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Body moult and autumn migration in the barn swallow *Hirundo rustica*: is there a cost of moulting late?

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The timing of moult in birds is thought to be constrained by physiological trade-offs. We studied barn swallows in central Spain to assess whether (a) body moult tends to be temporally separated from migration in adult and first-year birds, (b) it is related to an impaired fattening, and (c) its overlap with migration may involve adverse energetic effects. First-year swallows tended to moult early in the post-breeding period: the proportion of first-year birds in active moult was highest in July, and it decreased progressively until September. On the other hand, adult swallows tended to avoid moulting both in the post-breeding (July) and the migratory period (September), concentrating their moulting period in August. In all periods, swallows in active moult stored less fat than non-moulting ones, suggesting a faster depletion of energy resources by moulting birds. Swallows in active moult showed a better body condition — measured as body mass relative to body size and fat content — than non-moulting ones before migration (coinciding with the periods of highest frequency of moulting individuals), but the opposite was found during autumn migration. Our results support the existence of a physiological trade-off between body moult and migration, which could have fitness consequences; thus, if these activities overlap it would impair migration performance of swallows.

Introduction

The moult is one of the most costly activities in the annual cycle of birds. Feather production and thermoregulation during moult require large amounts of energy and proteins, whose consumption increases the basal metabolic rate of a moulting bird (Murphy & King 1992, Lindström *et al.* 1993). Because of this, each species has evolved different moult strategies which tend to place feather renewal away from other energy-demanding activities, such as reproduction or migration (Jenni & Winkler 1994, Kjellén 1994, Gwinner 1996).

It is widely recognised that the overlap of moult and reproduction impairs both breeding success and adult survival of birds (Hemborg 1998, Hemborg & Lundberg 1998, Hemborg *et al.* 1998), but little is known about the effects of overlapping moult and autumn migration. The general view is that moult would cause an extreme depletion of both energy and structural resources if it overlapped with such an energy-demanding activity as autumn migration (Jenni & Winkler 1994, Kjellén 1994). Consistent with this view, many long-distance migrants tend to start their moult while they are breeding, especially at high latitudes, so that they can complete both reproduction and moult before the onset of migration (Hemborg *et al.* 1998). It follows that a physiological trade-off between moult and migration could be a major determinant of the location of moult in the annual cycle of these species (Merilä 1997, Yuri & Rohwer 1997, Hemborg *et al.* 1998). However, since a proper experimental manipulation of the moult-migration overlap is not feasible, the possible trade-off between moult and migration has received little empirical support. In practice, this challenging question can only be addressed by studying the variation in physiological condition between moulting and non-moulting individuals during and outside migration. Although such non-manipulative approaches will probably never disentangle the causes and consequences of the moult-migration overlap, they can nonetheless provide valuable insights into the functional relationships between moult and migration (*see* Roff 1992, Stearns 1992, and references therein for discussion). Thus, these studies offer tests that will or will not support the predicted covariation between traits coming up from the hypothetical trade-off between moult and migration (Roff 1992, Stearns 1992).

In this study, we evaluate the changes in body condition in relation to moult in barn swallows (*Hirundo rustica*), before and during their autumn migration, in a locality of central Spain. The moult pattern of swallows is well known (Cramp 1988, Jenni & Winkler 1994). Both adult and juvenile birds undertake a complete post-nuptial (or post-juvenile) moult. Flight feathers are usually replaced in the African wintering grounds, although some individuals begin their moult in the Palearctic and suspend it during the autumn migration. Once in their wintering areas, these individuals are thought to resume the moult of flight feathers from the point in which they stopped it. This suspended moult has been interpreted as a way to avoid a stressing moult-migration overlap. Indeed, overlapping flight-feather moult and migration would be too expensive, not only because of the high energy output necessary for satisfying both activities, but also because having gaps in the wings would impair flight performance (Pennycuick 1989, Jenni & Winkler 1994, Kjellén 1994). Hence, almost no migrating swallows overlap the active moult of flight feathers with migration (3 per 1000 in our study site, *see also* Jenni & Winkler 1994). By contrast, body moult does not require so much energy and protein as flight-feather moult does (Murphy & King 1992, Lindström *et al.* 1993), and neither does it affect flight performance. Likely because of this comparatively low cost of body moult, many swallows renew a variable number of body feathers in Europe, doing so either before or during their autumn migration (Jenni & Winkler 1994). Therefore, the study of body moult of swallows in relation to migratory status can provide a suitable opportunity for investigating the effects of overlapping both activities.

