Contrasting sensitivity of nestling and fledgling Barn Swallow *Hirundo rustica* body mass to local weather conditions

RICHARD J. FACEY, JIM O. VAFIDIS, JEREMY A. SMITH, IAN P. VAUGHAN, & ROBERT J. THOMAS

1 Cardiff University, School of Biosciences, The Sir Martin Evans Building Museum Ave, Cardiff, UK, CF10 3AX

2 University of the West of England, Department of Applied Sciences, Bristol, UK, BS16 1QY

Corresponding author. Email: faceyrj@cardiff.ac.uk

Local weather can influence the growth and development of young birds, either indirectly, by modifying prey availability, or directly, by affecting energetic trade-offs. Such effects can have lasting implications for life history traits, but the nature of these effects may vary with the developmental stage of the birds, and over timescales from days to weeks. We examined the interactive effects of temperature, rainfall and wind speed on the mass of nestling and fledgling Barn Swallows *Hirundo rustica*, both on the day of capture and averaging weather across the time since hatching. At the daily timescale, nestling mass was negatively correlated with temperature, but the strength of this association depended on the level of rainfall and wind speed; nestlings were typically heavier on dry or windy days, and the negative effect of temperature was strongest under calm or wet conditions. At the early lifetime timescale (i.e. from hatching to post-fledging), nestling mass was negatively correlated with temperature at low wind speed. Fledgling body mass was less sensitive to weather; the only weather effects evident were a negative correlation with temperature at the daily scale under...
high rainfall that became slightly positive under low rainfall. These changes are consistent with weather effects on availability and distribution of insects within the landscape (e.g. causing high concentrations of flying insects), and with the effects of weather variation on nest microclimate. These results together demonstrate the impacts of weather on chick growth, over immediate (daily) and longer term (nestling/fledgling lifetime) timescales. This shows that sensitivity to local weather conditions varies across the early lifetime of young birds (nestling-fledgling stages) and illustrates the mechanisms by which larger scale (climate) variations influence the body condition of individuals.

Keywords: fitness wind speed, foraging ecology, rainfall, temperature.
The biotic and abiotic conditions experienced by an individual animal early in its development have
consequences not only for short term growth, development and immediate survival, but also for
longterm survival, reproductive success and social status (e.g. Richner et al. 1989, Magrath 1991, Naef-
Daenzer et al. 2001, Saino et al. 2012). In birds, chick growth and survival is associated with factors
linked to both the nesting attempt as a whole, such as hatching date, brood size, habitat quality and
et al. 2012, Crombie & Arcese 2018), and factors that may vary within the nesting attempt, such as
weather and food availability (Geiser et al. 2008, Salaberria et al. 2014, Crombie & Arcese 2018). A
range of studies has linked these factors to post-fledging and over-winter survival, and fecundity in
subsequent breeding seasons (e.g. Newton & Moss 1986, Greño et al. 2008, Öberg 2015), highlighting
the importance of understanding the factors influencing early stages of development, and the role
played by relatively short-term environmental factors during this period.

Weather is of particular interest in the context of understanding nestling development in wild
birds, given predictions of both shifts in average weather conditions and increases in the frequency
and magnitude of extreme weather events over the coming decades (IPCC 2014). Regional-scale
climate conditions, manifested as local-scale weather conditions and nest-scale microclimate, could
impact chick growth via direct mechanisms (e.g. by altering energetic costs; Sikamäki 1996, Dawson
et al. 2005) or indirectly (e.g. by altering prey availability; Ritz et al. 2005, Grüebler et al. 2008). The
relative importance of these different mechanisms is likely to vary according to an individual’s ability
to thermoregulate, its food demands and, later, its ability to self-provision, all of which change from
al. 2006). Despite this, the majority of studies has focused on the effects of local weather variation on
the nestling phase as a whole (e.g. Sikamäki 1996, Dawson et al. 2005, Ardia 2013, Mainwaring &
Hartley 2016), and on future post-fledging survival or recruitment (e.g. Greño et al. 2008, Obërg et al.
2014, Rodríguez et al. 2016). The effects of local weather on body condition in the weeks immediately
Temperature, rainfall and wind speed have been shown to affect nestling growth and development in a wide range of species. While warmer temperatures have been shown to increase nestling survival, feather development and body mass in many species (e.g. Podlesak & Blem 2001, Dawson et al. 2005, Ambrosini et al. 2006), extremely high or low temperatures have been linked to reduced growth rates, body condition and survival (e.g. Rodrigez & Barba 2016, Adreasoon et al. 2019, Imlay 2019). Rainfall has been shown to have a negative effect on nestling provisioning rates, survival, and fledging success (e.g. Arlettaz et al. 2010, Conrey et al. 2016, Crombie & Arcese 2018, but see Oppell et al. 2013). Negative effects of rainfall on nestling mass and growth have been shown in a number of species, for example, Cirl Bunting Emberiza cirlus (Evans et al. 1997), Pied Flycatcher Ficedula hypoleuca (Siikamäki 1996), Eurasian Bittern Botaurus stellaris (Kasprzykowski et al. 2014), Gambel’s White-Crowned Sparrow Zonotrichia leucophrys gambellii and Lapland Longspur Calcarius lapponicus (Pérez et al. 2016). Although the effects of rainfall on chick mass seem to be typically negative, this is not universal. For example, Kruuk et al. (2015) found a positive association between chick mass and high levels of precipitation during the nestling phase in the Superb Fairy-wren Malurus cyaneus.

