavioral means to save energy when feathers are lost, and tested the general prediction that house sparrows growing new feathers adjust their behavior to minimize the energy costs of foraging and to increase net energy gain from their food. To test these predictions we divided 18 house sparrows into three groups: 1) plucked – house sparrows from which we plucked 15 flight feathers; 2) cut – house sparrows in which the same 15 feathers were cut off at the calamus below the barbs; and 3) control – unmanipulated house sparrows with plumage intact. We recorded both the quantity of seeds the house sparrows ate and the time they spent foraging from assay food patches. We found that 'plucked' sparrows growing new feathers adjust their foraging behavior by reducing their feeding time and the number of visits to a food patch. This allowed them to increase their patch harvest rate while maintaining a steady body mass.

Most avian species replace their feathers at least once a year, molting completely (Murphy 1996). Molting entails direct energetic costs, mainly due to the metabolic cost of the physiological and anatomical adjustments that attend the growth of feathers (Schieltz and Murphy 1995, Murphy 1996, Hoye and Buttemer 2011), but also because of increased thermoregulatory costs resulting from impaired insulation (Murphy and King 1991, 1992, Lindström et al. 1993) and the biosynthesis of new feathers (Lindström et al. 1993). In addition, molting is associated with an indirect cost arising from compromised flight ability due to reduced wing area or wing span (Swaddle et al. 1996, Swaddle and Witter 1997, Hedenström and Sunada 1999, Guillemette et al. 2007). Clearly, feather replacement, either during molt or when feathers are lost otherwise, by accident or in an encounter with a predator for example, is energetically demanding. We assumed that birds replacing their feathers use behavioral means (e.g. foraging behavior) to save energy.

Observing a forager's patch use behavior can allow us to understand its foraging costs (Stephens and Krebs 1986). For instance, if an organism is foraging in a risky environment, optimal foraging theory (Charnov 1976, Stephens and Krebs 1986) intimates that the forager will quit foraging when the gained benefit, i.e. harvest rate (H), no longer exceeds the sum of its metabolic cost of foraging (C), the perceived cost of predation (P), and missed opportunity costs (MOC);

$H = C + P + MOC$ (Brown 1988, 1992). In a patch with diminishing returns, the amount of food left behind in a food patch (i.e. its giving up density, GUD) is a good proxy for the forager's patch quitting-harvest rate. Thus quantifying the quitting harvest rate or GUD of animals should reflect the individual's overall foraging costs in the patch (Brown 1988). In the present study, we examined patch use behavior by measuring giving up densities of house sparrows *Passer domesticus biblicus* allotted to three feather treatment groups: birds with their feathers plucked, cut or intact (control) to separate the energetic costs of replacing feathers from other costs attributable to missing flight feathers, since birds with cut feathers do not replace them until the next molt. We assumed that house sparrows from both the cut and the plucked treatments experienced a functional cost due to impaired flight ability and an energetic cost due to increased thermoregulatory demands (Senar et al. 2002), and that only house sparrows from the plucked treatment faced an additional energetic cost related to the growth of new feathers. Therefore, we predicted that the marginal value of energy ($\partial F/\partial e$, the effect of net energy gain on the forager's fitness), is higher for house sparrows with plucked feathers. Hence, house sparrows with plucked feathers should consume more food, i.e. have lower GUDs, and higher harvest rates than house sparrows from the other treatments.

Since we expected differences in energetic costs among the three feather treatment groups, due to differences in C, the metabolic cost of foraging, we allowed the sparrows to choose and forage from two different patch types. These two patches had the same amount of food, but differed in the level of difficulty of obtaining it. This allowed us to test whether house sparrows adjust their behavior according to their foraging costs. House sparrows had the choice of feeding either from a free-access tray, where all the food was within easy reach, i.e. their encounter rate with seeds was high; and a more 'natural' tray in which food was mixed in a substrate and where we assumed that finding food becomes harder as sparrows deplete the patch, i.e. seed encounter rate is progressively reduced with resultant diminishing returns. We predicted that house sparrows have higher GUD and lower harvest rates when foraging in the natural tray than in the free-access one. More specifically, since regrowth of feathers affects $\partial F/\partial e$ so that sparrows with plucked feathers are expected to ascribe a higher marginal value to energy gained from foraging than do the control birds, we predicted that their harvest rate increases and GUD decreases with increasing energetic demands for regrowth of feathers. We further predicted that any differences between house sparrows from the different feather treatment groups are exacerbated when foraging in the natural tray. Finally, we monitored changes in body mass of all the house sparrows throughout the experiment to test for possible effects of the feather treatments on body reserves.

