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SHORT NOTE

# The influence of environmental conditions on the body mass of Barn Swallows (*Hirundo rustica*) during spring migration

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**Abstract** The present study examines the effects of seven microclimatic factors on the arrival body mass of migrant Barn Swallows (*Hirundo rustica*) in the Aiguamolls de l'Empordà Natural Park, a site located in northeastern Spain. We used principal component analysis, followed by a general linear model procedure, to create a model that examines the relationships between body mass and weather-related events recently experienced during the spring migration. Our results suggest that local weather variation during the migratory flight clearly affects the body mass of Barn Swallows on a short time scale. This effect demonstrates the importance of the environmental conditions en route for migrating swallows and how these conditions might influence diverse events of the life cycle, such as the arrival time at the breeding grounds or the reproductive success.

**Keywords** Weather · Body mass · *Hirundo rustica* · Temperature

## Introduction

In the life cycle of long-distance migratory birds, one of the most energetically demanding activities, other than breeding and moulting, is migration. In these birds, the amount of energy necessary to complete a trip normally exceeds their storage capacity, so the regulation of fat reserves plays a crucial role. These energetic reserves are important not only for the trip itself, but also for arriving at the destination with sufficient reserves to assure the reproductive success of the individual (Sandberg and Moore 1996). The Barn Swallow (*Hirundo rustica*) is able to feed while migrating over favorable areas, and so they tend not to accumulate excessive fat before and during the journey (Turner 2006), unless they have to face great ecological barriers like the Saharan Desert (Rubolini et al. 2002). Traveling with relatively little fat and depending almost entirely on flying insects (Davis 1965; Mead 1983; Ormerod 1989, 1991), which are known to be profoundly affected by weather conditions (Williams 1940, 1961; Taylor 1963; Johnson 1969; Peng et al. 1992; Briers et al. 2003), makes the swallows especially susceptible to environmental conditions en route (Møller 1994b; Huin and Sparks 1998, 1999; Sparks and Braslavska 2001). Our objective was to investigate the effects of weather conditions on the body mass in the Barn Swallow during its spring passage northwards through northeastern Spain. We predicted that, in time-selected migrants like this species (sensu Alerstam and Lindström 1990) which are also specialized aerial feeders, factors that affect the availability of their prey, such as weather, should have a parallel effect on the birds' body mass. This should lead to a negative relationship between body mass upon arrival at the stopover site and the environmental factors related to poor weather.

## Methods

The study area was situated within the Aiguamolls de l'Empordà Natural Park, a coastal complex of saline

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**Table 1** The range of values of the meteorological variables used in this study (the values are the mean of the day of capture and the previous day at five stations following the theoretical migration route of Barn Swallows (*Hirundo rustica*) in northeastern Spain during the months of April and May between 1993 and 2002)

| | Units | Minimum | Maximum | Mean | SD |
|---|---|---|---|---|---|
| Mean temperature | °C | 8.4 | 22.9 | 15.2 | 2.7 |
| Relative humidity | % | 47.2 | 96.8 | 76.9 | 8.7 |
| Wind speed | m/s | 1.1 | 4.8 | 2.0 | 0.5 |
| Global radiation | W/m$^2$ | 3.5 | 27.3 | 18.9 | 4.4 |
| Rainfall | mm | 0.0 | 49.4 | 1.7 | 3.8 |
| Rainfall duration | h | 0.0 | 12.7 | 0.5 | 1.1 |
| Wind direction | | −1.0 | 1.0 | 0.06 | 0.7 |

and freshwater wetlands located in northeastern Spain (42°14′N, 3°06′E).

The data were collected as part of the Progetto Piccole Isole (Spina et al. 1993) during the spring migration in the years 1993–2002. A total of 3,376 Barn Swallows were captured with a fixed number of mist nets, and were ringed with an aluminum leg ring. Of these, 895 were classified as males, 1,381 as females, and 1,100 were not sexed according to Svensson (1992). The birds were weighed (to the nearest 0.1 g) and their flattened wing length was measured to the nearest 0.5 mm. In this study, we used the average body mass of days with ≥5 captures corrected for size, time and date. Body mass was correlated to fat score ($r = 0.53$, $P < 0.001$) and the results do not change substantially by using fat score in the calculations instead of weight.

