## Parental cooperation in a changing climate: fluctuating environments predict shifts in care division

### Journal:
*Global Ecology and Biogeography*

### Manuscript ID
GEB-2016-0012

### Manuscript Type:
Research Papers

### Date Submitted by the Author:
10-Jan-2016

### Complete List of Authors:
- Vincze, Orsolya; Debreceni Egyetem, Department of Evolutionary Zoology and Human Biology; Universitatea Babes-Bolyai, Hungarian Department of Biology and Ecology
- Kosztolánya, András; Debreceni Egyetem, Department of Evolutionary Zoology and Human Biology; Szent Istvan Egyetem, Department of Ecology
- Barta, Zoltán; Debreceni Egyetem, Department of Evolutionary Zoology and Human Biology
- Küpper, Clemens; University of Graz, Institute of Zoology
- AlRashidi, Monif; University of Ha'il, Department of Biology
- Amat, Juan; Estacion Biologica de Donana CSIC, Department of wetland Ecology
- Argüelles Ticó, Araceli; University of Bath, Department of Biology and Biochemistry
- Burns, Fiona; RSPB Centre for Conservation Science, RSPB Centre for Conservation Science
- Cavitt, John; Weber State University, Department of Zoology
- Conway, Warren; Texas Tech University, Department of Natural Resources Management
- Cruz-López, Medardo; Universidad Nacional Autónoma de México, Posgrado en Ciencias del Mar y Limnología
- Desuec-Medrano, Atahualpa Eduardo; Universidad Nacional Autónoma de México, Posgrado en Ciencias del Mar y Limnología
- dos Remedios, Natalie; University of Sheffield, Department of Animal and Plant Sciences
- Figuerola, J; CSIC, Sevilla, Wetland Ecology
- Galindo-Espinosa, Daniel; Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas
- García-Peña, Gabriel E.; CESAB- Centre de Synthèse et d’Analyse sur la Biodiversité, CESAB- Centre de Synthèse et d’Analyse sur la Biodiversité; Centre de Recherche IRD -UMR MIVEGEC, Maladies Infectieuses et Vecteurs: Ecologie, Génétique, Evolution et Contrôle
- Del Angel, Salvador Gómez; Universidad Nacional Autónoma de México, Posgrado en Ciencias del Mar y Limnología
- Gratto-Trevor, Cheri; Environment Canada, Prairie and Northern Wildlife Research Centre
- Jönsson, Paul; Lund University, Department of Biology
- Lloyd, Penn; University of Cape Town, Percy FitzPatrick Institute
- Montalvo, Tomás; Agència de Salut Pública de Barcelona, Servei de
| Keywords: | global change, climate, environmental stochasticity, seasonal environment, parental care, parental cooperation |
Parental cooperation in a changing climate: fluctuating environments predict shifts in care division


¹ MTA-DE “Lendület” Behavioural Ecology Research Group, Department of Evolutionary Zoology and Human Biology, University of Debrecen, Debrecen, H-4032, Hungary

² Evolutionary Ecology Group, Hungarian Department of Biology and Ecology, Babeş-Bolyai University, Cluj Napoca, RO–400006, Romania

³ Department of Ecology, Faculty of Veterinary Science, Szent István University, Budapest, H-1077, Hungary

⁴ Institute of Zoology, University of Graz, Universitätsplatz 2, 8010 Graz, Austria

⁵ Department of Biology, Faculty of Science, University of Ha’il, Ha’il, PO Box 2440, Saudi Arabia

⁶ Estación Biológica de Doñana (EBD-CSIC), calle Américo Vespucio s/n, Sevilla, 41092, Spain

⁷ Biodiversity Lab, Department of Biology and Biochemistry, University of Bath, Bath, BA1 7AY, United Kingdom

⁸ RSPB Centre for Conservation Science, RSPB, The Lodge, Sandy, Bedfordshire, SG192DL, United
of Life Sciences, Beijing Normal University, Beijing, 100875, China

State Key Laboratory of Biocontrol and College of Ecology and Evolution, Sun Yat-Sen University, Guangzhou, 510275, China

