information services
gwasanaethau gwybodaeth

2 # Contrasting sensitivity of nestling and fledgling Barn
3 # Swallow *Hirundo rustica* body mass to local weather
4 # conditions
5

6   RICHARD J. FACEY,[1]* JIM O. VAFIDIS,[2] JEREMY A. SMITH,[1] IAN P. VAUGHAN,[1] &
7   ROBERT J. THOMAS[1]
8

9   [1] *Cardiff University, School of Biosciences, The Sir Martin Evans Building Museum Ave,*
10   *Cardiff, UK, CF10 3AX*
11
12   [2] *University of the West of England, Department of Applied Sciences, Bristol, UK, BS16 1QY*

13

14   Corresponding author.

15   Email: faceyrj@cardiff.ac.uk

16
17

18   Local weather can influence the growth and development of young birds, either indirectly, by

19   modifying prey availability, or directly, by affecting energetic trade-offs. Such effects can have lasting

20   implications for life history traits, but the nature of these effects may vary with the developmental

21   stage of the birds, and over timescales from days to weeks. We examined the interactive effects of

22   temperature, rainfall and wind speed on the mass of nestling and fledgling Barn Swallows *Hirundo*

23   *rustica*, both on the day of capture and averaging weather across the time since hatching. At the daily

24   timescale, nestling mass was negatively correlated with temperature, but the strength of this

25   association depended on the level of rainfall and wind speed; nestlings were typically heavier on dry

26   or windy days, and the negative effect of temperature was strongest under calm or wet conditions. At

27   the early lifetime timescale (i.e. from hatching to post-fledging), nestling mass was negatively

28   correlated with temperature at low wind speed. Fledgling body mass was less sensitive to weather;

29   the only weather effects evident were a negative correlation with temperature at the daily scale under

30   high rainfall that became slightly positive under low rainfall. These changes are consistent with

31   weather effects on availability and distribution of insects within the landscape (e.g. causing high

32   concentrations of flying insects), and with the effects of weather variation on nest microclimate. These

33   results together demonstrate the impacts of weather on chick growth, over immediate (daily) and

34   longer term (nestling/fledgling lifetime) timescales. This shows that sensitivity to local weather

35   conditions varies across the early lifetime of young birds (nestling-fledgling stages) and illustrates the

36   mechanisms by which larger scale (climate) variations influence the body condition of individuals.

37

39   The biotic and abiotic conditions experienced by an individual animal early in its development have

40   consequences not only for short term growth, development and immediate survival, but also for

41   longterm survival, reproductive success and social status (e.g. Richner *et al.* 1989, Magrath 1991, Naef-

42   Daenzer *et al.* 2001, Saino *et al.* 2012). In birds, chick growth and survival is associated with factors

43   linked to both the nesting attempt as a whole, such as hatching date, brood size, habitat quality and

44   predator abundance (Podlesak & Blem 2001, Nilson & Gårdmark 2001, Mainwaring *et al.* 2009, Saino

45   *et al.* 2012, Crombie & Arcese 2018), and factors that may vary within the nesting attempt, such as

46   weather and food availability (Geiser *et al.* 2008, Salaberria *et al.* 2014, Crombie & Arcese 2018). A

47   range of studies has linked these factors to post-fledging and over-winter survival, and fecundity in

48   subsequent breeding seasons (e.g. Newton & Moss 1986, Greño *et al.* 2008, Öberg 2015), highlighting

49   the importance of understanding the factors influencing early stages of development, and the role

50   played by relatively short-term environmental factors during this period.

51   Weather is of particular interest in the context of understanding nestling development in wild

52   birds, given predictions of both shifts in average weather conditions and increases in the frequency

53   and magnitude of extreme weather events over the coming decades (IPCC 2014). Regional-scale

54   climate conditions, manifested as local-scale weather conditions and nest-scale microclimate, could

55   impact chick growth via direct mechanisms (e.g. by altering energetic costs; Sikamäki 1996, Dawson

56   *et al.* 2005) or indirectly (e.g. by altering prey availability; Ritz *et al.* 2005, Grüebler *et al.* 2008). The

57   relative importance of these different mechanisms is likely to vary according to an individual's ability

58   to thermoregulate, its food demands and, later, its ability to self-provision, all of which change from

59   hatching to post-fledging (Elmen *et al.* 1991, Siikamäki 1996, McCarty & Winkler 1999, Ambrosini *et*

60   *al.* 2006). Despite this, the majority of studies has focused on the effects of local weather variation on

61   the nestling phase as a whole (e.g. Sikamäki 1996, Dawson *et al.* 2005, Ardia 2013, Mainwaring &

62   Hartley 2016), and on future post-fledging survival or recruitment (e.g. Greño *et al.* 2008, Obërg *et al.*

63   2014, Rodríguez *et al.* 2016). The effects of local weather on body condition in the weeks immediately

64 after fledging remain largely unexplored, despite survival being at its lowest during this critical period

65 (Yackel Adams *et al.* 2006, Cox *et al.* 2014).

66   Temperature, rainfall and wind speed have been shown to affect nestling growth and development

67 in a wide range of species. While warmer temperatures have been shown to increase nestling survival,

68 feather development and body mass in many species (e.g. Podlesak & Blem 2001, Dawson *et al.* 2005,

69 Ambrosini *et al.* 2006), extremely high or low temperatures have been linked to reduced growth rates,

70 body condition and survival (e.g. Rodrigez & Barba 2016, Adreasoon *et al.* 2019, Imlay 2019). Rainfall

71 has been shown to have a negative effect on nestling provisioning rates, survival, and fledging success

72 (e.g. Arlettaz *et al.* 2010, Conrey *et al.* 2016, Crombie & Arcese 2018, but see Oppell *et al.* 2013).

