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

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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 predator abundance (Podlesak & Blem 2001, Nilson & Gårdmark 2001, Mainwaring *et al.* 2009, Saino *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 hatching to post-fledging (Elmen *et al.* 1991, Siikamäki 1996, McCarty & Winkler 1999, Ambrosini *et 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 after fledging remain largely unexplored, despite survival being at its lowest during this critical period (Yackel Adams *et al.* 2006, Cox *et al.* 2014).

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 gambelii* 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,* Grüebler *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 2001Schifferli *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, Grüebler & 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;

Table ***2***), 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/^{o}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 1g 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, Table ***2***). At the chick-lifetime scale, fledgling age was the only significant predictor of fledgling mass (LMM; marginal R^2 = 0.195;

Table **2**), 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 fledgling 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 (Grüebler *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 (Grüebler *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 (Grüebler *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 availability (Witter *et al.* 1994, Witter *et al.* 1995, Ratikainen & Wright 2013, Vafidis *et al.* 2014).

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 (Grüebler *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.*

2019). 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 (6^{th} to 18^{th} May 2014, mean ambient temperature inside stable = 23.92 ± 5.98 ^{O}C, outside = 12.74 ± 1.64 ^{O}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).

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		2008	2009	2010	2011	2012	2013	2014
Temperature	Mean ± sd	15.84 ± 2.12	15.62 ± 2.70	15.73 ± 3.05	14.60 ± 2.13	14.75 ± 2.80	15.58 ± 3.65	15.73 ± 2.81
	Minimum	9.90	8.25	6.80	9.80	8.10	7.63	9.91
	Maximum	20.55	21.75	20.50	19.55	21.65	23.82	22.93
Rainfall	Mean ± sd	3.80 ± 5.97	3.68 ± 8.37	2.30 ± 5.60	2.80 ± 4.66	3.63 ± 5.64	1.83 ± 4.75	3.59 ± 6.91
	Minimum	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Maximum	29.70	78.10	41.10	27.20	31.40	36.80	46.80
Wind Speed	Mean ± sd	9.71 ± 3.65	9.00 ± 3.46	7.97 ± 2.50	9.33 ± 3.56	8.96 ± 3.60	8.86 ± 3.44	8.47 ± 3.56
	Minimum	3.04	3.42	3.25	3.33	3.42	3.25	3.21
	Maximum	24.00	19.38	16.42	18.88	25.79	17.88	21.04

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.

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

[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 =≤ 0.05); non-significant terms retained in the final model are shown for completeness.

Life Stage	**Response variable**	**parameter estimate**	**se**	***t* value**	***P* value**
Nestlings	Age[1]	0.906	0.204	4.443	<0.001
	Day handled[3]	0.663	0.236	2.810	0.006
	Brood size	-0.803	0.200	-4.012	<0.001
	Time of day[2]	0.785	0.195	4.025	<0.001
	Temperature x Wind Speed	**-1.135**	**0.234**	**-4.857**	**<0.001**
Fledglings	Age[1]	-0.4653	0.1738	-2.677	0.013
	Day handled	0.3245	0.1792	1.811	0.107
	Brood size	-0.3539	0.1846	-1.917	0.072
	Nesting attempt	-0.6358	0.4321	-1.471	0.153
	Temperature x Wind speed	0.5316	0.2638	2.015	0.072

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