Meteorological data were obtained from Servei Meteorològic de Catalunya daily reports. The following weather parameters were used: rainfall duration and intensity, mean temperature, mean relative humidity, wind speed and direction, and global radiation (a variable that is related to sunlight). All are daily averages. Tables 1 and 2 show the descriptive statistics and the correlation matrix between these variables. Mass upon capture likely depends on conditions experienced prior to arrival; hence, we used the mean value of the day of capture and the values from the previous day obtained at five stations located 5 km (Sant Pere Pescador), 50 km (Cassà de la Selva), 130 km (Caldes de Montbui), 250 km (Vinyol), and 300 km (Amposta) south of the study area along the theoretical migration route (Fig. 1). In general, the data from all five stations showed high correlation, which indicated regional consistency in the effect of the weather during migration.

We estimated the effects of these variables on body mass using a general linear regression model of daily average weight (corrected for size, time and date) on year and the weather variables. Sex was initially incorporated as an additional factor, but a previous analysis pointed out that it was a nonsignificant factor in the model. The final equation shows data of pooled sexed and unsexed individuals.

Weather variables showed some degree of correlation (Table 2), so we performed a principal component analysis (PCA), to produce a set of uncorrelated variables (PC1, PC2 and PC3) that described the weather conditions experienced by Barn Swallows on the day of capture and the previous day (Table 3). The variance inflation factors (VIFs) obtained in the model suggested that collinearity should not have seriously biased our significance tests.

One assumption of our study is that the pool of migrants from which we drew samples arrived after their diurnal migration to rest, and that the variation in body condition over the course of their migratory flight is reflected in the mass of birds at first capture. The first capture does not

**Table 2** Pearson correlation matrix between weather variables

| | *T* | RH | WS | *R* | RD | GR | WD | Date |
|---|---|---|---|---|---|---|---|---|
| *T* | 1 | 0.13** | −0.33** | −0.19** | −0.25** | 0.46** | −0.04 | 0.76** |
| RH | 0.13** | 1 | −0.65** | 0.34** | 0.37** | −0.35** | 0.02 | 0.20** |
| WS | −0.33** | −0.65** | 1 | −0.02 | −0.02 | 0.03 | 0.01 | −0.31** |
| *R* | −0.19** | 0.34** | −0.02 | 1 | 0.95** | −0.59** | 0.07 | −0.04 |
| RD | −0.25** | 0.37** | −0.02 | 0.95** | 1 | −0.65** | 0.07* | −0.08* |
| GR | 0.46** | −0.35** | 0.03 | −0.59** | −0.65** | 1 | −0.10* | 0.35** |
| WD | −0.04 | 0.02 | 0.01 | 0.07 | 0.07* | −0.10* | 1 | −0.06 |
| Date | 0.76** | 0.20** | −0.31** | −0.04 | −0.08* | 0.35** | −0.06 | 1 |

*T* Mean temperature, *RH* relative humidity, *WS* wind speed, *GR* global radiation, *R* rainfall, *RD* rainfall duration, *WD* wind direction, *Date* date of capture (Julian day)

* Correlation is significant at the 0.05 level (two-tailed)

** Correlation is significant at the 0.01 level (two-tailed)


**Fig. 1** Map of the study site (Aiguamolls de l'Empordà, *star* symbol) with the location of the five meteorological stations (*square* symbols)

**Table 3** Varimax rotated components matrix for principal components analysis of the weather variables

| | Component | | |
|---|---|---|---|
| | PC1 | PC2 | PC3 |
| Rainfall | 0.918 | 0.129 | 0.008 |
| Rainfall duration | 0.894 | 0.096 | 0.028 |
| Global radiation | −0.876 | −0.015 | −0.066 |
| Wind speed | −0.027 | −0.899 | 0.005 |
| Relative humidity | 0.405 | 0.805 | 0.011 |
| Mean temperature | −0.524 | 0.581 | −0.017 |
| Wind direction | 0.051 | −0.004 | 0.998 |
| Eigenvalues | 2.92 | 1.75 | 0.99 |
| Percentage of variance | 41.80 | 25.14 | 14.12 |

necessarily represent the first day of arrival (Schaub et al. 2001) and, indeed, little is known about the birds' actual arrival or departure dates (Kaiser 1999). Nevertheless, the hourly pattern of catches suggests that in our study zone the swallows were captured mainly when they gathered on nocturnal roost sites after their diurnal migration. Also, the small number of recaptures (18 out of 3,376 birds ringed over 10 years) indicates high turnover, and, therefore, most of them are probably migrants that leave the zone the next morning, with a small proportion of local birds.