Manomet Center for Conservation Sciences, Manomet, MA 02345, USA

Schutzstation Wattenmeer Nationalparkhaus, Husum, D-25813, Germany

Istituto Superiore per la Protezione e Ricerca Ambientale (ISPRA), Ozzano dell’Emilia BO, 40064, Italy

School of Biology, University of St Andrews, St Andrews, KY16 9TH, United Kingdom

Point Blue Conservation Science, Petaluma, CA 94954, USA

Centre for Integrative Ecology, School of Life and Environmental Sciences, Faculty of Science, Engineering and the Built Environment, Deakin University, Burwood, 3125, Australia

Quest University Canada, Squamish, 3200, Canada

Department of Biology, University of Toliara, Toliara, Madagascar

E-mail addresses: orsolya.vincze@vocs.unideb.hu (OV), andras.kosztolanyi@gmail.com (AK), barta.zoltan@science.unideb.hu (ZB), clemens.kuepper@uni-graz.at (CK), mm_alrashedi@yahoo.com (MA), amat@ebd.csic.es (JAA), araceli.a.tico@gmail.com (AAT), fionaburns_21@hotmail.com (FB), JCAVITT@weber.edu (JC), warren.conway@ttu.edu (WCC), tod472@gmail.com (MCL), desucre@unam.mx (AEDM), ndosremedios@hotmail.co.uk (NdR), jordi@ebd.csic.es (JF), dgalindoe@gmail.com (DGE), ggp01@gmail.com (GGP), salvachavin@hotmail.com (SGdA), Cheri.Gratto-Trevor@ec.gc.ca (CGT), pauleric.jonsson@gmail.com (PJ), penn.lloyd@gmail.com (PL), tmontal@aspb.cat (TM), jep33@bath.ac.uk (JEP), raya.pruner@gmail.com (RP), quepinjia@gmail.com (PQ), liuy353@mail.sysu.edu.cn (YL), saalfeldst@gmail.com (STS), r.schulz@schutzstation-wattenmeer.de (RS), lorenzo.serra@isprambiente.it (LS), jsc20@st-andrews.ac.uk (JSC),
lstenzel@prbo.org (LS), mike.weston@deakin.edu.au (MAW), maiyasue@gmail.com (MY),
samazefania@yahoo.fr (SZ), T.Szekely@bath.ac.uk (TS)

Keywords
global change, climate, environmental stochasticity, seasonal environment, parental care, parental cooperation

Running head: Parental cooperation in fluctuating climate

*Correspondence to: Orsolya Vincze, Email: orsolya.vincze@vocs.unideb.hu, Tel: +36-52-512900/

Abstract word count: 201

Word count of the main body: 5096

Number of references: 56
ABSTRACT

Aim Parental care improves offspring survival and therefore has a major impact on reproductive success. Whilst the influence of ambient environment on parental care is increasingly recognised, the impacts of environmental fluctuations remain largely unexplored. Assessing the impacts of environmental stochasticity, however, is essential for understanding how populations will respond to climate change. Here we investigate the influence of environmental stochasticity on biparental care in a worldwide avian genus.

Location Global

Methods We assembled data on biparental care in 36 plover populations (Charadrius spp.), from six continents, collected over several decades between 1981 and 2012. Using a space-for-time approach we investigate how average temperature, temperature stochasticity (i.e. year to year variation) and seasonality during the breeding season influences parental cooperation during care.

Results We show that both average ambient temperature and its fluctuations influence parental cooperation during incubation. Male care relative to females increases with both mean ambient temperature and stochasticity in temperature. Remarkably, local climatic conditions fully explained within-species, population differences in parental cooperation, but not differences among species.

Main conclusions Taken together, these results imply that climate change might have a multifaceted influence upon the reproductive behaviour and demography of populations by influencing parental care strategies and breeding systems.

