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How does nest-box temperature affect nestling growth rate and breeding success in a parrot?

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Abstract. Climate change is predicted to affect many species by reducing range, habitat suitability and breeding success. Cavity-nesting species, already threatened by deforestation and declining natural hollows, may be particularly at risk because they are limited in nest-site location, and climatic alterations may further reduce usability of natural cavities. It is therefore essential to determine how cavity-users may be affected. We recorded internal nest-box temperatures and modelled the relationships of four temperature parameters (relating to mean temperature, variability in temperature, low temperature extremes and high temperature extremes) with breeding success and nestling growth in an Australian cavity-nesting parrot, the Crimson Rosella (*Platycercus elegans*). We found that less extreme low temperatures resulted in heavier nestlings; however, higher mean temperatures tended to result in lighter nestlings. Greater temperature variability tended to reduce fledging success; however, no temperature variables had a clear effect on clutch size or hatching success. Our findings indicate that there may be a complex relationship between nestling growth and temperature, and although less extreme cold temperatures may benefit nestlings, continued increases in mean temperature and variability may have negative consequences.

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Introduction

Microclimate at breeding sites has been found to be a crucial factor for breeding success in many bird (such as passerines, piciformes and apodiformes) and bat species, particularly in nest-boxes and hollows (e.g. Wiebe 2001; Dawson *et al.* 2005; Ardia *et al.* 2010; Catry *et al.* 2011). In birds, suboptimal conditions during egg incubation and offspring development can result in increased incubation periods and reduced embryonic growth, hatchling mass, nestling growth, body condition and immunity, and in extreme cases, heat stress and dehydration can result in death (Grant 1982; Murphy 1985; Bull 2003; Amat and Masero 2004; Ardia *et al.* 2006, 2010; Burton 2007).

Climate change is expected to lead not only to increasing mean temperatures, but also more variable temperatures and to increases in the frequency, intensity and length of extreme weather events such as heat waves and floods (Meehl *et al.* 2000; Meehl and Tebaldi 2004; Mitchell *et al.* 2006; Hegerl *et al.* 2011; Coumou and Rahmstorf 2012). The predicted changes in weather patterns coupled with other environmental concerns (e.g. habitat destruction and deforestation) are likely to negatively impact a broad spectrum of species that are sensitive to temperature such as bats (Sedgeley 2001), reptiles (Brewster *et al.* 2013; Pike 2014) and birds (Sekercioglu *et al.* 2008; Bellard *et al.* 2012; Şekercioglu *et al.* 2012). Species that are thought to be most at risk are those geographically isolated and confined to particular habitats, and those already close to their thermal

maximum (Jiguet *et al.* 2010; De Frenne *et al.* 2013; Moritz and Agudo 2013). For example, species that are confined to cavities for nesting may be more susceptible to increased temperature variability and extremes because these changes may reduce optimal breeding locations and conditions.

Cavity-nesting species are already limited by a continuing decline in the number of available hollows due to continued habitat alteration, fragmentation and degradation (Goldingay and Stevens 2009). This has caused displacement and limited breeding success and survival of many hollow-utilising species (Kerth *et al.* 2001; Sedgeley 2001; Goldingay and Stevens 2009). In Australia alone, ~300 species of birds, bats and arboreal marsupials that utilise tree cavities are potentially at risk due to this decline in tree hollows (Goldingay and Stevens 2009). Particularly at risk are parrots, which are among the most threatened taxa due to additional pressures such as hunting and disease (Renton 2002; Eastwood *et al.* 2014). The predicted alterations to our climate are likely to shift cavity microclimates, potentially rendering them inadequate or unusable, thereby exacerbating the pressure on species that utilise them. It is therefore essential to understand how nest-site microclimate affects reproductive success in obligate cavity-nesters in order to predict and mitigate potential impacts.

The use of artificial nest-boxes is now a well accepted strategy for supplementing existing hollows, improving habitat connectivity, reintroducing locally extinct species, and promoting easy

physical access to nests when surveying species in an area or studying a target species, with the result that many threatened species and research programs now depend heavily on nest-boxes (Evans *et al.* 2002; Beyer and Goldingay 2006; Catry *et al.* 2009). Nest-box characteristics such as construction material, wall thickness, canopy cover and aspect, contribute greatly to the resulting microclimate found within them (McComb and Noble 1981; Brittingham and Williams 2000; Sedgeley 2001; Gibbons *et al.* 2002; Bull 2003), which may determine nest-site preference and breeding success (Menkhorst 1984; Kerth *et al.* 2001; Wiebe 2001; Ardia *et al.* 2006).