73 Negative effects of rainfall on nestling mass and growth have been shown in a number of species, for

74 example, Cirl Bunting *Emberiza cirlus* (Evans *et al.* 1997), Pied Flycatcher *Ficedula hypoleuca* (Siikamäki

75 1996), Eurasian Bittern *Botaurus stellaris* (Kasprzykowski *et al.* 2014), Gambel's White-Crowned

76 Sparrow *Zonotrichia leucophrys gambelii* and Lapland Longspur *Calcarius lapponicus* (Pérez *et al.*

77 2016). Although the effects of rainfall on chick mass seem to be typically negative, this is not universal.

78 For example, Kruuk *et al.* (2015) found a positive association between chick mass and high levels of

79 precipitation during the nestling phase in the Superb Fairy-wren *Malurus cyaneus.*

80   Wind is an important meteorological variable that is likely to affect chick growth and development

81 through changes in prey abundance and availability Quinney *et al.* 1986, Dawson *et al. 2000,* Grüebler

82 *et al.* 2008, Møller 2013), and by altering the nest microclimate and costs of thermoregulation

83 (Salzman 1982, Bakken *et al.* 2002, Heenan & Seymour 2012, Gray & Deeming 2017). Only a few

84 studies have linked higher wind speeds to reduced nestling growth; for example in nestling Blue Tits

85 *Cyanistes caeruleus* (Mainwaring & Hartley 2016), Black-legged Kittiwakes *Rissa tridactyla*

86 (Christensen-Dalsgaard *et al.* 2018) and Eurasian Bittern (Kasprzykowski *et al.* 2014). However, in

87 contrast to rainfall and temperature, and despite growing evidence of its influence on reproductive

88 traits (Møller 2013, Irons *et al. 2017*), the impact of wind speed on chick growth has received less

89 attention and is less well known (Mainwaring & Hartley 2016, Irons *et al.* 2017). Similarly, the potential

90   for interactive effects between different weather variables has rarely been considered (but see

91   Dawson *et al.* 2000, Coe *et al.* 2015, Mainwaring & Hartley 2016, de Zwann *et al*. 2019 for examples),

92   despite the potential for synergistic or antagonistic relationships; for example, de Zwann *et al.* (2019)

93   found that the delay in nestling development in Horned Lark *Eremophila alpestris* chicks, induced by

94   cold temperatures, was exacerbated by precipitation.

95   Major effects of weather on nestling growth and development are not universal. Several studies

96   have found little or no effect of weather on chick growth (e.g. Bradbury *et al.* 2003, Gilroy *et al.* 2009).

97   Parents may be able to ameliorate weather impacts, at least over short periods, by adjusting the

98   frequency, timing or nature of food delivered to the nestlings (Dawson *et al.* 2000, Paiva *et al.* 2006).

99   Chicks too may be able to mitigate some of the negative effects on development, for example by

100   slowing growth rates or by prioritising the development of certain tissues over others (Lepczyk &

101   Karasov 2000, Metcalfe & Mongahan 2001Schifferli *et al*. 2014, Honarmand *et al.* 2017). However,

102   such nestling growth strategies are not without negative effects (Metcalfe & Monaghan 2001).

103   In the current study, we used a seven-year data set to investigate the combined and interactive

104   effects of three key weather variables (temperature, rainfall and wind speed) on the mass and growth

105   of nestlings in the Barn Swallow (hereafter 'Swallow')*.* The Swallow is a socially monogamous, aerial

106   insectivore with altricial young (Cramp 1988, Turner 2006), and so is expected to be particularly

107   sensitive to short-term weather variation*,* as the young rely on their parents to brood and to provision

108   them with food during both the nestling and immediate post-fledging stages*.* We examined the

109   relationship between multiple weather variables (temperature, rainfall and wind) and individual

110   Swallow mass during the nestling stage (8-12 days post-hatching) and fledgling stage (20-35 days post-

111   hatching), representing the dependent and semi-/fully-independent stages of development. In both

112   cases, separate analyses were carried out for short-term weather conditions (conditions on the day of

113   weighing for nestlings or day before for fledglings) and average weather conditions over their elapsed

114   lifetime (i.e. weather conditions from hatching until the time of weighing the nestling or fledgling,

115   hereafter 'lifetime'), to assess their importance at different temporal scales. We tested the following

116   directional predictions: i) Nestling body mass is positively related to temperature but negatively

117   related to wind speed and rainfall, at both daily and lifetime scales, due to impacts on, for example,

118   aerial insect abundance and parental provisioning rates; ii) Fledgling mass is sensitive to weather in

119   the short-term (daily scale), due to weather-related variation in insect abundance and activity, but is

120   less sensitive to weather in the long-term (lifetime scale), as fledglings are expected to be less

121   susceptible to food-limitation once they have completed their growth. Furthermore, we predict that

122   temperature, wind and rain will interact to modulate their separate effects on body mass.

123

124   ## METHODS

125   **Study Species and Site**

126   Swallow nests were monitored at an equestrian centre in Cardiff, Wales, UK (Cardiff Riding School, N

127   51° 29' 40.7292" W 3° 12' 21.258", 9m asl). The centre is surrounded by 10 hectares of intensively

128   grazed pasture dominated by Ryegrass *Lolium* spp. and Meadow Buttercup *Ranunculus acris,* and lies

129   immediately adjacent to *c.* 120 ha of urban parkland (Bute Park). Each year, 15-22 pairs of Swallows

130   nest in the stable buildings; pairs typically re-use the same nests both within and between seasons,

131   but occasionally swap nest locations between broods within a season (*c.* 2-3 pairs per year); these

132   alternative nests are always within the same or an adjacent stable (RJF pers. obs.).