INTRODUCTION

Climate change influences the ecology and life-history of animals (Both & Visser 2001, Bradshaw & Holzapfel 2006; Dunn & Winkler 2010). It is associated with phenological shifts in life-history (e.g. earlier spring and/or later autumn migration, earlier breeding), changes in geographical ranges and
For Peer Review

physiology, as well as population trends (Walther et al., 2002; Winkler et al., 2002; Végvári et al., 2010; Thompson et al., 2013; Vasseur et al., 2014; IPCC, 2014; Lawson et al., 2015). Although climate change has severe impacts on natural systems, our knowledge about how animals responds behaviourally to altered climate is surprisingly limited. Monitoring behaviour would however enable us to predict to what extent can behavioural plasticity mitigate the effects of climate change.

Investigations of climate change often only focus on the impacts of average temperatures on populations (Walther et al., 2002). Nevertheless, there is a growing awareness that increased temperature variability, as well as a greater frequency and magnitude of climate extremes may also have a significant effect on biological systems (Lawson et al., 2015, Thompson et al., 2013; Vasseur et al., 2014; IPCC 2014). Environmental uncertainty appears to increase with changing climatic conditions (Thompson et al., 2013; Vasseur et al., 2014; Lawson et al., 2015), therefore temperature fluctuations may represent a potentially large, but to date mostly neglected threat to living organisms. In this study we aim to understand how animals respond to climate change in terms of behaviour and how behavioural plasticity may mitigate the ecological impact of climate change. We investigate parental care that is a major contributor to reproductive success in a wide range of taxa. Therefore, parental behaviour might represent an important link between climate change and its impacts on populations, and it might change both in function of both average climatic conditions, as well as with its between-year and within-season variation (stochasticity and seasonality).

Parental care (i.e. parental behaviour that enhances the fitness of offspring and evolved for this function) is one of the most diverse social behaviours (Clutton-Brock 1991; McGraw et al., 2010; Royle et al., 2012). There is immense variation in the type and duration of care parents provide, the timing and duration of care-giving by each sex, and in ecological and morphological adaptations associated with
Whilst parental behaviour has been studied extensively in wild populations (Royle et al., 2012), evidence on how climate influences parental strategies is scant. Theoretical and empirical studies suggest that climate influences both the costs of care, i.e. the time and energy parents spend on rearing the young and the benefits of care, i.e. improved survival and recruitment of young (Clutton-Brock, 1991; Bonsall & Klug, 2011; Klug et al., 2012). For instance, ambient temperature may influence the energetic costs of care (e.g. food provisioning, offspring brooding), and thus affect parental survival (Webb et al., 2002; Bonsall & Klug, 2011; Klug et al., 2012). Climatic conditions also influence the dependence of young on care, that particularly increases in extremely cold or hot climates, or during times of resource shortages. Parental protection and provisioning substantially improve offspring survival under these harsh conditions, as opposed to more favourable conditions (Wilson, 1975; Clutton-Brock, 1991; Alrashidi et al., 2011, Bonsall & Klug, 2011). Although theoretical models suggest that increased climate variability will influence life-history trade-offs and thus parental care (Bonsall & Klug, 2011; Klug et al., 2012; Tökölyi et al., 2012), surprisingly little is known about the impact of these fluctuations on wild populations.