This study aimed to reveal how temperature variation at nest sites affects offspring growth and breeding success of a common and widely distributed hollow-breeding parrot species, the Crimson Rosella (*Platycercus elegans*). *P. elegans* has been widely studied in regards to its plumage colour diversity, vision, vocalisation and population structure (Joseph *et al.* 2008; Ribot *et al.* 2009, 2011, 2012, 2013; Berg and Bennett 2010; Knott *et al.* 2010, 2013; Carvalho *et al.* 2011). In addition, its breeding biology is well documented (Krebs 1998, 1999, 2001; Krebs and Magrath 2000). The species is a medium-sized (~35 cm long, 130 g) common parrot that occupies a wide range of mesic habitats and climatic zones in south-eastern Australia (Krebs 1998; Krebs and Magrath 2000). Like almost all parrots species, it is an obligate cavity-nester. The breeding season is mid-September to early January, with most pairs laying 3–8 eggs (Krebs 1998). The incubation period ranges from 16 to 28 days (Krebs 1998), but the range observed in our study was 14–19 days, with fledging occurring at 30–40 days old. It is an ideal study species due to its abundance, extensive early studies and willingness to breed in nest-boxes.

The objectives of this study were to determine the effects of nest-box temperature on nestling growth rates, clutch size, hatching success, and fledging success in *P. elegans* breeding in nest-boxes. We used temperature variables related to mean temperature, temperature variability (standard deviation), and high and low temperature extremes. We thereby sought to improve understanding of the effects of temperature variability and temperature extremes on reproductive success in birds, both with and without climate change. We predicted that less variable temperatures during the nestling period would result in heavier nestlings due to reduced thermoregulatory costs. We also predicted that temperature extremes would have negative effects at each reproductive stage, but that higher average temperatures might benefit reproductive success by reducing energetic costs.

Materials and methods

Ethics statement

This study conformed to the laws of Victoria, Australia (Deakin University Animal Ethics Committee approval A33-2008 and State research permit 10004759-3). The study was carried out on privately owned properties with permission.

Study sites

P. elegans nests were studied in dry sclerophyll eucalypt forests at two sites in Victoria which were ~50 km apart: Bellbrae (38.33°S, 144.26°E) and Steiglitz (37.88°S, 144.18°E). Although these sites

experience a temperate climate (Fig. 1), it is still important to investigate the potential effects of changing climate regimes, particularly as many threatened species reside in areas with similar climates (e.g. the Orange-Bellied Parrot, *Neophema chrysogaster*). Seventy-seven nest-boxes at Bellbrae and 80 at Steiglitz, which had been previously erected (Bellbrae in 2010, Steiglitz in 2008), were monitored from September to December 2011. Nest-boxes had been spaced at least 50 m apart and mounted 4–5 m from the ground on *Eucalyptus* spp. trunks, with all nest-boxes facing south-east. The nest-boxes used in this study were constructed of 19-mm treated pine and were 24 cm wide 28 cm deep × 42 cm high, with an entrance hole diameter of 7.5 cm and a sliding side door to allow us easy access to nests. A layer of red gum wood chips had been placed in each nest-box when erected.

Nestling measurements

Nest-boxes were checked weekly from 21 September 2011, which was before *P. elegans* commenced breeding. *P. elegans* lays eggs usually about two days apart and has a high level of hatching asynchrony (Krebs 1998). Nest-box checks were more frequent (every 2–3 days) closer to predicted hatching dates in order to accurately determine hatching dates. *P. elegans* made 29 breeding attempts in 25 out of our 157 nest-boxes.

After hatching, nests were checked every 2–4 days to record nestling mortality. Nestlings ($n=80$) were weighed using a Pesola scale (to nearest 0.25 g) every 4.3 ± 1.2 (s.d.) days, resulting in 376 weigh-ins. Any dead nestlings or unhatched eggs were collected and frozen for DNA analysis. Nestlings were initially marked for individual identification by trimming nails and down in specific combinations, and were later ringed with a standard metal band (Australian Bird and Bat Banding Scheme) when they had reached a suitable size. Within four days after hatching, blood (~200–400 μ L) was sampled from the brachial vein and stored in 100% ethanol for later DNA extraction and molecular sexing (see below). Disposable sterile needles were used for each individual to prevent cross-contamination. Genomic DNA was extracted from nestling blood samples using a standard ammonium acetate precipitation protocol and used for sexing using PCR as per Eastwood *et al.* (2015). Nestling sex was included in growth rate analyses.