Wind is an important meteorological variable that is likely to affect chick growth and development through changes in prey abundance and availability Quinney et al. 1986, Dawson et al. 2000, Grüeber et al. 2008, Møller 2013), and by altering the nest microclimate and costs of thermoregulation (Salzman 1982, Bakken et al. 2002, Heenan & Seymour 2012, Gray & Deeming 2017). Only a few studies have linked higher wind speeds to reduced nestling growth; for example in nestling Blue Tits Cyanistes caeruleus (Mainwaring & Hartley 2016), Black-legged Kittiwakes Rissa tridactyla (Christensen-Dalsgaard et al. 2018) and Eurasian Bittern (Kasprzykowski et al. 2014). However, in contrast to rainfall and temperature, and despite growing evidence of its influence on reproductive traits (Møller 2013, Irons et al. 2017), the impact of wind speed on chick growth has received less attention and is less well known (Mainwaring & Hartley 2016, Irons et al. 2017). Similarly, the potential...
for interactive effects between different weather variables has rarely been considered (but see Dawson et al. 2000, Coe et al. 2015, Mainwaring & Hartley 2016, de Zwann et al. 2019 for examples), despite the potential for synergistic or antagonistic relationships; for example, de Zwann et al. (2019) found that the delay in nestling development in Horned Lark *Eremophila alpestris* chicks, induced by cold temperatures, was exacerbated by precipitation.

Major effects of weather on nestling growth and development are not universal. Several studies have found little or no effect of weather on chick growth (e.g. Bradbury et al. 2003, Gilroy et al. 2009). Parents may be able to ameliorate weather impacts, at least over short periods, by adjusting the frequency, timing or nature of food delivered to the nestlings (Dawson et al. 2000, Paiva et al. 2006). Chicks too may be able to mitigate some of the negative effects on development, for example by slowing growth rates or by prioritising the development of certain tissues over others (Lepczyk & Karasov 2000, Metcalfe & Mongahan 2001, Schifferli et al. 2014, Honarmand et al. 2017). However, such nestling growth strategies are not without negative effects (Metcalfe & Monaghan 2001).

In the current study, we used a seven-year data set to investigate the combined and interactive effects of three key weather variables (temperature, rainfall and wind speed) on the mass and growth of nestlings in the Barn Swallow (hereafter ‘Swallow’). The Swallow is a socially monogamous, aerial insectivore with altricial young (Cramp 1988, Turner 2006), and so is expected to be particularly sensitive to short-term weather variation, as the young rely on their parents to brood and to provision them with food during both the nestling and immediate post-fledging stages. We examined the relationship between multiple weather variables (temperature, rainfall and wind) and individual Swallow mass during the nestling stage (8-12 days post-hatching) and fledgling stage (20-35 days post-hatching), representing the dependent and semi-/fully-independent stages of development. In both cases, separate analyses were carried out for short-term weather conditions (conditions on the day of weighing for nestlings or day before for fledglings) and average weather conditions over their elapsed lifetime (i.e. weather conditions from hatching until the time of weighing the nestling or fledgling, hereafter ‘lifetime’), to assess their importance at different temporal scales. We tested the following
directional predictions: i) Nestling body mass is positively related to temperature but negatively related to wind speed and rainfall, at both daily and lifetime scales, due to impacts on, for example, aerial insect abundance and parental provisioning rates; ii) Fledgling mass is sensitive to weather in the short-term (daily scale), due to weather-related variation in insect abundance and activity, but is less sensitive to weather in the long-term (lifetime scale), as fledglings are expected to be less susceptible to food-limitation once they have completed their growth. Furthermore, we predict that temperature, wind and rain will interact to modulate their separate effects on body mass.