To our knowledge, the overlap of body moult with migration has only been studied from an energetic perspective by Merilä (1997), who found migrating goldcrests (*Regulus regulus*) that had completed the post-juvenile moult to store more fat than those that overlapped moult and migration. Here we go a step further by studying the scheduling of body moult of barn swallows in relation to autumn migration, as well as the variation in body condition between individuals in active body moult and individuals not in active moult before or during migration. We also compare the performance of adult and first-year swallows for testing the role of recent reproductive investment in shaping the possible trade-off between moult and migration. If the moult scheduling is constrained by the need of migrating (Kjellén 1994, Holmgren & Hedenström 1995, Hemborg *et al.* 1998), then there should be an optimal timing for moult before the autumn migration, in which most moulting swallows should be concentrated. This moulting period should be narrower in adults provided that they also avoided a moult-reproduction overlap (Hemborg *et al.* 1998). On the other hand, if moulting body feathers actually increases energy expenditure, we predict that birds in active moult will face more difficulties with fattening and hence have less stored fat than non-moulting ones, as fat is the main source of energy for migrating birds (Alerstam & Lindström 1990, Blem 1990, Lindström *et al.* 1994, Merilä 1997, Jenni & Jenni-Eiermann 1998). Although a negative correlation between body moult and fat accumulation has already been found in the barn swallow (Pilastro *et al.* 1998, Pilastro & Spina 1999), its consideration is a pre-requisite in this paper if the migration-related cost of moult is to be evaluated. On the other hand, nothing is known about the possible variation of the effect of body moult upon fat storage depending on whether birds are in pre-migratory or migratory stage. Finally, if swallows are faced with an energetic trade-off between body moult and migration, we predict that overlapping activities will also translate into a loss of lean body mass (that is to say, a depletion of body components other than fat, such as proteins or water), as a consequence of energy stress (Klaasen 1996, Jenni & Jenni-Eiermann 1998).

Methods

The barn swallow in central Spain

The barn swallow is a small (18–19 g) passerine that visits Europe for reproduction (Cramp 1988). In the colonies neighbouring our study site, for instance, most broods fledge throughout July, although some few young from third clutches can fledge as late as during the first half of August (authors' unpublished data). While breeding, and also during some days after fledging, both adults and juveniles roost in the colonies. In the late breeding season (from mid July in central Spain), they begin to concentrate at night in communal roosts (*see* Cramp 1988, Ormerod 1991). Pre-migratory fat accumulation does not start until August (Pilastro & Magnani 1997, Pilastro *et al.* 1998), and recoveries in the Iberian Peninsula of swallows ringed further to the north are principally obtained from mid August to early October (Bernis 1971). Migration peaks in September (Bernis 1971, Ormerod 1991), when swallows cross the Mediterranean basin as shown by the large number of inter-roost recoveries obtained in Italy during this month (Pilastro *et al.* 1998). Therefore, we can consider those birds roosting in July to be in a post-breeding, pre-migratory stage, and those roosting in September to be migrating swallows landed at stopover. It is difficult to decide from phenology whether swallows captured in August are in a post-breeding or a migratory stage, but we find more prudent to consider them as a mix principally composed by local birds in a pre-migratory stage.

Study site and handling of swallows

We mist-netted swallows once a week from mid July to late September 1998, in a communal roost located in a partially inundated (up to 100-cm water depth) 20-ha reed bed (*Phragmites australis*) in the Tajo Valley, near Añover de Tajo, Central Spain (39°59´N, 3°46´W, 450-m elevation). We tape-lured swallows while they were gathering to get in the roost, starting around half an hour before the arrival of birds. By using this method, we captured 1759 individuals during the period of roost use (12 July–23 September). We first weighed swallows with a digital balance to the nearest 0.1 g, tagging them with standard aluminium rings and storing them in spacious cages until recording the measurements. In order to avoid that birds lost too much body mass due to stress during storage and handling, we suspended weighing after 3 hours from their capture. This caused the final number of processed individuals to be 1326 (93 adults and 1233 first-year birds; *see* ageing criteria in Jenni & Winkler 1994). We did not consider the sex of adult swallows because of their small sample size. We recorded the length of the third primary feather with a 0.5-mm precision pin ruler (Jenni & Winkler 1989), and the size of the subcutaneous fat deposit according to a 9-score scale (Kaiser 1993). We also evaluated the moult status of individuals. Although we originally coded the moult status in a three-value scale (no moult, moulting less than 20 body feathers or moulting more than 20 feathers), we finally considered whether or not swallows were in active body moult at the moment of their capture, in order to maintain sample sizes as balanced as possible. We checked body moult by searching for growing feathers in the back, crown, breast, neck and belly of swallows (*see* Jenni 1998 for further details on methods). Once processed, we placed the swallows in a safe site at the roost.