Measuring reproductive success

We recorded three measures of reproductive success: (1) clutch size, the total number of eggs laid for each nest; (2) hatching success, the number of chicks that hatched, controlling for clutch size (eggs that had signs of predation such as beak piercings or that were squashed or destroyed were excluded, as in Krebs (1998)); and (3) fledging success, the number of chicks that fledged, controlling for brood size (nestlings alive after 32 days of age were considered fledged if absent from the nest-box at the subsequent nest visit). Out of the 29 breeding attempts, 22 nests had at least one chick hatch, and 17 nests had at least one nestling successfully fledged; however, we had sufficient temperature data for only 18 nests for clutch size and hatching success analyses and 16 nests for fledging success analyses.

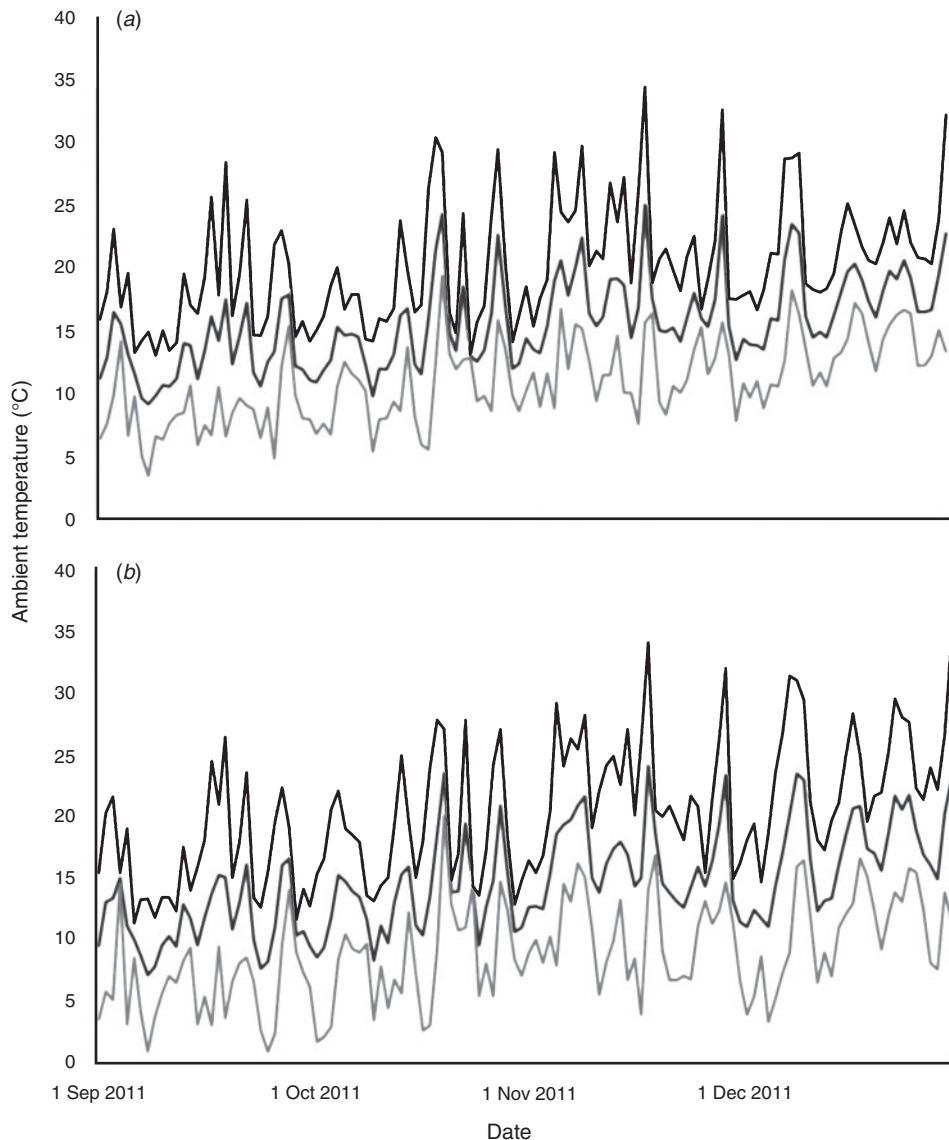


Fig. 1. Daily maximum (black), mean (medium grey) and minimum (light grey) ambient temperature for (a) Bellbrae and (b) Steiglitz during the *P. elegans* breeding season, 2011.