Material and methods

Animals

A total of 18 house sparrows were captured with mist nets on the Sede Boqer Campus of Ben-Gurion Univ. at Midreshet Ben-Gurion, Israel (30°51′17.17″N, 34°46′57.54″E, 480 m a.s.l.). House sparrows were captured in January 2008 between a minimum of two weeks to a maximum of a month before the beginning of the experiments. The birds were individually identified by banding them with standard Israel aluminum bands, and each treatment group (see below) was housed in a separate outdoor aviary (1.5 × 2 × 2.5 m), with free access to unhusked millet seeds and water ad libitum. There were equal numbers of male and female house sparrows in each of the experimental groups. All experiments were completed before the natural molting season of the house sparrows and all were released near their site of capture after the experiment in which they were subjects.

Foraging behavior

In mid-January 2008, the 18 house sparrows were divided into three groups of six individuals each: 1) plucked – each bird had a total of 15 feathers plucked, five from each wing, namely the 3rd and 6th primaries, 1st and 4th secondaries, and the 1st tertiary, and five rectrices; the 4th, 5th, and 6th from the right, and 5th and 6th from the left, following feather designation by Newton (1966); 2) cut: these had the same 15 feathers as in the plucked group cut off at the calamus below the barbs; and 3) control: six unmanipulated

house sparrows. At the peak of their annual complete moult, house sparrows replace several primaries, secondaries and rectrices simultaneously; thus our choice of 15 feathers is representative of the event that they naturally experience (Anderson 2006). Each morning at 06:00 birds were captured and weighed to ± 0.01, when we also checked for the onset of re-growth of the missing feathers in house sparrows from the plucked treatment. As soon as this occurred, passive integrated transponder (PIT) tags (TX148511B, Biomark, Boise, ID, USA) were implanted subcutaneously on their backs between the scapulars. A short incision was made laterally, just above the rib cage, and the tag was inserted with a microprobe. We sealed the incision with medical cyanoacrylate glue (Histoacryl®, TissueSeal, Ann Arbor, MI, USA). The tags were implanted so that we could quantify the foraging behavior of each individual (see below).

Quantifying house sparrow patch use behavior

During the experiment, each group of house sparrows was moved to an outdoor aviary (5 × 5 × 3 m with several branches for perching) for 5 d, where we placed two plastic food trays (28 × 38 × 8 cm): a free-access tray containing 5 g of seeds evenly spread on it, and a natural tray containing 3 g of seed thoroughly mixed with 3 dm³ of sand. We tested the three feather treatment groups in series, first the controls, then the house sparrows with cut feathers and last the house sparrows with plucked feathers. On any given day, five new sets of trays were presented to each group. Both the free-access and natural trays were replaced throughout each day, in the following sequence (time treatments): after 15 min; then after 120 min; then after 60 min; then after 180 min; and finally after 30 min. At the end of each period, the trays were gathered, and fresh trays were set out. The remaining seeds were collected by sifting the sand and debris, and weighed to ± 0.01 g to calculate the GUD. We quantified the time that sparrows spent in the trays by recording their PIT tag IDs with readers (Model SQID, Vantro Systems, Burnsville, MN, USA) placed under each seed tray, which recorded the presence of several birds at the feeders in an additive manner. From this information, we derived the cumulative amount of time sparrows spent in each tray and the number of visits they paid to each tray. By offering seed trays for different periods we could plot harvest rate curves (Kotler and Brown 1990). The positions of the free-access and natural trays within the aviary were alternated randomly to ensure the birds did not become accustomed to the position of a particular type of tray.

Statistical analyses

We used repeated-measures ANOVA (rm-ANOVA) to compare changes in body mass (m_b) of individuals from the different treatment groups throughout the experiment. We also used rm-ANOVA to test for differences in GUD, foraging time, and number of visits to the tray using time-treatment and feather treatment groups as categorical predictors, and sparrow ID as the random factor nested in feather treatment group. We used linear models to test the relationship between seeds consumed and cumulative time foraging to estimate the harvest rate for each feather treatment group.