The variables that were not normally distributed were logarithmically transformed. Wind direction is transformed by cosine function. Values close to 1 represent northern winds and values close to −1 mean southern winds. Two-tailed significance tests were used throughout. Time is given as GMT.

## Results

Table 3 is the summary result of a PCA analysis based on the weather data. The first three principal components accounted for 81% of the total variation in the weather data collected. The first axis (PC1) explained 42% of the variance and had strongly positive loading from rainfall amount and duration and strongly negative loading from radiation (sunlight). Additionally, the axis displayed a moderately negative loading from temperature. The second axis (PC2) explained 25% of the variance and had strongly positive loading from relative humidity, moderately positive loading from temperature, and strongly negative loading from wind speed. The third axis (PC3) explained 14% of the total variance and was positively correlated with the "northness" of wind direction (see "Methods").

The final model describing the body mass at first capture is given in Table 4. All three meteorological variables entered the equation and the model had a multiple correlation coefficient of 0.68, meaning that approximately 47% of the variation in body mass was accounted for by the equation. The partial correlation coefficient between body mass and PC2 was significant and positive. The PC1 and PC3 components showed a negative partial correlation that was also significant. PC2 was the most influential of all the variables in the model.

**Table 4** Summary of the GLM analysis for variables explaining body mass of migrant swallows passing over northeastern Spain

| Source | Type III sum of squares | *df* | Mean square | *F* | *P* value | *B* | Partial |
|---|---|---|---|---|---|---|---|
| Year | 6.1 | 9 | 0.6 | 3.4 | 0.001 | | |
| PC1 | 4.5 | 1 | 4.5 | 23.0 | 0.000 | −0.178 | −0.385 |
| PC2 | 14.7 | 1 | 14.7 | 74.9 | 0.000 | 0.384 | 0.602 |
| PC3 | 1.3 | 1 | 1.3 | 6.8 | 0.010 | −0.101 | −0.222 |

Body mass was corrected for size, time and date. We used the average body mass of days with ≥5 captures as the dependent variable. PC1, PC2 and PC3 are the component scores of the meteorological variables analyzed (Table 3). *B* represents the estimated coefficients, *Partial* is the partial correlation between the independent variable and the body mass (parameter estimates for each of the 10-year binary variables not shown). Overall model: $F_{12,132} = 9.4$, $r^2 = 0.47$, $P < 0.001$

## Discussion

This paper explores the meteorological conditions that can affect the body mass of migrating Barn Swallows arriving at a passage area in the spring in northeastern Spain. To do this, we proposed to link the body mass at arrival at the study site with the environmental conditions recently experienced south of the study area along the theoretical migration route (Fig. 1).

Our results showed a clear positive association between body mass and warmer days with calm winds and high humidity (as represented by PC2; Fig. 2). Body mass was negatively correlated with rainy, cloudy days (see PC1). Northern winds were found to have a weaker though significant negative effect (see PC3). These results suggest a sensitivity to environmental conditions of a pure aerial feeder bird, such as the Barn Swallow, and they show that in relatively poor conditions migratory birds fly with a fat load that might be lower than optimum. The weather conditions associated with higher body mass upon arrival at our study site in the spring are rising temperatures and humidity, clear skies (high sunlight), low rainfall, and low wind speed.

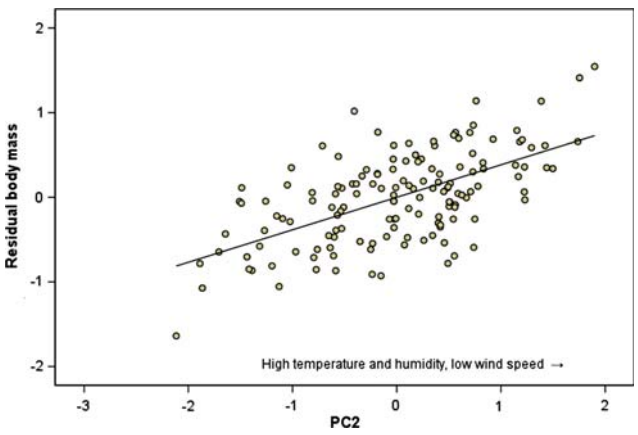


**Fig. 2** Mean residual body mass of Barn Swallows (*Hirundo rustica*) on stopover in northeastern Spain across the range of PC2 values (principal component score related positively to temperature and humidity and negatively to wind speed)