Assessing body condition of swallows

For a migrating bird, fat is the optimal source of energy during fasting, and its amount in the body largely determines the flight range from a given stopover site (Alerstam & Lindström 1990, Jenni & Jenni-Eiermann 1998). On the other hand, the development of pectoral muscle is a major determinant of flight endurance (Pennycuick 1989, Piersma 1998). Because of the importance of fattening ability and muscular power during migrations, birds experience physiological changes during the pre-migratory and migratory periods that favour the accumulation and consumption of fat (to the point that, in some species, birds put on fat up to double their body mass, even at the expense of strongly impaired flight performance, *see* Lind *et al.* 1999). But these physiological changes also allow sparing proteins from muscle and body water, so that fasting birds only begin to deplete muscular mass and to suffer dehydration during migrations when they are exposed to an intense energy stress (Klaasen 1996, Jenni & Jenni-Eiermann 1998, Piersma 1998). Thus, the body condition of a migrating bird may be assessed in two complementary ways. The size of fat stores will reflect the quantity of fuel available to the bird, while its lean body mass relative to body size will indicate the amount of other body components, especially pectoral muscle and water. The link between these two indices of body condition and fitness is straightforward in migrating birds, as both fattening and endurance abilities play a critical role in determining migration success (Alerstam & Lindström 1990, Jenni & Jenni-Eiermann 1998, Piersma 1998).

Statistical analyses

We studied fat contents considering fat as a continuous variable and applying parametric statistics. Since fat is measured on an ordinal instead of an interval scale, its analysis with parametric techniques would be only reliable provided that (a) its relationship with the actual content of body fat were linear, and (b) the distribution of fat scores fitted well a normal distribution (Brown 1996). Fat scores are linearly related to body fat in some bird species (Rogers 1991), but these two variables commonly better follow a quadratic relationship (Kaiser 1993). Although we have no way to study the relationship between fat scores and actual fat content of swallows, we attempted to improve the reliability of our estimates by exploring the fit of body mass to either the original fat scores and the squared fat scores (both log-transformed). Provided that fat storage is the main determinant of changes in body mass of migrating birds (Blem 1990, Jenni & Jenni-Eiermann 1998), we assumed that the better the linear relationship of a given fat index with body mass, the better its linear relationship with body fat (for further explanation *see* Herrera 1998). By simple regression, squared fat scores accounted for more variation in body mass (r^2 = 0.21; $F_{1,1320}$ = 359.65, P < 0.0001) than original fat scores (r^2 = 0.16; $F_{1,1320}$ = 252.85, P < 0.0001). Moreover, squared fat scores fitted a little better a normal distribution than original scores (Filliben's correlations: r^2 = 0.99 and r^2 = 0.94, respectively; *see* StatSoft 1999). Therefore, we considered the logarithm of the squared fat scores plus one as the final measure of stored fat.

We used the residual body mass relative to body size and level of fat stored by swallows as a measure of lean body mass (Brown 1996). To do so, we used the length of the third primary feather as a proper surrogate of body size (Gosler *et al.* 1998). Body mass of migrant passerines may vary through the migratory period (Blem 1990) and although we captured all swallows at the same time — while they were arriving on the roost — they could have lost body mass during their handling. To control for these effects, we conducted an one-way ANCOVA on body mass with time of weighing as the factor (first, second or third hour after capture) and length of the third primary feather, level of stored fat, and date of capture as covariates. Then, we used the residuals of this ANCOVA as measures of lean body mass relative to size (Brown 1996). Both the body mass and the length of the third primary were log-transformed to improve normality of residuals. We assigned the value 1 to the first day in which we captured swallows at the study site (12 July), squaring date values to linearize their relationship with body mass.

Differences in both the level of stored fat and the residual mass of swallows in relation to age, migration stage and moult status were tested by means of three-way ANOVA, and among-group differences were assessed with Tukey's tests.