To explore the impact of climate on parental care, we investigate incubation behaviour, the most common form of care in birds (Deeming, 2002; Székely et al., 2013). In nearly all bird species one (or both) parents incubate the eggs for several weeks, and in some cases for over two months (Deeming, 2002). By incubating the eggs, the parents keep egg temperature near the optimal for embryonic development by turning and warming or cooling the eggs in cold or hot climates, respectively (Deeming, 2002; AlRashidi et al., 2011; Vincze et al., 2013; Ghalambor & Martin, 2002; Royle et al., 2012). Ambient temperature is expected to have a particularly significant impact on incubation in ground-nesting birds, because their eggs and the incubating parent are not buffered against extreme
temperatures (Webb 1987; Deeming 2002; AlRashidi et al., 2011). In environments with ambient temperatures close to optimal embryonic development (35-39°C: Webb, 1987), in the absence of other constraints, one parent may provide sufficient incubation (Deeming 2002; AlRashidi et al., 2011; Vincze et al., 2013). If the environmental conditions, however, deviate from the optimal in either direction, one would expect increased parental effort by both sexes. However, male involvement in parental care during incubation is usually less remarkable than that of females, providing them with increased potential to alter their effort if needed (Auer et al., 2007). Consequently, we expect males' share relative to females' to increase under harsh ambient conditions. Under harsh environmental condition we mean high or low average temperatures or high interannual fluctuations of temperatures (stochasticity), since high between-year environmental fluctuations may increase the probability of extreme events to occur. Additionally, we test the effect of within breeding season environmental change. We predict increased male share in less seasonal, as well as in highly seasonal environments, in contrast to environments with medium seasonality. Under constant environmental circumstances extended parental care is predicted for both sexes as part of the tropical life-history syndrome (Wilson 1985), therefore in less seasonal environments male share should increase. Highly seasonal environments on the other hand restrict breeding time and remating opportunities, therefore it might increase the value of current relative to future broods. Therefore, highly seasonal environments may also select for increased male share relative to females.

In this study we use data from 36 plover populations. Plovers (Charadrius spp.) are ground nesting shorebirds with body mass ranging from approximately 20g to 50g. The ancestor of this monophyletic group likely evolved in temperate or cold climates of the Northern hemisphere (dos Remedios et al., 2015). Plovers breed on all continents except Antarctica in habitats as varied as arctic tundra, temperate
For Peer Review

181 grassland, tropical beaches, salt marshes, sand dunes, semi-deserts, deserts and high altitude mountain
182 lake shores (Piersma & Wiersma 1996). This immense variation in breeding environment provides an
183 excellent opportunity to conduct a geographically large-scale study, capturing a substantial range of
184 global ecological diversity. Plovers usually lay 2-4 eggs in uninsulated scrapes. Incubation is usually
185 carried out by both parents, although the extent of male involvement in incubation is highly variable
186 among species and populations (Vincze et al., 2013). In addition, the share of incubation by each sex
187 may vary throughout the day: in most species males tend to incubate at night, whereas females carry out
188 most of the daytime incubation (Vincze et al., 2013; but see St Clair et al., 2010a).

189 Here we investigate how climate influences parental behaviour using an extensive data set on parental
190 care that cover temperate and tropical habitats in both the northern and southern hemispheres (between
191 55°N to 52°S latitude, and between 145°E to 121°W longitude). To see how climate influence incubation
192 behaviour, we used the space-for-time substitution approach, i.e. we infer temporal trends from spatial
193 data, a powerful method in ecology (Pickett, 1989). First, we establish that how the division of parental
194 care varies across species, populations and over the day. Second, we test whether ambient temperature
195 and fluctuations in temperature influence the division of care between males and females.

196 METHODS

197 Fieldwork

198 Fieldwork was carried out in 36 breeding populations, and ranged from one to 16 breeding seasons per
199 population (Table S1). Parents were captured on their nest using funnel traps, noose mats, box traps or
200 bownet traps while incubating (see Székely et al., 2008 for general methodology, and specific
201 references in Table S1). For each captured bird we recorded the time of capture and sex of the captured
202 individual. In three populations (Florida, Monterey Bay, Cape Peninsula) capture data were augmented
by opportunistic observations of the incubating parent. Sex determination was based on plumage characteristics in the field and/or measurements (e.g. vent), sex-specific DNA markers (following methods in Parra et al., 2014; Gratto-Trevor, 2011), and, in a few cases, based on observations of copulation behaviour (Table S1).