Nest-box temperature

Sixty-three HOBO pendant temperature data loggers (Onset Computer Corporation, MA, USA) were deployed in nest-boxes from September to February. Loggers were placed in the top left-hand corner of the nest-boxes, and set to record temperature, date and time every 30 min. All nest-boxes in which a *P. elegans* nest occurred during the study were fitted with a logger (before hatching where possible). Loggers were collected in February 2012 and the data were downloaded and analysed. A subsample of our loggers was retrospectively tested on 7 May 2014 in an ice bath (as per Wilson and Verbeek 1995, and as recommended by the manufacturer). Loggers recorded temperatures from 0.1°C to 0.6°C, with a mean of 0.34°C. Although logger accuracy can drift over time, we did not detect much difference between original loggers (mean temperature 0.37°C) and recently purchased loggers (mean temperature 0.31°C). Loggers were randomly

allocated to nest-boxes; therefore these small differences were negligible.

Statistical analysis

All analyses were performed using SPSS 22 (SPSS Inc. 2013, Chicago, IL). Dependent variables were first visually assessed for normality, following Quinn and Keough (2002). Dates were converted into Julian date for all analyses.

Four temperature variables were calculated for each developmental period within each nest-box and for the period intervening each nestling weighing (the 'weighing periods'); however, as data for the egg-laying period were limited (the period between clutch initiation and clutch completion), we instead used incubation period temperature data (date of last-laid egg to hatching date) to analyse both clutch size and hatching success. Nestling period data (hatching date to fledging date) was used for fledging success

analyses. These four temperature variables were chosen to reflect variation in the mean temperature (T_{mean}), absolute variability in temperature ($T_{\text{variability}}$; standard deviation), and the magnitude of low and high extremes of temperature within nest-boxes (T_{low} and T_{high} ; 5th and 95th percentile values respectively). As we were interested in the effects of absolute variability in temperature (i.e. not relative to mean temperature), we chose to use standard deviation as our measure of variability.

To test which combination of temperature variables best predicted reproductive success or nestling growth, we used linear models (GLM; proc. MIXED with REML estimation, Gaussian distribution and identity link function) and model selection based on the Akaike Information Criterion corrected for small sample size (AIC_c). To obtain unbiased estimates of the most important temperature effects and parameter estimates (Burnham and Anderson 2002), our candidate models included all model subsets, totalling 16 candidate models (including the ‘null’ models, which included no temperature variables). To obtain parameter estimates, model averaging was undertaken for all plausible models up to a cumulative weight of 0.9; however, only models and parameters with a weight of at least 0.1 are presented. We chose to consider models as plausible if they had a weight more

than 0.1 because our results included many models with low weights (Burnham and Anderson 2002). Variables were considered to be important based on whether the 95% confidence interval of their estimates overlapped zero and if the parameter weight was >0.9 (Burnham and Anderson 2002). Overall and marginal measures of effect size for each reproductive success top model and parameter (η^2) were obtained using proc. UNIANOVA.

To analyse nestling growth we used nestling mass controlled for age in days. Nestling growth rate was approximately linear, but reaches a plateau after 26 days (Fig. 2), so analyses were restricted to nestlings from zero to 26 days old. Temperature variables and brood size were included as fixed effects, and hatching-date was included as a fixed covariate. To account for the repeated measures from nestlings and for nestlings being clustered within nest-boxes, we used mixed-effects models with both nestling identity and nest-box identity included as random intercepts in all growth rate models. Modelling site as a random intercept made no qualitative difference to conclusions (Fig. 2), so this term was excluded from further growth rate analysis, and data from both sites were grouped together.

Site was included as a fixed effect (as some models failed to converge when site was treated as a random effect), and lay-date was included as a fixed covariate (to control for seasonal confounds) for all reproductive success models. Clutch size was included as a fixed effect for all hatching success models, and brood size was included as a fixed effect for all fledging success models. *P. elegans* generally has only one breeding attempt and most breeding attempts overlapped temporally, therefore we assumed that each breeding pair was included in the analysis only once. Means and estimates are presented with standard error unless otherwise noted.