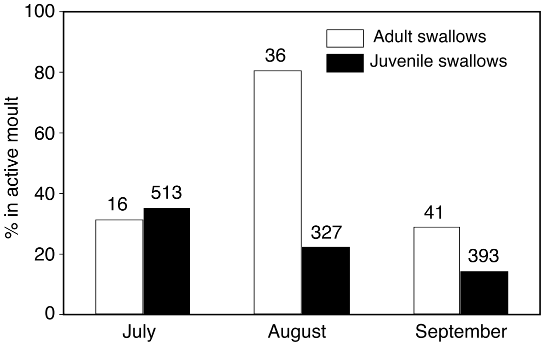

Fig. 1. Temporal scheduling of body moult in adult and juvenile barn swallows. Figures on the top of bars refer to total sample sizes.

Results

Temporal scheduling of moult

The scheduling of body moult along the study period varied between age classes (Fig. 1). Thus, a log-linear analysis of the frequency of adults and juveniles that were moulting in each month discarded the absence of a three-way interaction among age, month and moult status (goodness-of-fit test: χ^2_2 = 20.34, P < 0.0001). Juvenile swallows tended to moult early in the post-breeding period, as their proportion was highest in July and gradually decreased throughout the study period (χ^2_2 = 52.93, P < 0.0001). Adult swallows, however, tended to avoid moult both in July and September, concentrating their moult in August (χ^2_2 = 22.72, P < 0.0001). In this month, adults in active moult outnumbered non-moulting adults, suggesting the existence of a narrow time window for the moult of adults between reproduction and moult.

Moult status and body condition

Although swallows gradually increased their fat deposits from July to September, both age classes differed in their levels of stored fat through the study period (Table 1). First-year birds stored more fat than adults during July and August, but not during September, when adults showed even

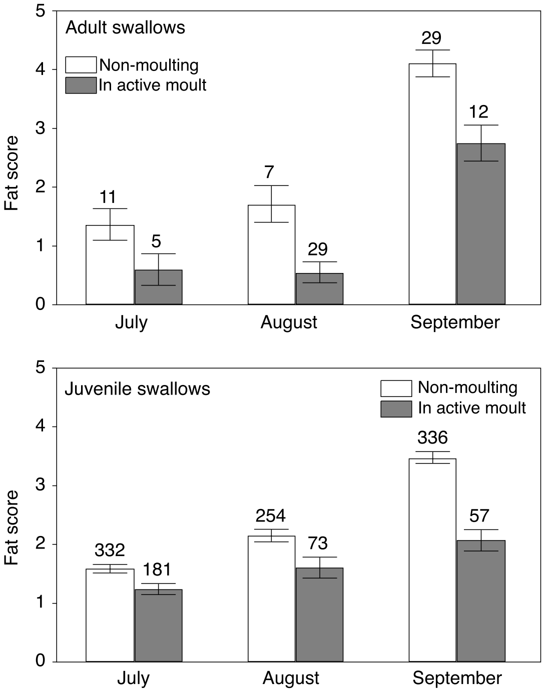

Fig. 2. Level of fat stored by adult and juvenile barn swallows throughout the study period in relation to moult status. The mean values with standard errors and sample sizes for both moulting and non-moulting swallows are shown.

larger fat stores than first-year swallows. Aside from this difference in fat dynamics between the age classes, individuals in active moult always accumulated less fat than non-moulting ones, regardless of age and month (Fig. 2, Tukey's tests for the described differences, all $P < 0.001$).

Altogether, the time of weighing, the level of stored fat, the length of the third primary and the date of capture accounted for 30% of the variation in body mass of swallows (Table 2). The level of stored fat alone explained around half of the variation accounted for by the model. Lean body mass, measured as the residual of this ANCOVA model, was always higher in adults than in first-year birds, and it decreased during the autumn migration (in September). But it varied in both age classes through the study period in relation to moult status (Table 3 and Fig. 3). Individuals in active moult were in a comparatively good body condition during the periods in which most individuals were moulting (cf. Fig. 1). Thus, individuals that were moulting during July showed a higher residual mass than the non-moulting ones in both age classes. However, the overlap between active body moult and migration was related to an impaired body condition in both adult and first-year swallows, as moulting individuals had a lower residual mass than non-moulting ones in September (Fig. 3, Tukey's tests for the described differences, all $P < 0.001$).

Table 1. Results of the three-way ANOVA analysing the variation in level of fat stored by swallows in relation to month, age and moult status.