Egg-laying date was defined as the date of clutch completion. This was either known, for nests that were found during egg-laying, or estimated by floating eggs or measuring egg mass relative to egg size (Székely et al., 2008; Fraga & Amat, 1996). Egg-laying dates were standardised separately for each population by subtracting the mean and dividing by the standard deviation of laying dates for a given population. Since males have a greater tendency to be at the nest during egg-laying and egg-hatching (Székely T & Kosztolányi A, pers. obs), we only included nests that were incubated for at least three days and but not longer than 20 days (incubation usually lasts for 25-26 days in small plovers, Piersma & Wiersma, 1996). If an individual was captured (or observed) several times, we only included its first record, in order to exclude birds with potentially altered behaviour due to previous disturbance. To investigate daily patterns of incubation behaviour, we divided the day into twelve 2-hour time periods following previous analyses of incubation patterns in small plovers (AlRashidi et al., 2011; Vincze et al., 2013). Records between 00h and 04h were not included in data analyses, since we lacked such data from most populations. To estimate parental care division between the sexes, we used the sex of incubating parent as binary response variable in statistical models. In total, 5,591 individuals were included in the dataset (Table S1).

**Consistency between captures and behavioural observations**

To test whether capture times reflected the daily routine of shared incubation between the sexes, we compared male share as estimated based on capture data with male share as estimated based on
continuous behavioural observations in six populations of two species, from which both capture data and behavioural data were available (see Vincze et al., 2013 for details on behavioural observations). Based on capture data, male share (%, capture) was calculated as the percentage of male captures of all captures (males plus females) at the nests during a given 2-hour time period. Based on behavioural observations, male share (%, behaviour) was calculated as the % of time when males incubated of the total time the nest was incubated by either parent in a given 2-hour time period. The relationship between capture-based and behavioural observation-based male share estimates was analysed using linear regressions for the six populations separately, where each 2-hour time period represented a datum. These data points were weighted by the number of captures in each 2-hour time period, since the precision of the male share (%, capture) estimate is expected to increase with the total number of individuals captured in a given time period.

**Climate data**

We extracted ambient temperature data from the University of East Anglia Climate Research Unit database (CRU, http://www.cru.uea.ac.uk/; version 3.10.01; Mitchell & Jones, 2005). The CRU database is a global dataset containing interpolated monthly average temperatures (°C) from 1901 onward in a grid of spatial coordinates (0.5 x 0.5 degrees). For each population we selected temperatures from 20 years prior to the last year of data collection (including the latter); this seemed sufficient to represent the ambient temperatures the plovers experienced in our study given that the largest temporal dataset based on captures spanned 16 years. Since our study focused on parental behaviour, we only used ambient temperatures from those months when capture data were collected in each population; these months are referred to as ‘the breeding season’. Using the same number of years for each population enabled us to estimate the three climate variables used here (see below) with similar precision in each population, irrespective of the number of data collection years in each of these.
Note that although results presented are based on climate data of 20 years, we carried out sensitivity analyses by repeating the analyses using 15, 10 and 5 years climate data prior to the last year of field data collection. These models yielded highly consistent results (see SI Appendix, Table S2).

We derived three variables to characterise ambient environment. (i) Average temperature at each site refers to mean temperature over the breeding season, calculated from monthly means for each breeding season and averaged over 20 years. (ii) Between-year variation was calculated as the standard deviation of each month’s average temperature across the 20 years, averaged over the breeding season for each population. (iii) Within-season temperature variation was obtained by calculating the average temperature for each month of the breeding season over 20 years, and then calculating the difference between the maximum and minimum monthly average temperatures. Therefore, the latter two variables refer to the average between-year and within-season variation in ambient temperature during breeding at a given site. Climate variables tend to be correlated (see for example Tökölyi et al., 2014), therefore to test whether collinearity exists in models containing all three temperature variables, we calculated variance inflation factors (VIFs) for models without interactions, using the “vif.mer” function (available at: https://github.com/aufrank/R-hacks/blob/master/mer-utils.R, last accessed on: 15 September 2014) in R (R Core Team, 2014). None of the three climatic variables had VIF > 2.52. Additionally, none of the correlation coefficients between pairs of climate variables across populations exceeded 0.55 (Pearson correlation). Therefore, collinearity between temperature variables does not seem to be a major issue in our analyses.