Results

Nestling growth

Two plausible models relating temperature to nestling growth were identified, with a combined likelihood of 76.8%. All top models included T_{mean} , $T_{\text{variability}}$ and T_{low} . The best model contained all four variables (Table 1). Nestling growth was positively related to higher T_{low} values, with a predicted mass increase of over 2 g per °C increase (Table 2, Fig. 3). Confidence intervals for T_{mean} overlapped zero but only by a small amount, indicating a tendency for T_{mean} to negatively affect nestling growth (Table 2). All except one of the hypothesised models relating temperature variables to nestling growth performed better than the null model, which was ranked 15th out of the 16 candidate models (Table 1). The value of ΔAIC_c for the null

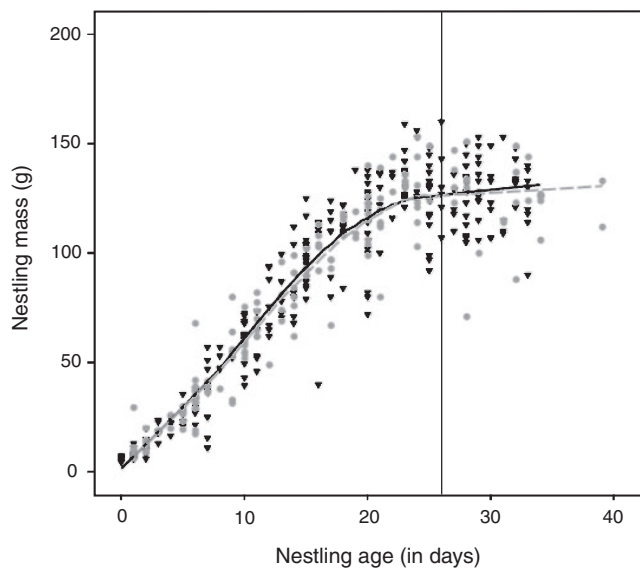


Fig. 2. Nestling mass versus nestling age in days for each weighing visit at Bellbrae (black triangles, weigh-ins $n=263$) and Steiglitz (grey circles, weigh-ins $n=113$), with Loess curve fit for site (Bellbrae: black; Steiglitz: grey dashed). Age of 27 days (vertical line) was considered the end of the linear growth phase.

Table 1. Plausible models and null model for growth rate of nestling *P. elegans* using nest-box temperature variables calculated for each weighing period

The weighing period is the period between each weighing (4.3 ± 1.2 , s.d., days). All models included nestling age in days and hatching-date as fixed covariates and brood size as a fixed effect. Abbreviations: T_{mean} , mean temperature; $T_{\text{variability}}$, calculated as standard deviation; T_{low} , low extreme temperature, calculated as 5th percentile temperature, T_{high} , high extreme temperature, calculated as 95th percentile value

Dependent variable	Model	AIC_c	ΔAIC_c	Akaike weight, w	Model likelihood
Mass (g, controlled for nestling age) (Weigh-ins $n=376$)	$T_{\text{mean}} + T_{\text{variability}} + T_{\text{low}} + T_{\text{high}}$	2845.511		0.486	
	$T_{\text{mean}} + T_{\text{variability}} + T_{\text{low}}$	2846.603	1.09	0.282	0.58
	Null model (rank: 15 of 16)	2902.692	57.18	0.000	0.00

Table 2. Model-averaged estimates for nest-box temperature parameters present in the plausible models for growth rate of nestling *P. elegans*
 Bold type indicates confidence intervals that do not overlap zero. All models included nestling age in days and hatching-date as fixed covariates and brood size as a fixed effect. Temperature variables were calculated for the periods between each weighing period (4.3 ± 1.2 s.d. days). Abbreviations: T_{mean} , mean temperature; $T_{\text{variability}}$, calculated as standard deviation; T_{low} , low extreme temperature, calculated as 5th percentile temperature; T_{high} , high extreme temperature, calculated as 95th percentile value

Dependent variable	Parameter	Estimates	s.e.	Parameter weight, w	Lower 95% CI	Upper 95% CI
Mass (g, controlled for nestling age) (Weigh-ins $n = 376$)	T_{low}	2.549	0.899	0.990	0.780	4.319
	T_{mean}	-1.375	0.805	0.912	-2.960	0.210
	$T_{\text{variability}}$	0.536	1.651	0.852	-2.712	3.785
	T_{high}	0.089	0.357	0.622	-0.613	0.792