METHODS

Study Species and Site

Swallow nests were monitored at an equestrian centre in Cardiff, Wales, UK (Cardiff Riding School, N 51° 29’ 40.7292” W 3° 12’ 21.258”, 9m asl). The centre is surrounded by 10 hectares of intensively grazed pasture dominated by Ryegrass Lolium spp. and Meadow Buttercup Ranunculus acris, and lies immediately adjacent to c. 120 ha of urban parkland (Bute Park). Each year, 15-22 pairs of Swallows nest in the stable buildings; pairs typically re-use the same nests both within and between seasons, but occasionally swap nest locations between broods within a season (c. 2-3 pairs per year); these alternative nests are always within the same or an adjacent stable (RJF pers. obs.).

Nest monitoring

Nests were monitored from April to September (inclusive) between 2008 and 2014. In each year, nest monitoring continued until no further clutches were initiated. Each nest was visited every three to four days, starting in late April, to record first egg date, hatching date, brood size, and chick survival and fledging success. If hatching was not observed directly, nestling age was estimated based on feather development (Turner 2006) and by comparison with chicks of known age; it was possible to examine all chicks within four days of hatching in all years. All breeding attempts were monitored until
the chicks had fledged or the attempt failed. Chicks were considered to have fledged when some or
all of the brood was absent from the nest on at least one monitoring visit, but observed to be alive on
subsequent visits (at approximately 20 days after hatching, Robinson 2015). A second breeding
attempt was considered to be any breeding attempt by the same female that followed a successful
first breeding attempt. Breeding attempts that resulted from re-nesting after a failed attempt were
not included in the study. To allow individual females to be assigned to each breeding attempt, they
were caught and ringed with a British Trust for Ornithology (BTO) metal numbered ring and a
combination of three plastic coloured leg rings to allow identification of individuals without the need
to recapture them.

To determine the effects of local weather conditions on individual mass (as a proxy for growth) we
used data from 248 nestlings (8–12 days old), and 75 fledglings: combined, these nestlings and
fledglings represented 79 broods. Throughout the study period, we aimed to ring and weigh all chicks
between eight and 12 days after hatching. At this age, tarsal development was sufficient to
accommodate metal rings and plastic rings (the latter fitted as part of another study) but young
enough to avoid premature fledging. All nestlings used in this study were those handled between 1700
and 2000hrs (British Summer Time, recorded to the nearest 30 minutes), when access to the study
site and nests was most practical. This represents approximately 61% of the young ringed during the
study; the remainder were either not weighed and/or were ringed under 5 days of age when young
enough to accommodate only a metal ring.

Individuals ringed as chicks were also re-caught post fledging -either intentionally, as part of other
studies, or unintentionally when targeting adult birds. Therefore, our sample of 75 fledglings
comprised 34 individuals weighed at both the nestling and fledgling stage, and 41 individuals weighed
as fledglings only. All fledglings were caught between 0500 and 0700hrs. Fledglings were captured at
dawn by placing a mist net across the entrance of the stable where they roosted. A minimum of 10
days elapsed between the ringing of nestlings and any subsequent re-capture as fledglings. All birds
were caught and ringed under BTO permit A5411 issued to RJF, following best practice guidelines
(Jenni 1998, Redfern & Clark 2001) and weighed to the nearest 0.1 g using an electronic balance (Satrue SA-500 http://www.satrue.com.tw/dp2.htm). Nestlings were ringed in all years, but fledglings were only caught from 2008 to 2011.