We then compared a linear regression with a quadratic regression, and selected the more appropriate model based on the Akaike information criterion (AIC). We rejected the null hypothesis at $\alpha = 0.05$. Data are reported as means ± 1 SE. All statistical analyses were done with R 3.0.2, using nlme package.

Results

Body mass

Sparrows assigned to the three feather treatment groups did not differ in their initial mean m_b ($F_{2,15} = 1.12$, $p = 0.4$; $m_{b\ (Control)} = 23.9 \pm 0.8$, $m_{b(Cut)} = 22.6 \pm 0.7$, $m_{b\ (Plucked)} = 23.8 \pm 0.4$). We found that the change in m_b with experimental day differed between groups (Fig. 1; $F_{2,374} = 3.66$, $p = 0.03$). Specifically, we found that sparrows from the control and 'cut' groups increased in m_b ($t_{374} = 5.44$, $\beta_{Control} = 0.37 \pm 0.11$; $t_{374} = -0.64$, $\beta_{Cut} = 0.43 \pm 0.08$, $p_{(Control-Cut)} = 0.5$), whereas sparrows from the plucked group maintained steady m_b ($t_{374} = 4.52$, $\beta_{Plucked} = 0.02 \pm 0.12$, $p_{(Plucked-Control)} = 0.001$, $p_{(Plucked-Cut)} = 0.006$).

Seeds consumed

We found no differences among the GUDs of the three feather treatment groups when they foraged in the free-access tray (Fig. 2A; $F_{2,48} = 1.06$, $p = 0.4$), but there were significant differences in GUD of sparrows that foraged in the natural tray (Fig. 2B; $F_{2,55} = 4.10$, $p = 0.02$), with sparrows from the plucked group having consistently lower GUD (Fig. 2B). Moreover, we found significant differences in GUDs between the two patch types (Fig. 2; $F_{1,22} = 68.34$, $p < 0.001$). Specifically, sparrows feeding in the natural tray ate significantly less seeds (1.73 ± 0.36 g) than sparrows feeding in the free-access tray (4.61 ± 0.17 g), when offered trays for 180 min. We found no relationship between tray type and feather treatment group (Fig. 2; $F_{2,22} = 1.53$, $p = 0.2$).
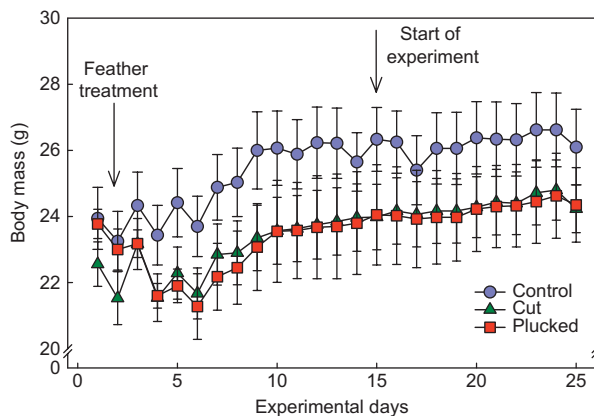