133

134   **Nest monitoring**

135   Nests were monitored from April to September (inclusive) between 2008 and 2014. In each year, nest

136   monitoring continued until no further clutches were initiated. Each nest was visited every three to

137   four days, starting in late April, to record first egg date, hatching date, brood size, and chick survival

138   and fledging success. If hatching was not observed directly, nestling age was estimated based on

139   feather development (Turner 2006) and by comparison with chicks of known age; it was possible to

140   examine all chicks within four days of hatching in all years. All breeding attempts were monitored until

141 the chicks had fledged or the attempt failed. Chicks were considered to have fledged when some or

142 all of the brood was absent from the nest on at least one monitoring visit, but observed to be alive on

143 subsequent visits (at approximately 20 days after hatching, Robinson 2015). A second breeding

144 attempt was considered to be any breeding attempt by the same female that followed a successful

145 first breeding attempt. Breeding attempts that resulted from re-nesting after a failed attempt were

146 not included in the study. To allow individual females to be assigned to each breeding attempt, they

147 were caught and ringed with a British Trust for Ornithology (BTO) metal numbered ring and a

148 combination of three plastic coloured leg rings to allow identification of individuals without the need

149 to recapture them.

150   To determine the effects of local weather conditions on individual mass (as a proxy for growth) we

151 used data from 248 nestlings (8–12 days old), and 75 fledglings: combined, these nestlings and

152 fledglings represented 79 broods. Throughout the study period, we aimed to ring and weigh all chicks

153 between eight and 12 days after hatching. At this age, tarsal development was sufficient to

154 accommodate metal rings and plastic rings (the latter fitted as part of another study) but young

155 enough to avoid premature fledging. All nestlings used in this study were those handled between 1700

156 and 2000hrs (British Summer Time, recorded to the nearest 30 minutes), when access to the study

157 site and nests was most practical. This represents approximately 61% of the young ringed during the

158 study; the remainder were either not weighed and/or were ringed under 5 days of age when young

159 enough to accommodate only a metal ring.

160   Individuals ringed as chicks were also re-caught post fledging -either intentionally, as part of other

161 studies, or unintentionally when targeting adult birds. Therefore, our sample of 75 fledglings

162 comprised 34 individuals weighed at both the nestling and fledgling stage, and 41 individuals weighed

163 as fledglings only. All fledglings were caught between 0500 and 0700hrs. Fledglings were captured at

164 dawn by placing a mist net across the entrance of the stable where they roosted. A minimum of 10

165 days elapsed between the ringing of nestlings and any subsequent re-capture as fledglings. All birds

166 were caught and ringed under BTO permit A5411 issued to RJF, following best practice guidelines

167 (Jenni 1998, Redfern & Clark 2001) and weighed to the nearest 0.1 g using an electronic balance

168 (Satrue SA-500 http://www.satrue.com.tw/dp2.htm). Nestlings were ringed in all years, but fledglings

169 were only caught from 2008 to 2011.

170

171 **Weather data**

172 Daily mean ambient temperature (^{o}C, mean of the daily maximum and daily minimum values), daily

173 mean wind speed (km/h) and total daily rainfall (mm) were obtained from a UK Meteorological Office

174 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

175 equipment failure, some data were missing from the Bute Park time series for parts of 2007, 2010 and

176 2011 for one or both of the rainfall and temperature variables. To fill in these gaps in the time series,

177 data were obtained from a second Met Office weather station (St Athan; 51°24'18"N, -3°26'24", 49m

178 asl) approximately 18.7 km to the south-east. Linear regression models were fitted to predict mean

179 temperature and total rainfall in Bute Park, using the temperature and rainfall records for St Athan (n

180 = 529 days; temperature R^2 = 0.915; rainfall R^2 = 0.761), and predictions generated for missing Bute

181 Park data records (temperature n = 550 days, rain n = 366 days). Mean daily wind speed (km/h) data

182 were also obtained from St Athan, as these data were not available from Bute Park. The three weather

183 variables were only weakly correlated with each other (r = 0.005 to 0.026) and so their effects on

184 chicks could be analysed in the same statistical models (see below).

185 Daily weather data were summarised over two timescales relating to the development of individual

186 chicks: i) the day of handling in the case of nestlings, or in the case of fledglings (which were all caught

187 around sunrise), the day prior to capture, and ii) the time elapsed between hatching and handling,

188 either as a nestling (mean = 9.9 ± 2.0 days) or as a fledgling (mean = 26 ± 3.4 days). Mean values were

189 calculated for temperature and wind, and the cumulative total across this period was calculated for

190 rainfall.

191

192 **Statistical analysis**

193   The effects of local weather variation on the body masses of nestling and fledgling Swallows were

194   investigated using linear mixed-effects models (LMMs), fitted using the R package "lme4" (Bates et al.