Weather data

Daily mean ambient temperature (°C, mean of the daily maximum and daily minimum values), daily mean wind speed (km/h) and total daily rainfall (mm) were obtained from a UK Meteorological Office weather station (Bute Park; 51°29’16.7”N 3°11’17.0”W, 9m asl), 1.5 km south of the study site. Due to equipment failure, some data were missing from the Bute Park time series for parts of 2007, 2010 and 2011 for one or both of the rainfall and temperature variables. To fill in these gaps in the time series, data were obtained from a second Met Office weather station (St Athan; 51°24’18”N, -3°26’24”, 49m asl) approximately 18.7 km to the south-east. Linear regression models were fitted to predict mean temperature and total rainfall in Bute Park, using the temperature and rainfall records for St Athan (n = 529 days; temperature $R^2 = 0.915$; rainfall $R^2 = 0.761$), and predictions generated for missing Bute Park data records (temperature n = 550 days, rain n = 366 days). Mean daily wind speed (km/h) data were also obtained from St Athan, as these data were not available from Bute Park. The three weather variables were only weakly correlated with each other ($r = 0.005$ to 0.026) and so their effects on chicks could be analysed in the same statistical models (see below).

Daily weather data were summarised over two timescales relating to the development of individual chicks: i) the day of handling in the case of nestlings, or in the case of fledglings (which were all caught around sunrise), the day prior to capture, and ii) the time elapsed between hatching and handling, either as a nestling (mean = 9.9 ± 2.0 days) or as a fledgling (mean = 26 ± 3.4 days). Mean values were calculated for temperature and wind, and the cumulative total across this period was calculated for rainfall.

Statistical analysis
The effects of local weather variation on the body masses of nestling and fledgling Swallows were investigated using linear mixed-effects models (LMMs), fitted using the R package “lme4” (Bates et al. 2015). All analysis was undertaken using R statistical software, version 3.5.1 (R Development Core Team 2017).

We fitted four LMMs to test the effects of weather variation upon body mass: each model examined a different combination of the two life stages (nestling and fledgling) and two timescales (day of handling and period since hatching). Collinearity between variables was assessed using pair plots and variance inflation factors (VIF), with a threshold of VIF <3 considered to represent sufficiently low levels of collinearity (Zuur et al. 2010). Each of the four starting models contained mean ambient temperature, mean wind speed and total rainfall, either for the day of handling or the period between hatching and handling, and all possible two-way interactions. In addition, age, date of handling (day 1 = 1st April), time of day, brood size and nesting attempt (first or second) were included in the starting models, to control for heterogeneity introduced by seasonal and diurnal changes, and changes between successive nesting attempts. With the exception of nesting attempt, all variables were standardised to have a mean of zero and a standard deviation of one, prior to model fitting. While nesting attempt and day of handling could both be considered proxies for seasonal effects, both were included in the starting models as parent birds can make different investment decisions in relation to first and second broods (Møller 1991, Grüepler & Naef-Daenzer 2010) and weather effects on first and second attempts reared in the same nest have been shown to vary seasonally (Salaberria et al. 2014), both of which may impact chick mass, for example through reduce provisioning rates. Adult female identity was used as a random factor in each model, to account for repeated observations (chicks and nesting attempts) from the same female; of the 48 females in the data set for the ‘chick’ models, ten were represented by more than one breeding attempt within the same year across the whole study period, but only three were represented in more than one season (one in three years and two in two years). None of the 27 adult females in the ‘fledgling’ models were represented in more than one year, and only two within the same year. Year was considered for inclusion in all models to
account for other sources of temporal variation (e.g. food abundance), but was highly co-linear with other fixed effects (VIF > 4, maximum VIF = 40), so was excluded from the models.

In all cases, the final models were selected using stepwise removal of explanatory variables until there was no further reduction in the AIC (Burnham & Anderson 2002). Model validation procedures followed Zuur et al. (2007) and Thomas et al. (2017). The explanatory power of the model was assessed using the marginal $R^2$ (Nakagawa & Schielzeth 2013), which is based solely on the fixed effects in the model (cf. the conditional $R^2$ which is based on the whole model fixed and random effects combined), calculated using the ‘MuMin’ package (Bartón 2019).

RESULTS

Mean ± sd brood size across the study period was 4.33 g ± 0.92 (range 3 - 6), mean nestling mass (all ages combined) was 21.88 g ± 2.79 (11.3-28.7g), and mean fledgling mass 18.0 g ± 1.34 (15.4 – 22.0).