Figure 1. The relationship between body mass (means $\pm$ SE) and experimental day for three groups of house sparrows: red squares denote sparrows with plucked feathers; green triangles denote sparrows with the same feathers cut at the base of the calamus; and blue circles denote sparrows with intact plumage (controls).
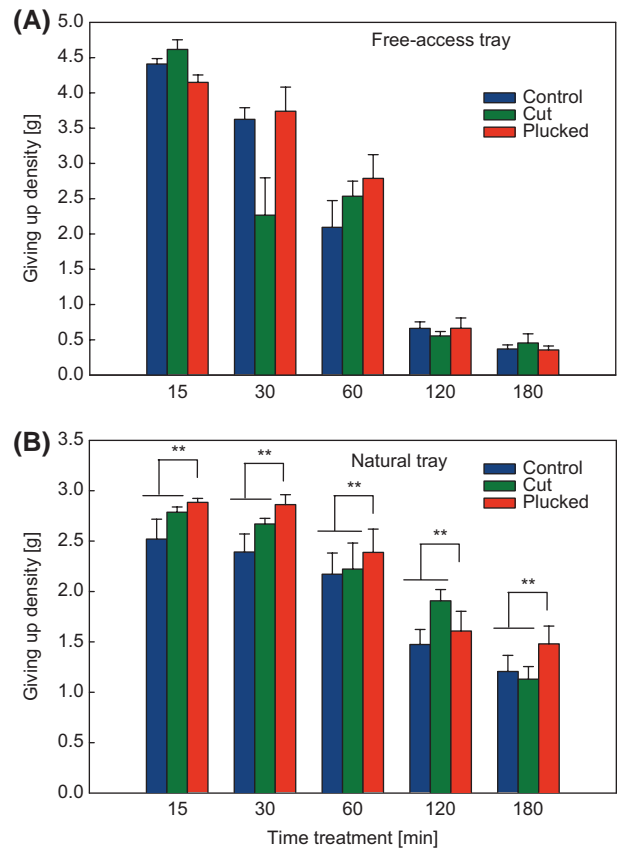

Figure 2. (A) Means $\pm$ SE of giving up densities (GUD) of house sparrows feeding on seeds in free-access foraging trays for each of three treatment groups: sparrows with plucked feathers; sparrows with the same feathers cut at the base of the calamus; and sparrows with intact plumage. (B) Means $\pm$ SE of giving up densities (GUD) in house sparrows (same three treatments) feeding in 'natural trays' in which the seeds were mixed with sand. ** denotes for $p < 0.01$. See text for details.

Foraging time

We found that the cumulative time spent foraging in the free-access tray was dependent on the total time a tray was left out for foraging (Fig. 3A; treatment × time – $F_{8,54} = 2.32$, $p = 0.03$). Sparrows from the plucked group spent significantly less time at the food tray than the other two feather treatment groups during the longer sessions (120 and 180 min). We found a similar relationship for sparrows foraging in the natural tray (Fig. 3B; interaction – $F_{8,56} = 3.43$, $p = 0.003$), where again, sparrows from the plucked group spent significantly less time at the food tray than the other two feather treatment groups.