Source of variation	df	Mean square	*F*	*P*
Month	2	44.098	72.69	< 0.0001
Age	1	1.547	2.55	0.11
Moult status	1	22.670	37.37	< 0.0001
Month × age	2	6.679	11.01	< 0.0001
Month × moult status	2	0.623	1.03	0.36
Age × moult status	1	0.764	1.26	0.26
Month × age × moult status	2	0.630	1.04	0.35
Residual	1314	0.607		

Table 2. One-way ANCOVA modelling the variation in body mass of swallows in relation to body size, fat contents, time of handling and date. The residuals of the model have been used as measures of fat-free body mass relative to body size of swallows (controlling for the other confounding variables). The percentage of variation of body mass accounted for by each independent variable (r^2) is also shown.

Source of variation	df	Mean square	*F*	r^2 (%)
Model	5	0.536	110.91*	29.74
Factor				
Time of weighing	2	0.051	10.47*	1.47
Covariates				
Level of stored fat	1	0.553	114.38*	14.28
Date of capture	1	0.181	37.46*	7.80
Third primary	1	0.439	90.83*	6.19
Residual	1310	0.005		

* $P < 0.0001$

Discussion

The different temporal scheduling of moult in adult and juvenile swallows suggests that the optimal timing of moult changes with age. Thus, first-year birds seem to moult as soon as possible after independence, which would allow them to replace some contour feathers before starting migration (Yuri & Rohwer 1997). This may explain why in August juvenile swallows in active moult are scarcer than adults, given that first-year, inexperienced individuals face more difficulties for fattening than adults and hence could need more time after moult to get ready for migration (Pilastro & Magnani 1997). Supporting these differential rates of fat accumulation, in July and August adult swallows had less stored fat than first-year birds, but in September reached on average half a score more fat than first-year individuals, irrespective of their moult status. Like first-year birds, adult swallows tended to avoid moulting in September, when moult would overlap with migration. However, they also seemed to avoid moulting in July, as they concentrated moult in August. This might indicate that most adults cannot face feather renewal as early as juvenile birds, but still they avoid a moult–migration overlap by moulting in a narrow period between reproduction and migration. Through this strategy, adult swallows could optimise the allocation of energy to moult and hence could improve their survival chances after breeding effort (Yuri & Rohwer 1997, Hemborg & Lundberg 1998).

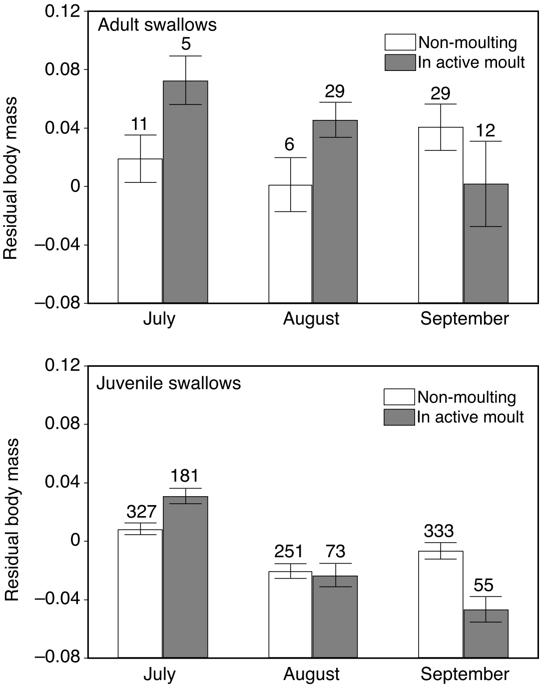

Fig. 3. Relationships between body moult and residual mass (fat-free body mass relative to body size) of adult and juvenile barn swallows throughout the study period. Means, standard errors and sample sizes for both moulting and non-moulting swallows are shown.

Table 3. Results of the three-way ANOVA for the monthly variation in body condition of swallows in relation to age and moult status.