Daily weather variation across the period can be seen in Error! Reference source not found.

The effects of weather on nestling mass

Nestling mass was sensitive to local weather variation at both the daily and lifetime temporal scales. At both the daily time-scale (LMM; marginal $R^2 = 0.339$; Table 1) and lifetime scale (LMM; marginal $R^2 = 0.265$;
chick body mass showed a negative relationship with temperature, although this was mediated by the interactive effects of wind speed (both time-scales) and rainfall (daily time-scale only). At the daily time-scale, nestling body mass declined with ambient temperature, but the rate of decline was negatively related to both wind speed and rainfall; mass decreased with temperature at twice the rate under calm compared to windy conditions, and declined at three times the rate under wet compared to dry conditions (Fig. 1). At the lifetime scale, nestling body mass was negatively related to temperature under calm conditions (at a rate of -0.89 g/°C); however, as wind speed increased, the relationship between body mass and temperature was no longer evident (Fig. 2). In the lifetime model, there was a small positive, seasonal effect; there was a 0.01 g difference between different individuals of the same age, and from the same sized brood, but weighed on consecutive days. Breeding attempt was not retained in any of the chick models. Both the daily and lifetime model showed effects of a similar magnitude for the increase in body mass with time of day (1.11 g and 1.18 g per hour, respectively) and a negative effect of brood size (-0.76 g and -0.89 g per additional chick in the brood). Predictably, chick mass was shown to increase with age, at a rate of approximately 1 g per day of age (1.1 g/day and 0.8 g/day). Chick mass declined with brood size at a rate of approximately 0.8-0.9 g per chick increase in brood size.

The effects of weather on fledgling mass

In contrast to the nestling stage, fledgling mass was only sensitive to weather at the daily scale (LMM; marginal $R^2 = 0.293$; Table 1). At this timescale, fledgling mass was negatively related to temperature under wet conditions, but the relationship between mass and temperature was reversed under dry conditions (Fig. 3). The two-way interaction between temperature and wind was included in the final model but the relationship with fledgling mass was non-significant ($P = 0.063$, $P = 0.063$, $P = 0.063$, $P = 0.063$).
Table 2). At the chick-lifetime scale, fledgling age was the only significant predictor of fledgling mass (LMM; marginal $R^2 = 0.195$);
with no evidence of any effects of weather across the fledglings’ lifetime influencing body mass. Fledgling mass was predicted to decline by a rate of 0.1 g per day of age.

**DISCUSSION**

We examined the effects of temperature, rainfall and wind-speed on the mass of nestling and fledging Swallows over two temporal scales: the daily scale (short-term) and at the scale of the individual chick’s lifetime (long-term). Mass variations during both the nestling and post-fledging stages were associated with short-term (daily) variation in ambient temperature, rainfall and wind speed, but only nestling mass was found to be affected by weather conditions at the lifetime scale. The current study provides evidence of the complex effects of multiple weather variables on an individual’s development, and specifically that these effects vary with the stage of development.

We found a complex relationship between nestling mass, and temperature, rainfall and wind speed, with evidence of interactive effects between temperature and rainfall, and temperature and wind speed. In the short-term, increased rainfall and increased wind speed both had a negative effect on nestling mass. While this study was unable to evaluate invertebrate prey abundance concurrently with the growth of nestlings, these interactive relationships are consistent with how weather changes the distribution and density of invertebrate prey in the landscape (Grüebl et al. 2008). For example, aerial insect densities are higher along hedgerows and trees, compared to adjacent fields, at low temperatures coupled with high wind speeds (Grüebl et al. 2008). This is probably the reason that Swallows show a preference for foraging near boundary features in poor weather (Evans et al. 2010); by exploiting this ‘honey pot’ effect of concentrated food availability, parent Swallows may be able to provision their chicks effectively, even under cold and windy conditions (Pérez et al. 2008). The boundary effect is reduced by higher temperatures, lower wind speeds and higher rainfall, as insects become more active and more evenly distributed across the landscape (Grüebl et al. 2008).