195   2015). All analysis was undertaken using R statistical software, version 3.5.1 (R Development Core

196   Team 2017).

197   We fitted four LMMs to test the effects of weather variation upon body mass: each model

198   examined a different combination of the two life stages (nestling and fledgling) and two timescales

199   (day of handling and period since hatching). Collinearity between variables was assessed using pair

200   plots and variance inflation factors (VIF), with a threshold of VIF <3 considered to represent sufficiently

201   low levels of collinearity (Zuur *et al.* 2010). Each of the four starting models contained mean ambient

202   temperature, mean wind speed and total rainfall, either for the day of handling or the period between

203   hatching and handling, and all possible two-way interactions. In addition, age, date of handling (day 1

204   = 1st April), time of day, brood size and nesting attempt (first or second) were included in the starting

205   models, to control for heterogeneity introduced by seasonal and diurnal changes, and changes

206   between successive nesting attempts. With the exception of nesting attempt, all variables were

207   standardised to have a mean of zero and a standard deviation of one, prior to model fitting. While

208   nesting attempt and day of handling could both be considered proxies for seasonal effects, both were

209   included in the starting models as parent birds can make different investment decisions in relation to

210   first and second broods (Møller 1991, Grüebler & Naef-Daenzer 2010) and weather effects on first

211   and second attempts reared in the same nest have been shown to vary seasonally (Salaberria *et al.*

212   2014), both of which may impact chick mass, for example through reduce provisioning rates. Adult

213   female identity was used as a random factor in each model, to account for repeated observations

214   (chicks and nesting attempts) from the same female; of the 48 females in the data set for the 'chick'

215   models, ten were represented by more than one breeding attempt within the same year across the

216   whole study period, but only three were represented in more than one season (one in three years and

217   two in two years). None of the 27 adult females in the 'fledgling' models were represented in more

218   than one year, and only two within the same year. Year was considered for inclusion in all models to

219 account for other sources of temporal variation (e.g. food abundance), but was highly co-linear with

220 other fixed effects (VIF >4, maximum VIF = 40), so was excluded from the models.

221   In all cases, the final models were selected using stepwise removal of explanatory variables until

222 there was no further reduction in the AIC (Burnham & Anderson 2002). Model validation procedures

223 followed Zuur *et al.* (2007) and Thomas *et al.* (2017). The explanatory power of the model was

224 assessed using the marginal R^2 (Nakagawa & Schielzeth 2013), which is based solely on the fixed

225 effects in the model (cf. the conditional R^2 which is based on the whole model fixed and random effects

226 combined), calculated using the 'MuMin' package (Bartón 2019).

227

228 RESULTS

229 Mean ± sd brood size across the study period was 4.33 g ± 0.92 (range 3 - 6), mean nestling mass (all

230 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).

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

232

233 **The effects of weather on nestling mass**

234 Nestling mass was sensitive to local weather variation at both the daily and lifetime temporal scales.

235 At both the daily time-scale (LMM; marginal R^2 = 0.339; Table 1) and lifetime scale (LMM; marginal R^2

236 = 0.265;

237   Table **2**), chick body mass showed a negative relationship with temperature, although this was

238   mediated by the interactive effects of wind speed (both time-scales) and rainfall (daily time-scale

239   only). At the daily time-scale, nestling body mass declined with ambient temperature, but the rate of

240   decline was negatively related to both wind speed and rainfall; mass decreased with temperature at

241   twice the rate under calm compared to windy conditions, and declined at three times the rate under

242   wet compared to dry conditions (Fig. 1). At the lifetime scale, nestling body mass was negatively

243   related to temperature under calm conditions (at a rate of -0.89 g/^{o}C); however, as wind speed

244   increased, the relationship between body mass and temperature was no longer evident (Fig. 2). In the

245   lifetime model, there was a small positive, seasonal effect; there was a 0.01 g difference between

246   different individuals of the same age, and from the same sized brood, but weighed on consecutive

247   days. Breeding attempt was not retained in any of the chick models. Both the daily and lifetime model

248   showed effects of a similar magnitude for the increase in body mass with time of day (1.11 g and 1.18

249   g per hour, respectively) and a negative effect of brood size (-0.76 g and -0.89 g per additional chick in

250   the brood). Predictably, chick mass was shown to increase with age, at a rate of approximately 1g per

251   day of age (1.1 g/day and 0.8 g/day). Chick mass declined with brood size at a rate of approximately

252   0.8-0.9 g per chick increase in brood size.

253

254   **The effects of weather on fledgling mass**

255   In contrast to the nestling stage, fledgling mass was only sensitive to weather at the daily scale (LMM;

256   marginal R^2 = 0.293; Table 1). At this timescale, fledgling mass was negatively related to temperature

257   under wet conditions, but the relationship between mass and temperature was reversed under dry

258   conditions (Fig. 3). The two-way interaction between temperature and wind was included in the final

259   model but the relationship with fledgling mass was non-significant (P = 0.063,

260   Table *2*). At the chick-lifetime scale, fledgling age was the only significant predictor of fledgling mass

261   (LMM; marginal R^2 = 0.195;

262   Table *2*), with no evidence of any effects of weather across the fledglings' lifetime influencing body

263   mass. Fledgling mass was predicted to decline by a rate of 0.1 g per day of age.

264

265   DISCUSSION

266   We examined the effects of temperature, rainfall and wind-speed on the mass of nestling and fledgling

267   Swallows over two temporal scales: the daily scale (short-term) and at the scale of the individual

268   chick's lifetime (long-term). Mass variations during both the nestling and post-fledging stages were

269   associated with short-term (daily) variation in ambient temperature, rainfall and wind speed, but only

270   nestling mass was found to be affected by weather conditions at the lifetime scale. The current study

271   provides evidence of the complex effects of multiple weather variables on an individual's

272   development, and specifically that these effects vary with the stage of development.