Source of variation	df	Mean square	*F*	*P*
Month	2	0.024	5.58	0.0039
Age	1	0.087	19.76	< 0.0001
Moult status	1	0.002	0.53	0.47
Month × age	2	0.002	0.52	0.60
Month × moult status	2	0.035	8.08	< 0.001
Age × moult status	1	0.010	2.20	0.14
Month × age × moult status	2	0.003	0.72	0.49
Residual	1300	0.004		

Consistent with our predictions, body moult always involved putting on less fat, both in adult and first-year swallows and whether or not they were migrating (*see also* Pilastro *et al.* 1998). When interpreting between-individual differences in fat contents, however, one should bear in mind that fat dynamics may be affected by other factors aside from energy requirements. Carrying much fat impairs flight performance and hence predator avoidance (Lind *et al.* 1999), which makes birds administrate their fat stores at levels that are at neither the environmental nor the physiological optima (Witter & Cuthill 1993). To reduce exposure to predators, birds that have access to adequate food sources — for example dominant birds in a flock or birds that occupy food-rich habitats — usually store less fat than birds that face problems to get food (Witter & Cuthill 1993). During migration, however, birds need to put on much fat to assure migration success (Jenni & Jenni-Eiermann 1998), and hence the non-energetic costs of fat storage loss importance. For example, in an experiment with bluethroats (*Luscinia svecica*), Lindström *et al.* (1990) showed that dominant birds keep their fat stores at low levels outside migration, but put on more fat than subordinates at stopovers during migration. Since the migratory flight range primarily depends on the size of fat stores (Alerstam & Lindström 1990), migrating birds are strongly pressed to accumulate fat even at the expense of impaired flight performance (Lind *et al.* 1999). Therefore, energetic costs of moult provide the most plausible explanation for the negative relationship between moult and fat storage. The energy output would be on average larger in moulting birds than in non-moulting ones (Murphy & King 1992, Lindström *et al.* 1993), and hence swallows would be unable to put on so much fat when moulting as would be under normal conditions.

The timing of moult, clearly separated from both reproduction and migration, could be affected by physiological trade-offs (Sibly & Calow 1986, Roff 1992, Stearns 1992). This is consistent with what we have found because: (1) our results support that moulting body feathers takes energy so as to impair migratory fattening, and (2) overlapping moult and migration involved a decrease in residual mass of swallows compared to non-moulting ones, such a relationship being at variance with that observed before migration. Swallows that moulted during the pre-migratory stages (in July, and likely also in August for adults, *see* Fig. 3) enjoyed a better body condition than non-moulting ones, as measured by their fat-free body mass relative to body size. However, the energetic costs of moult became detrimental when moulting effort overlapped with migration effort, as shown by the loss of residual mass in moulting swallows compared to non-moulting ones when they were migrating. This loss of lean body mass suggests that energy stress in relation to the moult-migration overlap is high enough to cause the depletion of body resources other than fat, such as proteins from muscles (Brown 1996, Jenni & Jenni-Eiermann 1998, Piersma 1998). Birds avoid consuming muscles before and during migration (Biebach 1998, Piersma 1998), and both the loss of muscular mass and dehydration are usual symptoms of energy stress in migrating birds (Klaasen 1996, Jenni & Jenni-Eiermann 1998). According to this, the decrease in residual mass of swallows related to a moult-migration overlap likely translates into an impaired migration performance, which together with an enlarged risk of starvation, may well have important fitness consequences for swallows.

In summary, this paper describes the adverse energetic effects of the moult-migration overlap in a passerine bird. Our integrated study of moult scheduling and different measures of body condition supports the view that competition between moult and migration for limited energy resources available to the individual constrains the timing of body moult in the annual cycle of both adult and juvenile swallows (Sibly & Calow 1986, Roff 1992, Stearns 1992). Not all swallows engage in moulting in the Palearctic, and those that do so, rarely replace many feathers as they will complete moult in their winter quarters (Jenni & Winkler 1994). But to allocate surplus energy to moult part of the plumage in the Palearctic may be rewarding for individuals enjoying a good condition before migration. This could mitigate their moulting effort in their African wintering grounds, which would improve both their winter survival and their preparation for spring migration (Hasselquist *et al.* 1988, Kjellén 1994, Yuri & Rohwer 1997). In turn, these improvements could lead to an early arrival to the breeding areas or a better condition during breeding (Marra *et al.* 1998), which could increase both the chances of reproduction and the reproductive success of swallows the next breeding season (Møller 1994, Sandberg & Moore 1996, Verboven & Visser 1998). However, overlapping moult and migration likely reduces the chances of successful completion of the migratory journey. It has been suggested that adjusting the timing of moult should be the easiest way to solve the optimal allocation of energy to reproduction, moult and migration (Kjellén 1994, Hemborg *et al.* 1998). Accordingly, our results suggest that energetic constraints play a role in shaping a relevant selective pressure for swallow populations, as long as survival might be impaired by the costs of moulting late.

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