Parent Swallows do not appear to increase their energy expenditure sufficiently to maintain provisioning rates to compensate for low insect availability (Turner 2006, Schifferli et al. 2014). This
could explain the negative relationships between nestling mass and temperature, which is especially
strong under calm conditions; the combination of low wind speed and higher temperatures reduces
the ‘honey pot’ of concentrated food abundance, while potentially increasing the difficulty of catching
invertebrates due to increased insect activity at higher temperatures. The effect of rainfall only at the
shorter temporal scale is suggestive that it is the duration, rather than the quantity, of rain that is
most disruptive to foraging Swallows. At the timescale of the chick’s lifetime, Swallows appear to be
able to organise their foraging bouts to take advantage of good foraging opportunities when weather
conditions allow.

Contrary to hypothesis one, and to previous studies (e.g. Fernaz et al. 2012), we found that nestling
mass had a negative relationship with ambient temperature. Temperature may influence nestling
mass indirectly, by affecting insect activity/availability - and thus parental provisioning rates - over a
daily timescale, or over the lifetime of a nestling, as discussed above. Overall, invertebrate activity and
abundance tends to be reduced under cooler conditions (Bryant 1973, Turner 1983, Jenni-Eiermann
et al. 2008); a higher body mass under cool conditions is consistent with the use of strategic deposition
of fat reserves as a buffer against starvation under conditions with low or unpredictable food

A second, but not mutually exclusive, possibility is that weather affects chick mass via the nest-
microclimate. Warmer nest environments can reduce the cost of self-maintenance activities, allowing
individual nestlings to invest more in growth (Podlesak & Blem 2001, Dawson et al. 2005; Ambrosini
et al. 2006). For example, Dawson et al. (2005) found that by experimentally warming Tree Swallow
Tachycineta bicolor nests to reduce chicks’ energetic demands, chicks had greater survival rates during
the nestling stage, faster feather development and were heavier, compared to chicks in control nests.
The body heat from livestock in the buildings in which Swallows breed, or the buildings themselves,
can provide a thermal advantage to the nest environment in cold weather (Grüebl et al. 2010, Imlay
et al. 2018). Conversely, very high nest temperatures may reduce nestling mass through evaporative
heat loss and dehydration (Ardia 2013, Rodríguez & Barba 2016, Andreasson et al. 2018, Imlay et al.
This may be particularly pertinent for species nesting in anthropogenic structures, such as hirundines. For example, Imlay et al. (2019) found that Cliff Swallow *Petrochelidon pyrrhonota* nests under barn roofs were subject to higher peak ambient temperatures, with chicks reared during periods of high temperatures having lower mass. This effect was greater under metal than under wooden roofs. The population studied here nests in a similar context – nesting within stables 10-15cm immediately below corrugated bitumen sheet roofing which reaches high temperatures under direct sunlight – and while temperature data were not collected from within the stables throughout the entire study period, the temperature within the stables was substantially warmer than ambient temperature outside (6th to 18th May 2014, mean ambient temperature inside stable = 23.92 ± 5.98°C, outside = 12.74 ± 1.64°C). Increased ventilation of the buildings and nests as a result of higher wind speeds (Gray & Deeming 2017, Heenan & Seymour 2012) would be expected to prevent or at least reduce thermal stress in nestlings.

Taken together, our results are consistent with the negative effect of temperature being the result of increased evaporative heat loss, especially as nestling mass only had a negative relationship with temperature at low wind speeds. However, our results are in keeping with Schifferli et al. (2014), who found the body mass of nestling Barn Swallows to be higher on colder days, likely as a buffer against lower adult provisioning under colder conditions. Further work is therefore recommended to investigate weather-mediated effects on the nest-microclimate, and the implications of nest microclimate for chick growth.