Visits to the food trays

There was a difference in number of visits to the free-access tray (Fig. 4A; $F_{2,54} = 5.03$, $p = 0.01$), to which sparrows from the plucked group consistently paid fewer visits than sparrows from the other feather treatment groups. We also found a difference in number of visits to the natural tray (Fig. 4B; interaction – $F_{8,56} = 2.07$, $p = 0.05$); sparrows from the plucked group paid fewer visits to it than the other
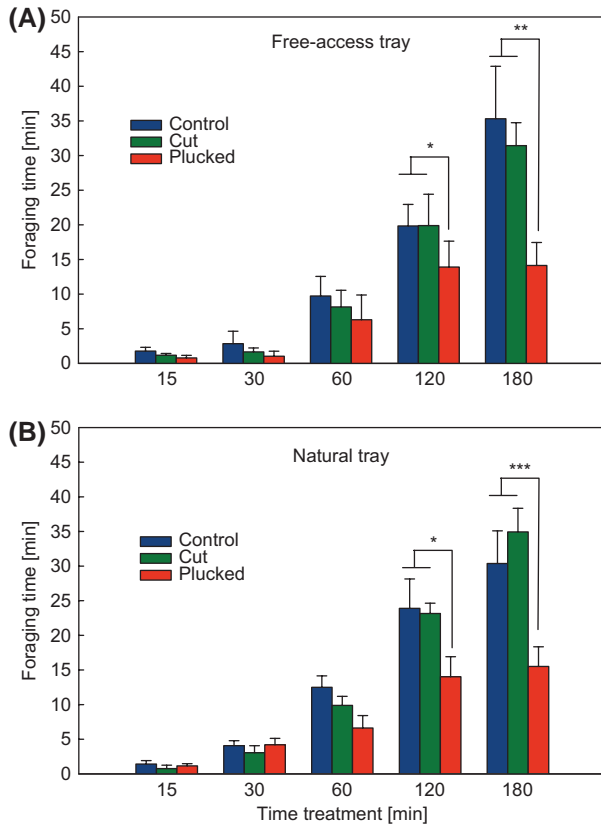
Figure 3. (A) Means $\pm$ SE of cumulative foraging time of house sparrows feeding from free-access trays for each of three treatment groups: sparrows with plucked feathers; sparrows with the same feathers cut at the base of the calamus; and sparrows with intact plumage. (B) Means $\pm$ SE of foraging time of house sparrows (same three treatments) feeding in natural trays. * denotes for $p < 0.05$; ** denotes for $p < 0.01$; and *** denotes for $p < 0.001$. See text for details.
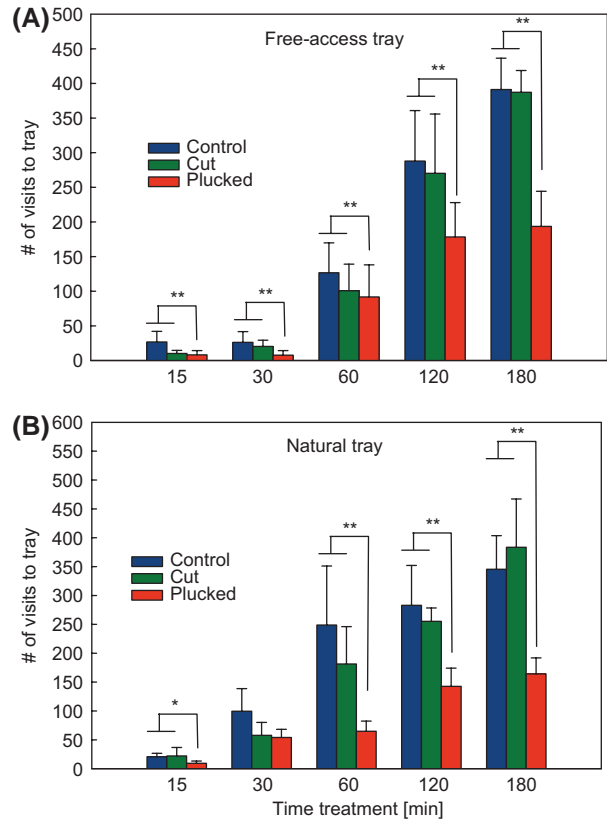
Figure 4. (A) Means $\pm$ SE of number of visits to free-access foraging trays of house sparrows from three treatment groups: sparrows with plucked feathers; sparrows with the same feathers cut at the base of the calamus; and sparrows with intact plumage. (B) Means $\pm$ SE of number of visits to natural trays of house sparrows (same three treatments). * denotes for $p < 0.05$; and ** denotes for $p < 0.01$. See text for details.

two feather treatment groups, with the exception of the 30 minutes session, where the differences between the groups were not significant.

Harvest rate

For the free-access trays, we found a significant quadratic relationship between seeds consumed and cumulative time spent foraging for all groups (Fig. 5A; $F_{6,57} = 56.92$, $p < 0.001$, $R^2 = 0.84$). The regression coefficients for this relationship were higher for sparrows with plucked feathers (Table 1; $\beta_1 - p_{(control-plucked)} < 0.001$, $p_{(cut-plucked)} = 0.02$; $\beta_2 - p_{(control-plucked)} < 0.001$, $p_{(cut-plucked)} = 0.007$) than for sparrows from the control and cut groups (Table 1; $\beta_1 - p_{(control-cut)} = 0.2$; $\beta_2 - p_{(control-plucked)} = 0.1$), indicating that sparrows with plucked feathers consumed seeds faster. In the natural trays, we found a significant linear relationship between seeds consumed and cumulative time spent foraging in the tray for both the treatment and control groups (Fig. 5B; $F_{3,67} = 140.8$, $p < 0.001$, $R^2 = 0.86$). Again, the regression coefficient of the relationship was greater in sparrows with plucked feathers (Table 1; $p_{(plucked-control)} = 0.002$, $p_{(plucked-cut)} < 0.001$) than sparrows from the control and cut groups

$(p_{(control-cut)} = 0.2)$, indicating that sparrows with plucked feathers consumed seeds faster.

Discussion

House sparrows regrowing lost feathers adjust their foraging behavior, as was evident from three different variables, namely GUD, foraging time, and number of visits to food patches. Since we observed some of these responses only in sparrows whose feathers we plucked, we tentatively conclude that they are related to physiological processes associated with feather growth and not to other consequences related to missing feathers, such as impaired flight or insulation capabilities.