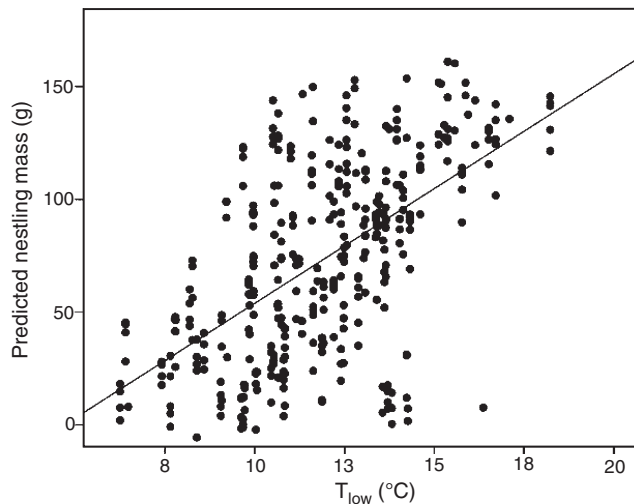


Fig. 3. Relationship between mass of *P. elegans* nestlings and low temperature extremes (T_{low} ; 5th percentile values) inside nest-boxes (weigh-ins $n = 376$). Nestling mass shown are predicted values from the most plausible model, controlling for hatch-date (jdate), sex, age, sex \times age and brood size. Basic regression line is used for reference only.

model is greater than 57, which suggests that the null model is highly implausible compared with the two most well supported models (Burnham and Anderson 2002).

Reproductive success

The most well supported model (Akaike weight 0.175–0.556) for each measure of reproductive success included all four temperature variables, suggesting that the hypothesis best supported by our data was that all temperature variables contributed to predicting reproductive success (Table 3). No temperature parameter estimate was found to have a confidence interval that did not overlap zero (Table 4). Furthermore, model-averaged standard errors were often larger than the estimated effect size (Table 4). However, $T_{\text{variability}}$ showed a tendency to negatively affect fledging success (95% CI estimate -8.703 to 0.425 , parameter weight 0.955), and was also the most highly weighted predictor for all reproductive success variables.

Top model R^2 values were similar across clutch size (0.639), hatching success (0.617) and fledging success (0.736), suggesting that our models containing all four temperature parameters do explain a high proportion of the variance in each measure of reproductive success. ΔAIC_c values of null models compared with the top model for each reproductive success measure are

greater than 5, and in the case of fledging success, greater than 10, suggesting that for all three reproductive success measures the null models were much less supported by the data compared with the top models (Burnham and Anderson 2002).

Discussion

Our study demonstrates that nest-box temperatures are potentially important for some aspects of reproduction in a common, widespread Australian parrot, most notably in terms of nestling growth rates. The clearest finding arising from our study was that less extreme low temperature in nest-boxes (T_{low}) was an important predictor of increased nestling growth rate. In addition, there were indications of negative relationships between nestling growth and mean nest-box temperature (T_{mean}), and between temperature variability in nest-boxes ($T_{\text{variability}}$) and fledging success; however, confidence intervals for these parameters slightly overlapped zero, suggesting that further investigation is required. In contrast, we found no clear evidence of relationships between clutch size and hatching success and any individual nest-box temperature parameters. Under scenarios of a changing climate, predictions generally focus on rising mean temperatures and increased extremes, with heatwaves and other extreme climatic events predicted to occur more often in southern Australia, and many other locations worldwide (Meehl and Tebaldi 2004; McKechnie and Wolf 2010; IPCC 2013). Our study is one of the first to investigate the effects of a comprehensive number of temperature variables on all major stages of nestling growth and reproduction, in addition to the effects of mean temperatures.

Nestling growth rates

The positive effects of less extreme low temperatures on nestling growth are consistent with Ardia *et al.* (2010), and Brewster *et al.* (2013), who found that experimentally cooled nests and high-cost thermoregulation treatments resulted in nestlings and lizard hatchlings respectively with lower mass. This is most likely due to an increased amount of energy spent on thermoregulation in environments with low temperatures, preventing young organisms from allocating more energy to growth (Dawson *et al.* 2005; Cunningham *et al.* 2013). This suggests that cold spells could be most detrimental to nestlings, which could result in setbacks in growth and delayed fledging. These analyses included brood size as a covariate; however, our findings were unchanged when brood size was excluded, indicating that they are robust. Our potential finding that higher mean temperatures tended to be negatively related to growth rates contradict many studies that have found that nestling body mass is positively related to mean temperature

Table 3. Plausible models and null models for clutch size, hatching success and fledging success of *P. elegans*, using nest-box temperature variables from the incubation period and the nestling period

Site was included as a fixed effect for all analyses. Clutch size was included as a covariate for hatching success analyses, and number of chicks was included in fledging success analyses. Abbreviations: T_{mean} , mean temperature; $T_{\text{variability}}$, calculated as standard deviation; T_{low} , low extreme temperature, calculated as 5th percentile temperature; T_{high} , high extreme temperature, calculated as 95th percentile value