273   We found a complex relationship between nestling mass, and temperature, rainfall and wind

274   speed, with evidence of interactive effects between temperature and rainfall, and temperature and

275   wind speed. In the short-term, increased rainfall and increased wind speed both had a negative effect

276   on nestling mass. While this study was unable to evaluate invertebrate prey abundance concurrently

277   with the growth of nestlings, these interactive relationships are consistent with how weather changes

278   the distribution and density of invertebrate prey in the landscape (Grüebler *et al.* 2008). For example,

279   aerial insect densities are higher along hedgerows and trees, compared to adjacent fields, at low

280   temperatures coupled with high wind speeds (Grüebler *et al.* 2008). This is probably the reason that

281   Swallows show a preference for foraging near boundary features in poor weather (Evans *et al.* 2010);

282   by exploiting this 'honey pot' effect of concentrated food availability, parent Swallows may be able to

283   provision their chicks effectively, even under cold and windy conditions (Pérez *et al.* 2008). The

284   boundary effect is reduced by higher temperatures, lower wind speeds and higher rainfall, as insects

285   become more active and more evenly distributed across the landscape (Grüebler *et al.* 2008).

286   Parent Swallows do not appear to increase their energy expenditure sufficiently to maintain

287   provisioning rates to compensate for low insect availability (Turner 2006, Schifferli *et al.* 2014). This

13

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 (6th to 18th 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

340   fledgling mass. This is suggestive of mechanisms that allow smaller siblings to compete with larger

341   nest-mates, and thus facilitate similar mass at fledging (Lepczyk & Karasov 2000, Schifferli *et al*. 2014,

342   Stier *et al*. 2015, Honarmand *et al.* 2017). Synchronised fledging can result in a higher level of adult

343   provisioning for all juveniles, compared to those nestlings that remain in the nest after their siblings

344   have fledged (Nilsson & Svensson 1996; Nilsson & Gårdmark 2001). As skeletal development cannot

345   be compensated for later in life, due to early bone ossification (Schew & Ricklefs 1998), it is more

346   advantageous for smaller (i.e. later-hatched) siblings to prioritise increasing body mass and skeletal

347   development over wing-feather development (Mainwaring *et al.* 2001) which can be compensated for

348   during the post-fledging stage.

349   The results presented here demonstrate the importance of considering the interactive effects of

350   multiple weather variables over multiple timescales when examining the impacts of weather on chick

351   growth. In this study, we have interpreted these effects on nestling and fledgling body mass in relation

352   to likely changes in nest micro-climate, and food availability and distribution. Further studies could

353   examine the effects of weather during the nestling and fledgling stages on subsequent survival and

354   recruitment into the breeding population. Determining the relative importance of these effects in

355   relation to population size and persistence may be an important and fruitful avenue of future research,

356   given current climatic trends.

357

358   Data Availability

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

360

REFERENCES

Adams, A.A.Y., Skagen, S.K. and Savidge, J.A. 2006. Modeling post-fledging survival of Lark Buntings in response to ecological and biological factors. Ecology 87: 178–188.

Ambrosini, R., Ferrari, R.P., Martinelli, R., Romano, M. and Saino, N. 2006. Seasonal, meteorological, and microhabitat effects on breeding success and offspring phenotype in the Barn Swallow, *Hirundo rustica*. Ecoscience 13: 298–307.

Andreasson, F., Nord, A. and Nilsson, J.Å. 2018. Experimentally increased nest temperature affects body temperature, growth and apparent survival in blue tit nestlings. J Avian. Biol. 49: jav-01620.

Ardia, D.R. 2013. The effects of nestbox thermal environment on fledging success and haematocrit in Tree Swallows. Avian Biol. Res. 6: 99–103.

Arlettaz, R., Schaad, M., Reichlin, T.S. and Schaub, M. 2010. Impact of weather and climate variation on Hoopoe reproductive ecology and population growth. J. Ornithol. 151: 889–899.

Bakken, G.S., Williams, J.B. and Ricklefs, R.E. 2002. Metabolic response to wind of downy chicks of Arctic-breeding shorebirds (Scolopacidae). J. Exp. Biol. 205: 3435-3443.

Barton, K. 2019. MuMIn: Multi-Model Inference. R package version 1.43.6. https://CRAN.R-project.org/package=MuMIn

Burnham, K.P. and Anderson, D.R. 2002. Model Selection and Inference: A Practical Information-Theoretic Approach. 2nd Edition, Springer-Verlag, New York.

Bradbury, R.B., Wilson, J.D., Moorcroft, D., Morris, A.J. and Perkins, A.J. 2003. Habitat and weather are weak correlates of nestling condition and growth rates of four UK farmland passerines. Ibis 145: 295–306.

Bryant, D. M. 1975. Breeding Biology of House Martins *Delichon Urbica* In Relation to Aerial Insect Abundance. Ibis 117: 180-216.

Charman, E.C., Smith, K.W., Dillon, I.A., Dodd, S., Gruar, D.J., Cristinacce, A., Grice, P. V. and Gregory, R.D. 2012. Drivers of low breeding success in the Lesser Spotted Woodpecker *Dendrocopos minor* in England: testing hypotheses for the decline. Bird Study 59: 255–265.

395 Christensen-Dalsgaard, S., May, R.F., Barrett, R.T., Langset, M., Sandercock, B.K. and Lorentsen, S.H.

396   2018. Prevailing weather conditions and diet composition affect chick growth and survival in the

397   black-legged kittiwake. Mar. Ecol. Prog. Ser. 604: 237–249.

398 Coe, B.H., Beck, M.L., Chin, S.Y., Jachowski, C.M.B. and Hopkins, W. a. 2015. Local variation in weather

399   conditions influences incubation behavior and temperature in a passerine bird. J Avian. Biol. 46:

400   1–10.

401 Conrey, R.Y., Skagen, S.K., Yackel Adams, A.A. and Panjabi, A.O. 2016. Extremes of heat, drought and

402   precipitation depress reproductive performance in shortgrass prairie passerines. Ibis 158: 614–

403   629.