Various studies analyzing the arrival of swallows to their breeding areas have shown that the environmental conditions in the passage areas of North Africa and Europe are very important, both for the arrival time (Vansteenwegen 1992; Møller 1994a, 2004; Huin and Sparks 1998; Sparks et al. 2001; Sparks and Braslavska 2001; Møller and Mërila 2006; Szép and Møller 2005; Gordo and Sanz 2007) as well as for the body condition upon arrival of this species (Ninni et al. 2004). It is important to know the factors that affect both of these characteristics since they directly influence the reproductive success of the swallows. It is known that early arriving birds have a higher probability of acquiring the best territories and mates. Also, an early beginning of nest building allows for an increase in the quantity and quality of offspring produced (Møller 1994a). A good physical condition is probably important during the period immediately following arrival, for example, during mate display (Fransson and Jakobsson 1998; Smith and Moore 2003). Indeed, the high mean spring weight in our study area (18.65 g) relative to either the Balearic Islands (16.97 g; unpublished data from the Piccole Isole project), the south of Spain (17.64 g; ANSE ringing group, in litt.) or Morocco (16.0 g; Ash 1969) suggest that most swallows that arrive at our study area devote time to fat accumulation whilst actively migrating.

Our results, which analyzed swallows captured during migration in a passage area, agree with these studies and show that the swallows are very dependent on the conditions found en route, which can affect body condition over a short time scale. This effect can be due to the trade-off that many Palaearctic birds face during the spring migration: (1) these birds are conditioned to arrive as rapidly as possible at their breeding grounds since early arrivals have a strong selective advantage (Møller 1994a), and (2) they also, however, have to build sufficient reserves both for the trip and to meet the exigencies that arise during the onset of the breeding season, like territory establishment, mating, or nesting (Sandberg and Moore 1996). The birds that face this trade-off need to efficiently utilize the food resources during migration, presumably eating at their maximum capacity (Lindström 1991) and, therefore, cannot compensate when something changes the availability of food. The food supply of hirundines is strongly correlated with the weather (Jones 1987). Therefore, any change in the weather conditions should also influence the body mass of the migratory birds. Several authors have shown this effect of the weather on the body mass of roosting swallows in

the autumn's pre-migratory phase before travelling to their winter areas (Ormerod 1989; Pilastro and Magnani 1997). However, to our knowledge, this is the first study dealing with spring migration, a period in which the selective pressure to travel quickly is stronger (Fransson 1995; Bauchinger and Klaassen 2005).

We conclude that relatively small changes in the local weather in the passage areas can affect the body condition of the migrating swallows. As a consequence, depending on the duration and severity of these conditions, this effect could produce changes in the time of arrival at the breeding grounds, as well as changes in the physical condition at arrival, both of which could, in turn, affect the reproductive success.

## Zusammenfassung

Der Einfluss der Umweltbedingungen auf den Energievorrat von Rauchschwalben (*Hirundo rustica*) während des Frühjahrszuges

Die vorliegende Studie untersucht die Effekte von sieben mikroklimatischen Faktoren auf die Körpermasse ziehender Rauchschwalben (*Hirundo rustica*) zur Zeit der Ankunft im Naturpark Aiguamolls de l'Empordà in Nordostspanien. Wir haben mit Hilfe einer Hauptkomponentenanalyse (PCA) und einem Verfahren zur Erstellung genereller linearer Modelle (GLM) ein Modell entwickelt, das die Beziehungen zwischen Körpermasse und mit dem Wetter verbundenen Ereignissen, die kurz zuvor während des Frühjahrszuges erlebt wurden, untersucht. Unsere Ergebnisse lassen darauf schließen, dass lokale Wetterschwankungen während des Zuges die Körpermasse von Rauchschwalben kurzfristig deutlich beeinflussten. Dieser Effekt zeigt die Bedeutung der Umweltbedingungen während des Zuges für ziehende Schwalben und wie diese Bedingungen verschiedene Ereignisse im Lebenszyklus beeinflussen können, wie z.B. die Ankunftszeit im Brutgebiet oder den Fortpflanzungserfolg.

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