Dependent variable	Model	AIC _c	Δ AIC _c	Akaike weight, w	Model likelihood
No. of eggs ($n = 18$)	$T_{\text{mean}} + T_{\text{variability}} + T_{\text{low}} + T_{\text{high}}$	59.630		0.175	
	$T_{\text{mean}} + T_{\text{variability}} + T_{\text{low}}$	60.126	0.50	0.137	0.78
	$T_{\text{mean}} + T_{\text{variability}} + T_{\text{high}}$	60.533	0.90	0.111	0.64
	Null model (rank: 15 of 16)	65.140	5.51	0.011	0.06
No. of chicks (controlled for clutch size) ($n = 18$)	$T_{\text{mean}} + T_{\text{variability}} + T_{\text{low}} + T_{\text{high}}$	60.322		0.249	
	$T_{\text{mean}} + T_{\text{variability}} + T_{\text{low}}$	61.417	1.10	0.144	0.58
	$T_{\text{variability}} + T_{\text{low}} + T_{\text{high}}$	61.719	1.40	0.124	0.50
	Null model (rank: 16 of 16)	67.814	7.49	0.006	0.02
No. of fledglings (controlled for brood size) ($n = 16$)	$T_{\text{mean}} + T_{\text{variability}} + T_{\text{low}} + T_{\text{high}}$	46.285		0.556	
	$T_{\text{variability}} + T_{\text{low}} + T_{\text{high}}$	48.303	2.02	0.203	0.36
	Null model (rank: 14 of 16)	56.631	10.35	0.003	0.01

Table 4. Model-averaged estimates for nest-box temperature parameters present in the plausible models for clutch size, hatching success and fledging success of *P. elegans*

Site was included as a fixed effect for all analyses. Clutch size was included as a covariate for hatching success analyses, and no. of chicks was included in fledging success analyses. Temperature variables were calculated from the incubation and nestling periods. Partial Eta² was calculated from the top model (see Table 3). Abbreviations: T_{mean} , mean temperature; $T_{\text{variability}}$, calculated as standard deviation; T_{low} , low extreme temperature, calculated as 5th percentile temperature, T_{high} , high extreme temperature, calculated as 95th percentile value

Dependent variable	Parameter	Estimates	s.e.	Parameter weight, w	Lower 95% CI	Upper 95% CI	Partial Eta ²
No. of eggs ($n = 18$)	$T_{\text{variability}}$	0.484	1.116	0.818	-1.861	2.828	0.004
	T_{mean}	-0.048	0.545	0.628	-1.192	1.097	0.007
	T_{high}	0.164	0.229	0.581	-0.317	0.644	0.036
	T_{low}	0.113	0.303	0.571	-0.525	0.750	0.010
	$T_{\text{variability}}$	-0.351	1.378	0.830	-3.246	2.543	0.004
No. of chicks (controlled for clutch size) ($n = 18$)	T_{low}	0.409	0.752	0.723	-1.171	1.988	0.091
	T_{mean}	0.093	0.608	0.677	-1.183	1.370	0.001
	T_{high}	-0.206	0.245	0.615	-0.721	0.309	0.079
	$T_{\text{variability}}$	-4.139	2.153	0.955	-8.703	0.425	0.055
No. of fledglings (controlled for brood size) ($n = 16$)	T_{low}	-1.356	2.309	0.886	-6.252	3.539	0.043
	T_{high}	0.750	4.085	0.836	-7.909	9.409	0.146
	T_{mean}	0.356	3.202	0.731	-6.431	7.144	0.005
	$T_{\text{variability}}$						

(Siikamäki 1996; Eeva *et al.* 2002; Dawson *et al.* 2005; Pipoly *et al.* 2013; Chausson *et al.* 2014). These studies were all conducted in the Northern Hemisphere in colder regions than our study, which could explain this contradictory finding. A study by Murphy (1985), also conducted in the Northern Hemisphere but in a region that experiences a similar climate to our study sites, did find that mean temperature had a negative effect on nestling mass in Eastern Kingbirds. This suggests that it is essential to take the climatic profile of study sites into account when comparing findings across studies. Additional studies investigating the effects of temperature should be undertaken in warmer regions and in the Southern Hemisphere to increase knowledge that can be used to implement local management programs with confidence.