404 Cox, W.A., Thompson, F.R., Cox, A.S. and Faaborg, J. 2014. Post-fledging survival in passerine birds and

405   the value of post-fledging studies to conservation. J. Wildl. Manage. 78: 183–193.

406 Cramp, S. (ed.) 1998. The Birds of the Western Palearctic, Vol. 5. Oxford: Oxford University Press

407 Crombie, M.D. and Arcese, P. 2018. Temporal variation in the effects of individual and environmental

408   factors on nest success. The Auk 135: 326–341.

409 Dawson, R.D., Lawrie, C.C. and O'Brien, E.L. 2005. The importance of microclimate variation in

410   determining size, growth and survival of avian offspring: experimental evidence from a cavity

411   nesting passerine. Oecologia 144: 499–507.

412 de Zwaan, D.R., Camfield, A.F., MacDonald, E.C. and Martin, K. 2019. Variation in offspring

413   development is driven more by weather and maternal condition than predation risk. Funct. Ecol.

414   33: 447–456.

415 ~~Dunn, E.K. 1975. The Role of Environmental Factors in the Growth of Tern Chicks. J. Anim. Ecol. 44:~~

416   ~~743-754.~~

417 Emlen, S.T., Wrege, P.H., Demong, N.J. and Hegner, R.E. 1991. Flexible growth rates in nestling white-

418   fronted bee-eaters: a possible adaptation to short-term food shortage. The Condor 93: 591–597.

419 Evans, A.D., Smith, K.W., Buckingham, D.L. and Evans, J. 1997. Seasonal variation in breeding

420   performance and nestling diet of Cirl Buntings *Emberiza cirlus* in England. Bird Study 44: 66–79.

421 Evans, K.L., Bradbury, R.B. and Wilson, J.D. 2010. Selection of hedgerows by Swallows *Hirundo rustica*

422   foraging on farmland: the influence of local habitat and weather. Bird Study, 50: 8-14

423 Fernaz, J.M., Schifferli, L. and Grüebler, M.U. 2012. Ageing nestling Barn Swallows *Hirundo rustica*: an

424   illustrated guide and cautionary comments. Ring. Migr. 27:65-75.

425 Gilroy, J.J., Anderson, G.Q. a., Grice, P. V., Vickery, J. a., Watts, P.N. and Sutherland, W.J. 2009.

426   Breeding on Arable Farmland. Bird Study 56: 221–232.

427 Gorman, H.E. and Nager, R.G. 2004. Prenatal developmental conditions have long-term effects on

428   offspring fecundity. Proc. R. Soc. Lond. B. 271: 1923–1928.

429 Gray, L.A. and Deeming, D.C. 2017. Effect of air movement on the thermal insulation of avian nests.

430   Bird Study 64: 492–501.

431 Greño, J.L., Belda, E.J. and Barba, E. 2008. Influence of temperatures during the nestling period on

432   post-fledging survival of great tit *Parus major* in a Mediterranean habitat. J Avian. Biol. 39: 41–

433   49.

434 Grüebler, M.U. and Naef-Daenzer, B. 2010. Brood overlap and male ornamentation in the double-

435   brooded barn Swallow. Behav. Ecol. 21: 513–519.

436 Grüebler, M.U., Korner-Nievergelt, F. and Von Hirschheydt, J. 2010. The reproductive benefits of

437   livestock farming in barn Swallows *Hirundo rustica*: quality of nest site or foraging habitat? J. Appl.

438   Ecol. 47: 1340–1347.

439 Grüebler, M.U., Morand, M. and Naef-Daenzer, B. 2008. A predictive model of the density of airborne

440   insects in agricultural environments. Agr. Ecosyst. Environ. 123: 75–80.

441 Heenan, C.B. and Seymour, R.S. 2012. The Effect of Wind on the Rate of Heat Loss from Avian Cup-

442   Shaped Nests. PLoS ONE 7: e32252

443 Hegyi, G. and Török, J. 2007. Developmental plasticity in a passerine bird: an experiment with collared

444   flycatchers *Ficedula albicollis*. J Avian. Biol. 38: 327–334.

445   Honarmand, M., Goymann, W. and Naguib, M. 2010. Stressful Dieting: Nutritional Conditions but Not

446   Compensatory Growth Elevate Corticosterone Levels in Zebra Finch Nestlings and Fledglings. PLoS

447   ONE 5: e12930.

448   Honarmand, M., Krause, E.T. and Naguib, M. 2017. Implications of nutritional stress as nestling or

449   fledgling on subsequent attractiveness and fecundity in zebra finches (*Taeniopygia guttata*).

450   PeerJ 5: e3628.

451   Imlay, T.L., Nickerson, D. and Horn, A.G. 2019. Temperature and breeding success for cliff Swallows

452   (*Petrochelidon pyrrhonota*) nesting on man-made structures: Ecological traps? Can. J. Zool. 97:

453   429–435.

454   IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the

455   Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team,

456   R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzer [Online]. Available at:

457   http://www.ipcc.ch/report/ar5/syr/

458   Irons, R.D., Scurr, A.H., Rose, A.P., Hagelin, J.C., Blake, T. and Doak, D.F. 2017. Wind and rain are the

459   primary climate factors driving changing phenology of an aerial insectivore. Proc. R. Soc. Lond. B

460   284: e20170412.

461   Jenni, L. (ed.) 1998. EURING Swallow Project Field Manual. EURING

462   Jenni-Eiermann, S., Glaus, E., Grüebler, M., Schwabl, H. and Jenni, L. 2008. Glucocorticoid response to

463   food availability in breeding Barn Swallows (*Hirundo rustica*). Gen. Comp. Endocr. 155: 558–565.