Foraging behavior

There were significant differences in the rates at which the sparrows harvested seeds (Fig. 5); sparrows with plucked feathers had higher harvest rates than sparrows from the cut and control groups, both in the free-access and the natural trays. There was no difference in GUD among
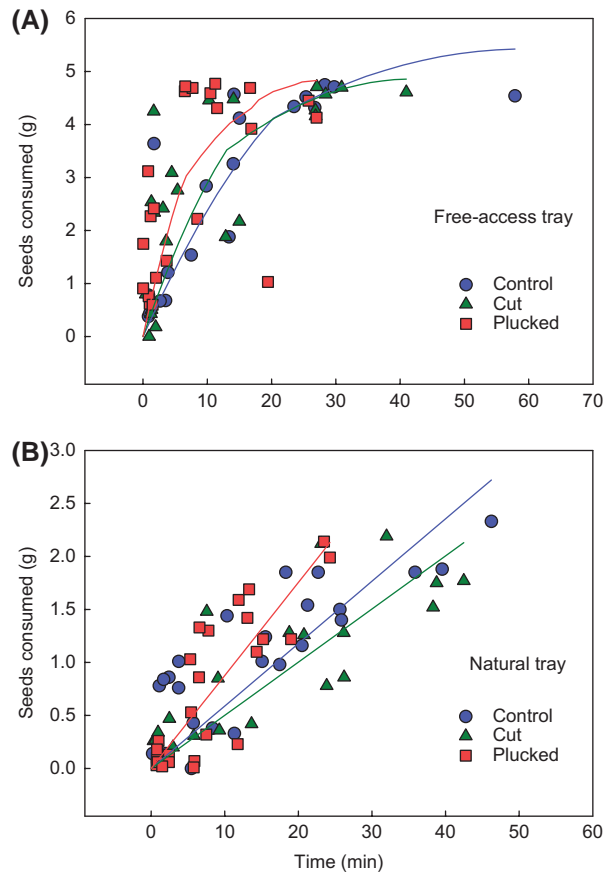
Figure 5. Harvest rate curves (seeds consumed [g] against cumulative time spent foraging [min]) for three groups of house sparrows: red squares denote sparrows with plucked feathers; green triangles denote sparrows with the same feathers cut at the base of the calamus; and blue circles denote sparrows with intact plumage (controls). (A) Sparrows feeding on free-access trays (quadratic regression: $F_{3,57} = 56.92$, $p < 0.001$, $R^2 = 0.84$); control: seeds $[g] = 0.27 \times$ time $[min] - 0.003 \times$ time^2 $[min^2]$, cut: seeds $[g] = 0.35 \times$ time $[min] - 0.006 \times$ time^2 $[min^2]$, plucked: seeds $[g] = 0.58 \times$ time $[min] - 0.017 \times$ time^2 $[min^2]$. See text for details; and (B) sparrows feeding in the natural patches (linear regression: $F_{3,67} = 140.8$, $p < 0.001$, $R^2 = 0.86$); control: seeds $[g] = 0.059 \times$ time $[min]$, cut: seeds $[g] = 0.050 \times$ time $[min]$, plucked: seeds $[g] = 0.09 \times$ time $[min]$.

sparrows feeding from the free-access trays (Fig. 2A). However, although sparrows with plucked feathers ate the same quantity of seeds as the other treatment groups, they did it in a shorter period of time. The lack of differences in GUD in the free-access trays is explained by the observation that sparrows from all treatment groups exhausted the seeds in

Table 1. Regression coefficients $\pm$ SE derived from the quadratic and linear analyses used to fit the amount of seeds consumed by house sparrows [in g] in each of three feather treatment groups to the amount of cumulative time spent foraging [in min] in the free-access and natural tray, respectively. See text for details.