Reproductive success

Clutch size is perhaps one of the most well studied life-history traits of birds (e.g. Hochachka 1990; Winkler and Allen 1996; Krebs 1998; Winkler *et al.* 2002; Masello and Quillfeldt 2004;

Valkama and Korpimäki 1999). Although temperature can affect clutch size indirectly via influencing food availability (Winkler *et al.* 2013), internal nest cavity temperature has also been found to be correlated with clutch size, potentially because cooler cavities may be more energetically costly to females (Wiebe 2001). Our findings that temperature did not affect clutch size corresponds with the findings of Brown and Brown (1999) and Chase *et al.* (2005); however, Eeva *et al.* (2002) did find that clutch sizes of a population of Pied Flycatcher (*Ficedula hypoleuca*) demonstrated a positive relationship with greater mean temperatures. Eeva *et al.* (2002) carried out this study on two populations of pied flycatcher, and this relationship was observed within the population located in a subarctic zone, but not within the population located in a temperate zone. This suggests that birds may adjust clutch size only if they experience severe conditions, although Wiebe (2001) did find a relationship between clutch size and greater mean cavity temperature in Northern Flickers (*Colaptes auratus*) in a temperate region.

Mean ambient temperature has been found to be both positively (e.g. Eeva *et al.* 2002) and negatively (e.g. Chase *et al.* 2005) related to hatching success, which may be attributed to differences in climate profiles or nesting strategy. We found no evidence of a relationship between temperature and hatching success, which was also the result of a similar study by Wiebe (2001). The detrimental effects of low temperatures and temperature variability on embryo development during incubation are well known (Carey 1996; Hepp *et al.* 2006; Nord and Nilsson 2011). Low temperatures result in greater heat loss from eggs, increasing the time and energy required to reheat to ideal temperatures (Carey 1996; Pipoly *et al.* 2013; Windsor *et al.* 2013). This can also lead to reduced parental incubation attendance, and therefore extended incubation periods, as they allocate more time to foraging activities (Ardia *et al.* 2010). However, the length of incubation periods in *P. elegans* does not decrease over the season (Krebs 1998), suggesting that any extra female energy costs may be offset by male foraging efforts during incubation (Krebs 2001). If *P. elegans* females are therefore more attentive incubators, this could explain why no effect of temperature was found in our study.

Both warmer and cooler temperatures have been found to affect fledging success (e.g. Eeva *et al.* 2002; Dawson *et al.* 2005; Ardia *et al.* 2006, 2010; Perez *et al.* 2008; DuRant *et al.* 2012; Cunningham *et al.* 2013). This is likely due to increased thermoregulatory costs (e.g. Catry *et al.* 2011; Cunningham *et al.* 2013); however, the direction of the response may depend on the species, and habitat. Although we found no clear relationship in our study, our findings suggest that greater temperature variability, as measured by standard deviation, may have a tendency to reduce fledging success. To our knowledge, no study has investigated the effect of standard deviation on fledging success; however, our findings suggest that it may be useful to include this temperature variable in future studies (Vasseur *et al.* 2014). A multiyear study located in a more variable climate may be necessary to fully explore this aspect.

In conclusion, global climate change is predicted to cause an increase in environmental variability and unpredictability (Meehl *et al.* 2000; Hegerl *et al.* 2011; IPCC 2013), but there remains a paucity of data about how this will affect wildlife populations. Many studies focus simply on mean temperature; however, our findings highlight the need to investigate a range of temperature parameters. For example, our results suggest that investigating methods to minimise the intensity of low temperature extremes could have important implications for management of cavity-nesting species and the increasing numbers of conservation and species-recovery programs that depend heavily on nest-boxes. Our findings highlight the need for future studies to analyse temperature in detail to better determine what effects climate change and associated extreme events will have on reproducing populations, and which species may be most sensitive. As has been found in lizards (Iraeta *et al.* 2007) and bats (Williams and Brittingham 1997; Kerth *et al.* 2001; Sedgeley 2001), birds may also exert active control over nest temperatures by selecting cavities with optimal temperature profiles (Hooge *et al.* 1999; Ardia *et al.* 2006) and future work should investigate the capacity of birds to exert such choice and the subsequent effects of it on reproductive success. Finally, improving the thermal environment of nest-boxes, including

improved insulative properties, should be an important consideration in management of obligate cavity-nesters to improve populations' ability to cope with unexpected, temporary climate extremes such as heat waves (Welbergen *et al.* 2008; Garnett *et al.* 2013). Such improved design may be particularly effective to buffer small populations, which are highly vulnerable to stochastic disturbances, and which may already rely heavily on artificial nests.

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