464   Kasprzykowski, Z., Polak, M. and Chylarecki, P. 2014. Effects of Weather Conditions, Time of Breeding,

465   Brood Size and Hatching Order on Eurasian Bittern Nestling Growth in a Food-Rich Fishpond

466   Habitat. Ann. Zool. Fenn. 51: 477–487.

467   Kruuk, L.E.B., Osmond, H.L. and Cockburn, A. 2015. Contrasting effects of climate on juvenile body size

468   in a Southern Hemisphere passerine bird. Global Change Biol.21: 2929–2941.

469   Lepczyk, C.A. and Karasov, W.H. 2000. Effect of Ephemeral Food Restriction on Growth of House

470   Sparrows. The Auk 117: 164–174.

471   LOTEM, A. 1998. Differences in begging behaviour between Barn Swallow, *Hirundo rustica*, nestlings.

472   Anim. Behav. 55: 809–818.

473   Magrath, R.D. 1991. Nestling Weight and Juvenile Survival in the Blackbird, *Turdus merula*. The J. Anim.

474   Ecol. 60: 335-351.

475   Mainwaring, M.C. and Hartley, I.R. 2016. Local weather conditions have complex effects on the growth

476   of blue tit nestlings. J. Therm. Biol. 60: 12–19.

477   Mainwaring, M.C., Rowe, L. V., Kelly, D.J., Jonathan, G., Stuart, B. and Hartley, I.R. 2009. Hatching

478   Asynchrony and Growth Trade-Offs Within Barn Swallow Broods. The Condor 111: 668–674.

479   Mccarty, J.P. 2001. Variation in Growth of Nestling Tree Swallows Across Multiple Temporal and

480   Spatial Scales Variation in Growth of Nestling Tree Swallows Across. The Auk 118: 176–190.

481   Mccarty, J.P. and Winkler, D.W. 1999. Relative importance of environmental variables in determining

482   the growth of nestling Tree Swallows *Tachycineta bicolor*. Ibis 141: 286–296.

483   Metcalfe, N.B. and Monaghan, P. 2001. Compensation for a bad start: Grow now, pay later? TREE

484   16:254–260.

485   Møller, A.P. 1991. Double broodedness and mixed reproductive strategies by female Swallows. Anim.

486   Behav. 42: 671–679.

487   Møller, A.P. 2013. Long-term trends in wind speed, insect abundance and ecology of an insectivorous

488   bird. Ecosphere 4: 1-11.

489   Naef-Daenzer, B., Widmer, F. and Nuber, M. 2001. Differential post-fledging survival of great and coal

490   tits in relation to their condition and fledging date. J. Anim. Ecol. 70: 730–738.

491   Nakagawa, S. and Schielzeth, H. 2013. A general and simple method for obtaining R^2 from generalized

492   linear mixed-effects models. Methods Ecol. Evol. 4: 133–142.

493   Newton, I. and Moss, D. 1986. Post-fledging survival of Sparrowhawks *Accipiter nisus* in relation to

494   mass, brood size and brood composition at fledging. Ibis 128: 73–80.

495   Nilsson, J.-Å. and Gårdmark, A. 2001. Sibling competition affects individual growth strategies in marsh

496   tit, *Parus palustris*, nestlings. Anim. Behav. 61: 357–365.

497 Öberg, M., Arlt, D., Pärt, T., Laugen, A.T., Eggers, S. and Low, M. 2015. Rainfall during parental care

498 reduces reproductive and survival components of fitness in a passerine bird. Ecol. Evol. 5: 345–

499 356.

500 Oppel, S., Hilton, G.M., Allcorn, R., Fenton, C., Matthews, A.J. and Gibbons, D.W. 2013. The effects of

501 rainfall on different components of seasonal fecundity in a tropical forest passerine. Ibis 155:

502 464–475.

503 Paiva, V.H., Ramos, J.A., Catry, T., Pedro, P., Medeiros, R. and Palma, J. 2006. Influence of

504 environmental factors and energetic value of food on Little Tern *Sterna albifrons* chick growth

505 and food delivery. Bird Study 53: 1–11.

506 Pérez, J.H., Ardia, D.R., Chad, E.K. and Clotfelter, E.D. 2008. Experimental heating reveals nest

507 temperature affects nestling condition in Tree Swallows (*Tachycineta bicolor*). Biol. Letters 4:

508 468–471.

509 Pérez, J.H., Krause, J.S., Chmura, H.E., Bowman, S., McGuigan, M., Asmus, A.L., Meddle, S.L., Hunt,

510 K.E., Gough, L., Boelman, N.T. and Wingfield, J.C. 2016. Nestling growth rates in relation to food

511 abundance and weather in the Arctic. The Auk 133: 261–272.

512 Podlesak, D.W. and Blem, C.R. 2001. Factors Associated with Growth of Nestling Prothonotary

513 Warblers. The Wilson Bulletin. 113: 263–272.

514 Quinney, T.E., Hussell, D.J.T. and Ankney, C.D. 1986. Sources of Variation in Growth of Tree Swallows.

515 The Auk 103 389–400.

516 R Core Team (2019). R: A language and environment for statistical computing. R Foundation for

517 Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

518 Ratikainen, I.I. and Wright, J. 2013. Adaptive management of body mass by Siberian jays. Anim. Behav.

519 85: 427–434.

520 Redfern, C.P.F. & Clark, J.A. 2001. Ringers Manual. BTO Thetford

521 Richner, H., Schneiter, P. and Stirnimann, H. 1989. Life-History Consequences of Growth Rate

522   Depression: An Experimental Study on Carrion Crows (*Corvus corone corone* L.). Funct. Ecol. 3:

523   617-624.