Consistent with hypothesis two, fledgling mass was less sensitive to weather in the long term. Fledgling mass was only significantly affected by weather at a daily timescale; specifically by the interactive effects of daily temperature and rainfall. In contrast, weather over the lifetime of fledged Swallows had no effect on fledgling mass, suggesting that body mass is more likely to be driven by a need to maintain a wing-loading appropriate for an active, aerial insectivore (Møller 2016, Ricklefs 1967, Ricklefs 1968). Consistent with previous studies, brood size was a significant predictor of nestling mass (Lotem 1998, Saino et al. 2001, Saino et al. 2003) at both time scales, but was not a predictor of
fledgling mass. This is suggestive of mechanisms that allow smaller siblings to compete with larger
nest-mates, and thus facilitate similar mass at fledging (Lepczyk & Karasov 2000, Schifferli et al. 2014,
Stier et al. 2015, Honarmand et al. 2017). Synchronised fledging can result in a higher level of adult
provisioning for all juveniles, compared to those nestlings that remain in the nest after their siblings
have fledged (Nilsson & Svensson 1996; Nilsson & Gårdmark 2001). As skeletal development cannot
be compensated for later in life, due to early bone ossification (Schew & Ricklefs 1998), it is more
advantageous for smaller (i.e. later-hatched) siblings to prioritise increasing body mass and skeletal
development over wing-feather development (Mainwaring et al. 2001) which can be compensated for
during the post-fledging stage.

The results presented here demonstrate the importance of considering the interactive effects of
multiple weather variables over multiple timescales when examining the impacts of weather on chick
growth. In this study, we have interpreted these effects on nestling and fledgling body mass in relation
to likely changes in nest micro-climate, and food availability and distribution. Further studies could
examine the effects of weather during the nestling and fledgling stages on subsequent survival and
recruitment into the breeding population. Determining the relative importance of these effects in
relation to population size and persistence may be an important and fruitful avenue of future research,
given current climatic trends.

Data Availability

Data will be made available via the Dryad Digital Repository (weblink to be included).

The authors thank the staff at Cardiff Riding School for allowing us to use the site and for putting up
with our occasional nuisance; in particular, we thank Penny Pembridge and Gloria Garrington for
permission to use the site, and Michaela Platt for keeping us up to date on the Swallows, and for
providing coffee. In addition, we would like to thank the reviewers for their comments which greatly
improved the manuscript, Dr Anthony Carvaggi for helpful discussions, and Dr Andrew Lucas for
comments on an early draft of the paper. All capture and handling work was carried out under license by the British Trust for Ornithology on behalf of the UK Statutory Nature Conservation Agencies.
REFERENCES


<table>
<thead>
<tr>
<th></th>
<th>2008</th>
<th>2009</th>
<th>2010</th>
<th>2011</th>
<th>2012</th>
<th>2013</th>
<th>2014</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Temp</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean ± sd</td>
<td>15.84 ± 2.12</td>
<td>15.62 ± 2.70</td>
<td>15.73 ± 3.05</td>
<td>14.60 ± 2.13</td>
<td>14.75 ± 2.80</td>
<td>15.58 ± 3.65</td>
<td>15.73 ± 2.81</td>
</tr>
<tr>
<td>Minimum</td>
<td>9.90</td>
<td>8.25</td>
<td>6.80</td>
<td>9.80</td>
<td>8.10</td>
<td>7.63</td>
<td>9.91</td>
</tr>
<tr>
<td>Maximum</td>
<td>20.55</td>
<td>21.75</td>
<td>20.50</td>
<td>19.55</td>
<td>21.65</td>
<td>23.82</td>
<td>22.93</td>
</tr>
<tr>
<td><strong>Rainfall</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean ± sd</td>
<td>3.80 ± 5.97</td>
<td>3.68 ± 8.37</td>
<td>2.30 ± 5.60</td>
<td>2.80 ± 4.66</td>
<td>3.63 ± 5.64</td>
<td>1.83 ± 4.75</td>
<td>3.59 ± 6.91</td>
</tr>
<tr>
<td>Minimum</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Maximum</td>
<td>29.70</td>
<td>78.10</td>
<td>41.10</td>
<td>27.20</td>
<td>31.40</td>
<td>36.80</td>
<td>46.80</td>
</tr>
<tr>
<td><strong>Wind Speed</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean ± sd</td>
<td>9.71 ± 3.65</td>
<td>9.00 ± 3.46</td>
<td>7.97 ± 2.50</td>
<td>9.33 ± 3.56</td>
<td>8.96 ± 3.60</td>
<td>8.86 ± 3.44</td>
<td>8.47 ± 3.56</td>
</tr>
<tr>
<td>Minimum</td>
<td>3.04</td>
<td>3.42</td>
<td>3.25</td>
<td>3.33</td>
<td>3.42</td>
<td>3.25</td>
<td>3.21</td>
</tr>
<tr>
<td>Maximum</td>
<td>24.00</td>
<td>19.38</td>
<td>16.42</td>
<td>18.88</td>
<td>25.79</td>
<td>17.88</td>
<td>21.04</td>
</tr>
</tbody>
</table>
Table 1. Model outputs for daily effects of local weather on nestling and fledgling mass. All main effects for each of the weather variables were included in the global models, but only the interaction terms are shown here. Significant weather-related terms are shown in bold ($P \leq 0.05$); non-significant terms retained in the final model are shown for completeness.