**Statistical analyses**

Since no population-level phylogenetic hypothesis is available for the 36 plover populations studied here, we used mixed-effects models to analyse relationships between care division and environmental
data. To account for the phylogenetic non-independence we included population and species identity as random factors. We used the sex of parents (male or female) captured on the nest as the response variable in binomial models. Species, population and nest identity were included as nested random factors in all models. Although we only used one capture per individual, nest identity was included as a random factor in the models to control for potential non-independence of male and female behaviour for a given nest. Time period was included in models as a fixed factor with 10 levels (i.e. 2 hour windows, between 04h and 24h). The three temperature variables were standardised, using the “scale” function implemented in R, to ease model fitting and comparing the effects. The standardised variables were included in the models as second order orthogonal polynomials, because of the expected non-linear effects (see above, Vincze et al. 2013). Although we also tested the effects of laying date, it was excluded from further models because it did not correlate with the sex of the parent captured.

We built four mixed effects models. First, to test how care division varies throughout the day and across species and populations we constructed a model that included time period and the random factors of species, population and nest IDs (model 1). Second, to test whether the daily pattern of incubation differed between plover species and populations, we built two models: in one of these models additionally to the terms in model 1 we included the species x time period interaction (model 2), whereas in the other the population x time period interaction was included (model 3).

Third, to investigate the effects of ambient temperature, and its fluctuations between years and within-seasons, we constructed a model (model 4) that included the time period factor, the three temperature variables (i.e., mean, within-season and between year variation), and two-way interactions between the time period and temperature variables. The significance of each predictor was assessed by removing it from the model and comparing the resulting model to the original using likelihood ratio statistics (see
Mixed models were built using the “glmer” function, as implemented in the “lme4” package (version 1.1-7, Bates et al., 2015) in R (version 3.1.1, R Core Team, 2014).

**Daily routines of parental care in different climate scenarios**

To investigate the impact of climate on daily routines during incubation, we removed from model 4 the non-significant interaction and quadratic terms for between-year variation (Table 1), and used this resulting model for predictions. We predicted the effect of the three temperature variables on daily routines of care division for nine climate scenarios. For each temperature variable, we calculated the predicted values for the 10 time periods at the 2.5% quantile, median and 97.5% quantile value of the temperature variable in question, while the other two temperature variables were kept at their median values. Only fixed effects were taken into account when extracting model predictions.

**RESULTS**

**Consistency between captures and behavioural observations**

Capture-based behavioural estimates reflect parental care division in plovers, since capture-based estimates of male share were highly correlated with estimates of male share obtained by behavioural observations (Figure 1, $R^2 = 0.61 - 0.97$, $n = 6$ populations).

**Incubation routines in different populations**

Incubation routines differed between different plover species and populations (models 2 & 3, Table 1). On the one hand, in species like *C. melodus*, males and females spent comparable time on incubation throughout the day (Figure 2). On the other hand, incubation routines followed a diurnal pattern in
species such as *C. alexandrinus*, *ruficapillus* and *modestus* (Figure 2). Furthermore, there were considerable differences in daily pattern of incubation among the different populations of the same species (Figure 2).

**Ambient environment, between- and within-season variation**

Mean ambient temperature, as well as between- and within-season variation in temperature strongly influenced parental care division (model 4, Table 1). Male share of incubation generally increased with mean ambient temperature. This effect was, however, dependent on time of the day as indicated by the significant interaction between time period and mean ambient temperature. For example, during daylight hours (8 – 20 h) males’ share of incubation increased with mean ambient temperature, though the increase was non-linear and varied depending on the specific time window (Figure 3a).

Temperature fluctuations also predicted incubation (Figure 3b and c). Between-year variation tended to have a linear influence on daily shifts: male share of incubation increased with variation in temperature between years and this effect was similar throughout the day (Figure 3b). Within-season temperature change also predicted shifts in daily routines of males relative to females: with increasing change in temperature during the breeding season, male share decreased between 6 h and 16 h. The effect of within-season temperature variation was however strongly non-linear early in the morning and in the evening (Figure 3c).