Feather treatment	Free-access tray		Natural tray
	β_1	β_2	β
Control	0.27 ± 0.04	-0.003 ± 0.001	0.059 ± 0.004
Cut	0.35 ± 0.06	-0.006 ± 0.002	0.050 ± 0.004
Plucked	0.58 ± 0.07	-0.017 ± 0.004	0.090 ± 0.010

these trays. Therefore, the increased harvest rate of the sparrows with plucked feathers suggests they reduced foraging time in the free-access tray due to higher *MOC*, and moved to the alternative food patch more quickly than sparrows from the other treatment groups. As predicted, in the natural tray we found that sparrows with plucked feathers had lower GUDs than sparrows from the cut and control groups (Fig. 2B). Therefore, these sparrows increased their harvest rate by increasing their food intake as well as reducing the time they spent foraging, probably to meet with their increased energy demands.

Differences in the quantity of seeds eaten (Fig. 2) and harvest rates (Fig. 5) between the two patch types can possibly be explained by *C*, the metabolic cost of foraging. Sparrows missing feathers may be less efficient at finding food and flying about because of reduced maneuverability due to their missing flight feathers, but only sparrows with plucked feathers are faced with the increased metabolic cost of regrowing their feathers. Therefore, the magnitude of the change in *C* should differ between sparrows with plucked feathers and sparrows with cut feathers. One way in which sparrows can minimize *C* is by being less active; by decreasing the number of sorties to food patches, for example. Indeed, we found that sparrows with plucked feathers paid fewer visits to the patches without changing the cumulative time they spent foraging during the shorter feeding sessions (Fig. 3–4). We infer from these results that sparrows with plucked feathers significantly increased the duration of their foraging visits compared to control sparrows and sparrows with cut feathers; thereby increasing their harvest rate (Fig. 5).

We reason, then, that sparrows replacing plucked feathers allocated their time use differently than did the cut and control groups. This may have been achieved 1) at the cost of reducing their levels of alertness (e.g. vigilance and apprehensiveness). In other words, the house sparrows reduced their attentiveness to predators and as a result their foraging efficiency increased; 2) by reduced interference or increased facilitation by conspecifics at the food patch; or 3) by both 1) and 2). Assuming that the reduction in foraging time of house sparrow sparrows with plucked feathers is a consequence of reduced interference by conspecifics, then one would expect to see a decrease in flock size in a food patch (Johnson et al. 2001, Vahl et al. 2005), whereas if it results from increased facilitation, e.g. some individuals serve as 'sentinels' and watch for predators while group mates forage, then one would expect to see relatively larger flocks of house sparrows with plucked feathers foraging together (Clark and Mangel 1986, Hollén et al. 2008). In this regard, Lendvai et al. (2004) found that house sparrows facing higher energy demands increased scrounging behavior compared to counterparts that faced lower energy demands. This could explain the change we observed in the foraging time allocation of house sparrows with plucked feathers, however, since we only have a measure of the time spent in the food patch for each individual, we cannot account for differences in the behavior of house sparrows from the different feather treatment groups while foraging. Nevertheless, we tentatively conclude that there is a difference in foraging behavior that is associated with the growth of new feathers, and we suggest that it is associated with increased metabolic demands due to feather growth.

From the above we infer that foraging house sparrows balance their conflicting energy demands by decreasing the time they devote to harvesting in a food patch and increasing their food intake. The result is that house sparrows with plucked feathers exploit food patches more efficiently than house sparrows that are not growing feathers, as is evident from their GUDs and harvest rates. Interestingly, we also found that house sparrows with plucked feathers did not increase m_b, unlike house sparrows with cut feathers (Fig. 1), implying yet again that there is an energetic cost exclusive to house sparrows, and likely other birds, re-growing feathers.

Conclusions

Because of the increased energy requirements of feather replacement, molting in birds is typically timed to coincide with life-history periods with fewer other strenuous demands. However, birds may also lose feathers outside their molting season, and are therefore expected to modify their energy balance regulation whenever growing new feathers. Yet, most of our understanding of the energy balance regulation of birds regrowing their feathers is derived from studies that focus on physiological adjustments, while behavioral adjustments are often ignored. In the present study, we examined the foraging behavior of birds regrowing their feathers. We found that birds with plucked feathers increase their harvest rate of seeds and they consume more food than birds with cut feathers and controls. We reason that house sparrows replacing their feathers compensated for an increased energy demand by reducing foraging activity.

List of symbols and abbreviations
m_b body mass
MR metabolic rate
$\partial F/\partial e$ marginal value of energy
P predation cost
GUD giving up density
H quitting harvest rate
C metabolic cost of foraging

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