524 Ricklefs, R.E. 1967. Relative Growth, Body Constituents, and Energy Content of Nestling Barn Swallows

525   and Red-Winged Blackbirds. *The Auk* 84: 560-570.

526 Ricklefs, R.E. 1968. Weight Recession in Nestling Birds. The Auk 85: 30-35.

527 Ritz, M.S., Hahn, S. and Peter, H.-U. 2005. Factors affecting chick growth in the South Polar Skua

528   (*Catharacta maccormicki*): food supply, weather and hatching date. Polar Biol. 29: 53–60.

529 Robinson, R.A. 2005. BirdFacts: profiles of birds occurring in Britain & Ireland. BTO, Thetford

530   (http://www.bto.org/birdfacts, accessed on 17 September 2018)

531 Rodríguez, S. and Barba, E. 2016. Nestling growth is impaired by heat stress: An experimental study in

532   a mediterranean Great Tit population. Zool. Stud. 55: 55-40.

533 Saino, N., Incagli, M., Martinelli, R., Ambrosini, R. and Moller, A.P. 2001. Immunity, growth and begging

534   behaviour of nestling Barn Swallows *Hirundo rustica* in relation to hatching order. J Avian. Biol.

535   32: 263–270.

536 Saino, N., Romano, M., Ambrosini, R., Rubolini, D., Boncoraglio, G., Caprioli, M. and Romano, A. 2012.

537   Longevity and lifetime reproductive success of Barn Swallow offspring are predicted by their

538   hatching date and phenotypic quality. J. Anim. Ecol. 81: 1004–1012.

539 Saino, N., Suffritti, C., Martinelli, R., Rubolini, D. and Møller, A.P. 2003. Immune response covaries with

540   corticosterone plasma levels under experimentally stressful conditions in nestling barn Swallows

541   (*Hirundo rustica*). Behav. Ecol. 14: 318–325.

542 Salaberria, C., Celis, P., López-Rull, I. and Gil, D. 2014. Effects of temperature and nest heat exposure

543   on nestling growth, dehydration and survival in a Mediterranean hole-nesting passerine. Ibis 156:

544   265–275.

545 Salzman, A.G. 1982. The Selective Importance of Heat Stress in Gull Nest Location. Ecology 63: 742–

546   751.

547 Schifferli, L., Grüebler, M.U., Meijer, H. a J., Visser, G.H. and Naef-Daenzer, B. 2014. Barn Swallow

548 *Hirundo rustica* parents work harder when foraging conditions are good. Ibis 156: 1–11.

549 Seress, G., Hammer, T., Bókony, V., Vincze, E., Preiszner, B., Pipoly, I., Sinkovics, C., Evans, K.L. and

550 Liker, A. 2018. Impact of urbanization on abundance and phenology of caterpillars and

551 consequences for breeding in an insectivorous bird. Ecol. Appl. 28: 1143–1156.

552 Siikamäki, P. 1996. Nestling growth and mortality of Pied Flycatchers *Ficedula hypoleuca* in relation to

553 weather and breeding effort. Ibis 138: 471–478.

554 Stier, A., Massemin, S., Zahn, S., Tissier, M.L. and Criscuolo, F. 2015. Starting with a handicap: effects

555 of asynchronous hatching on growth rate, oxidative stress and telomere dynamics in free-living

556 great tits. Oecologia 179: 999–1010.

557 Thomas, R. J., Lello, J., Medieros, R., Pollard, A., Seward, A., Smith, J., Vafidis, J. and Vaughan, I.

558 2017. Data analysis with R statistical software; a guidebook for scientists. – Eco-Explore, Machen,

559 Wales, UK

560 Turner, A. K. 1983. Time and energy constraints on the brood size of Swallows, *Hirundo rustica*, and

561 sand martins, *Riparia riparia.* Oecologia 59: 331-338.

562 Turner, A.K. 2006. The Barn Swallow. Bloomsbury Publishing.

563 Vafidis, J.O., Vaughan, I.P., Jones, T.H., Facey, R.J., Parry, R. and Thomas, R.J. 2014. Habitat use and

564 body mass regulation among warblers in the Sahel region during the non-breeding season. PLoS

565 ONE 9(11).

566 Witter, M.S., Cuthill, I.C. and Bonser, R.H.C. 1994. Experimental investigations of mass-dependent

567 predation risk in the European starling, *Sturnus vulgaris*. Anim. Behav. 48: 201–222.

568 Witter, M.S., Swaddle, J.P. and Cuthill, I.C. 1995. Periodic Food Availability and Strategic Regulation of

569 Body Mass in the European Starling, *Sturnus vulgaris*. Funct. Ecol. 9: 568-574.

570 Zuur, A.F., Ieno, E.N. and Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical

571 problems. Methods Ecol. Evol. 1: 3–14.

572 Zuur, A.F., Ieno, E.N. and Smith, G.M. 2007. Analysing ecological data. Springer.

573 **Error! Reference source not found.**

		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

574

575

576

577

578 **Table 1.** Model outputs for daily effects of local weather on nestling and fledgling mass. All main
579 effects for each of the weather variables were included in the global models, but only the interaction
580 terms are shown here. Significant weather-related terms are shown in bold ($P \leq 0.05$); non-
581 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*

582

583 **Table 2.** Model outputs for long-term (lifetime) effects of local weather on nestling and fledgling mass.

584 All main effects for each of the weather variables were included in the global models, but only the

585 interaction terms are shown here. Significant weather-related terms are shown in bold ($P =\le 0.05$);

586 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*

587