Once the three temperature variables were included in the models, the variance explained by population decreased considerably from 0.115 (model 1) to 0.005 (model 4). In contrast, the variance explained by species changed very little from 0.184 (model 1) to 0.191 (model 4).
Daily routines in different climate scenarios

With increasing mean ambient temperature and between-year variation, male share increases during daylight hours, while in the case of mean temperate this happened at the expense of a lowered share of care during the early morning hours (Figure 4a,b). Furthermore, with increasing within-season temperature variation, male share in incubation decreases during daylight hours (Figure 4c).

DISCUSSION

Three major insights have emerged from our study regarding the effect of environment on parental behaviour. First, male contribution to parental care was strongly influenced by ambient temperature. Second, temperature effects on behaviour varied with time of the day. Therefore, not just overall care division changed with changing environmental conditions, but the daily routine of care division was also affected. Specifically, male share of parental care increased with mean temperature and between-year variation in temperature during daylight hours. When conditions became harsher, i.e. the mean temperature and or the between-year unpredictability of temperature was high, males generally increased their effort relative to females during incubation. Finally, geographic variation in care division within species was largely explained by local ambient temperatures, although the differences between different species persisted even after controlling for climatic effects. The latter suggests that different plover populations respond in similar ways to ambient environment, reflecting phenotypic plasticity in behaviour. In contrast, there is substantial species difference in parental care, reflecting a strong phylogenetic effect.

Our results highlight that not only the average environmental conditions, but also their between- and within-season variation play a pivotal role in shaping care division and daily routines of parental care in biparental species. Environmental uncertainty influences reproduction (e.g. breeding initiation, song
display) and life-history (e.g. egg size, clutch size, age of sexual maturity; Lips, 2001; Dewar & Richard, 2007; Botero et al., 2009; Bonsall & Klug, 2011). In addition, unpredictable environmental variation influences mating systems (Botero & Rubenstein, 2012), and may promote the evolution of cooperative breeding strategies (Rubenstein & Lovette, 2007; Jetz & Rubenstein, 2011; but see Gonzalez et al., 2013 for opposite effect). Here we show that parental cooperation is also strongly influenced by predictable and stochastic climate variations.

We propose that more cooperative male behaviour is driven by the need to protect the embryo better under higher frequencies of extreme events (Deeming, 2002; AlRashidi et al., 2011). The expected changes in care division are most likely to occur during mid-day leading to altered daily routines of parental care. As climate change models predict both an increase in temperature and greater frequency of extreme events (Vasseur et al., 2014; IPCC, 2014; Lawson et al., 2015), our findings suggest that pattern of parental care will shift in the near future in biparental species. Such shifts may include greater diurnal incubation responsibilities for the sex with the more variable parental contribution (usually males in birds and mammals, Clutton-Brock, 1991). On the one hand, these shifts may help to maintain hatching success and hatchling condition in the provisioned brood under worsening environmental conditions (Reid et al., 2002). On the other hand, they may preclude the sex that increases parental effort from performing other activities (Dunning, 2002; Reid et al., 2002; Bulla et al., 2014). For instance, a greater share of care division by a given sex may constrain its foraging time, or may reduce its ability to attract further mates or provision other broods, therefore may directly influence mating systems (e.g. Reid et al., 2002). These effects would be especially important in species with flexible and variable parental care and mating systems (e.g. Reid et al., 2002; Kosztolányi et al., 2006).

Periodicity over the day drives daily behavioural routines (Houston & McNamara 1999). Similar to
earlier studies (AlRashidi et al. 2011, Vincze et al., 2013), we found significant daily variation in care provisioning by each sex in specific plover populations. A novel aspect of our current study is that we relate variations in daily routines of care to variation in environmental variables. Our results suggest that behavioural response to temperature changed during the day, in particular, behaviour around midday seemed to be most influenced. This suggests that breeding routines are driven by avoiding extreme hot temperatures. These results may contribute to a detailed theoretical treatment of daily parental routines. The current lack of such models hampers our ability to provide a more detailed explanation for the effect of environmental conditions on daily routines and hence to guide further empirical investigations.