<table>
<thead>
<tr>
<th>Life Stage</th>
<th>Response variable</th>
<th>parameter</th>
<th>estimate</th>
<th>se</th>
<th>$t$ value</th>
<th>$P$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>1</td>
<td></td>
<td>1.332</td>
<td>0.208</td>
<td>6.409</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Brood size</td>
<td></td>
<td></td>
<td>-0.699</td>
<td>0.192</td>
<td>-3.641</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Nestling</td>
<td>Time of day$^2$</td>
<td></td>
<td>0.877</td>
<td>0.194</td>
<td>4.532</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Temperature x Rainfall</td>
<td></td>
<td>-1.858</td>
<td>0.808</td>
<td>-2.299</td>
<td>0.023</td>
</tr>
<tr>
<td></td>
<td>Temperature x Wind speed</td>
<td></td>
<td>0.552</td>
<td>0.227</td>
<td>2.429</td>
<td>0.016</td>
</tr>
<tr>
<td>Age$^1$</td>
<td></td>
<td></td>
<td>-0.419</td>
<td>0.152</td>
<td>-2.748</td>
<td>0.008</td>
</tr>
<tr>
<td>Fledgling</td>
<td>Day handled$^3$</td>
<td></td>
<td>0.392</td>
<td>0.177</td>
<td>2.222</td>
<td>0.033</td>
</tr>
<tr>
<td></td>
<td>Temperature x Rainfall</td>
<td></td>
<td>-1.022</td>
<td>0.311</td>
<td>-3.285</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Temperature x Wind speed</td>
<td></td>
<td>0.596</td>
<td>0.310</td>
<td>1.922</td>
<td>0.063</td>
</tr>
</tbody>
</table>

$^1$ Days after hatching where day of hatching = day 0
$^2$ 17:00-20:00hrs
$^3$ Day 1 = 1 April
Table 2. Model outputs for long-term (lifetime) effects of local weather on nestling and fledgling mass. All main effects for each of the weather variables were included in the global models, but only the interaction terms are shown here. Significant weather-related terms are shown in bold ($P \leq 0.05$); non-significant terms retained in the final model are shown for completeness.

<table>
<thead>
<tr>
<th>Life Stage</th>
<th>Response variable</th>
<th>parameter</th>
<th>estimate</th>
<th>se</th>
<th>$t$ value</th>
<th>$P$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age¹</td>
<td></td>
<td></td>
<td>0.906</td>
<td>0.204</td>
<td>4.443</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td></td>
<td>Day handled³</td>
<td></td>
<td>0.663</td>
<td>0.236</td>
<td>2.810</td>
<td>0.006</td>
</tr>
<tr>
<td>Nestlings</td>
<td>Brood size</td>
<td></td>
<td>-0.803</td>
<td>0.200</td>
<td>-4.012</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td></td>
<td>Time of day³</td>
<td></td>
<td>0.785</td>
<td>0.195</td>
<td>4.025</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td></td>
<td>Temperature x Wind Speed</td>
<td></td>
<td>-1.135</td>
<td>0.234</td>
<td>-4.857</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>Fledglings</td>
<td>Brood size</td>
<td></td>
<td>-0.3539</td>
<td>0.1846</td>
<td>-1.917</td>
<td>0.072</td>
</tr>
<tr>
<td></td>
<td>Nesting attempt</td>
<td></td>
<td>-0.6358</td>
<td>0.4321</td>
<td>-1.471</td>
<td>0.153</td>
</tr>
<tr>
<td></td>
<td>Temperature x Wind speed</td>
<td></td>
<td>0.5316</td>
<td>0.2638</td>
<td>2.015</td>
<td>0.072</td>
</tr>
</tbody>
</table>

¹ Days after hatching where day of hatching = day 0
² 17:00-20:00hrs
³ Day 1 = 1 April