Since male contribution to care correlates with other aspects of breeding systems (e.g. 0% male care usually associated with polygyny, whereas 100% male care may be associated with polyandry and sex role reversal, Searcy & Yasukawa, 1995, Liker et al., 2013), our work suggests that breeding systems will also respond to changes in ambient temperature. To follow up this line of investigation, it would be interesting to study how brood care patterns, frequency of polygamy and extra pair paternity may vary in relation to environmental fluctuations (e.g. in temperatures, food, resource quality, and territory quality). Since these reproductive behaviours make fundamental contributions to reproductive success, we believe it is imperative to assess the impact of climate change not only on parental behaviour, but on other aspects of breeding systems including mate choice, mating system, and pair bonding.

Care division within a species varied with between-population differences in climatic conditions. Local adaptation is unlikely since many plover species show low genetic differentiation (Funk et al. 2007, Küpper et al., 2012, Eberhardt-Phillips et al., 2015). It is more likely that sex roles during biparental care are phenotypically plastic within species, and are modulated by local conditions. This interpretation
is consistent with previous studies, which have demonstrated behavioural plasticity according to local environments during incubation (Al Rashidi et al., 2011, Vincze et al., 2013). Another consequence of the observed flexibility in parental behaviour is that these populations might effectively be able to cope with changing climate at least within the climate range studied here. More climate resilience may be achieved by phenological changes (e.g. Chambers et al., 2008).

Although we found highly significant relationships between environmental fluctuation, its within-year variability, parental care division and its daily routines, the theoretical bases of these relationships have not been fully explored (Klug et al., 2012). Previous theoretical analyses of care and life history traits pointed out that environmental unpredictability can have sophisticated and counter-intuitive influences on provision of care (Klug et al., 2012). To model these future scenarios, it is essential to assess how different aspects of climate influence contemporary populations. Since changing climate may alter the costs and benefits of parental care (Clutton-Brock, 1991; Royle et al., 2012; IPCC, 2014), climate change is likely to affect the reproductive success of individuals that, in turn, will be likely to have an impact on population growth and resilience. We call for new theoretical models to tease apart the effects of ambient environment, social environment and life-histories on care provisioning and its daily pattern.

Using parental care data from an exceptionally wide geographic range, we have shown that incubation, a major component of parental care in birds, is significantly related to mean and variation of ambient temperatures. Daily patterns of care division between the sexes are strongly affected by temperatures. Theoretical explorations show that ambient temperature, as well as its predictable and unpredictable fluctuations, will influence diurnal incubation patterns (Bonsall & Klug, 2011; Klug et al., 2012). We recommend follow up studies building upon our research framework by augmenting these analyses with other climatic variables (e.g. precipitation, wind), and using a variety of response variables such as
mating system, brood survival and life-histories. In addition, we encourage the development of theoretical models investigating the influence of environmental fluctuations on parental care and breeding system.

ACKNOWLEDGEMENTS

Fieldwork and blood sampling was authorized by relevant authorities: Hungary (Environmental Ministry and Kiskunság National Park), Australia (Department of Primary Industries and Environment and Parks Victoria, #F10005850), Argentina (Centro Nacional Patagonico, Dr. Luis Bala), Ceuta (#SGPA/DGVS/01367/11), San Quintín Bay (Dirección General de Vida Silvestre SGPA/DGVS/02078/12), Llobregat Delta (Ministry of Environment #660117), Fuente de Piedra (Consejería de Medio Ambiente, Junta de Andalucía), Farasan (Saudi Wildlife Commission), California (U.S. Fish and Wildlife (USFWS) #TE807078 and U. S. Geological Survey (USGS) #09316), Madagascar (Ministry of Environment, Forests and Tourism of the Republic of Madagascar #053/11/MEF/SG/DGF/DCB.SAP/SCB and #132/10/MEF/SG/DGF/DCB.SAP/SSE; Service de la Gestion de la Faune et de la Flore, Direction de la Valorisation des Resources Naturelles, Ministère de l’Environnement et des Forêts Madagascar #080N-EA06/MG11; Madagascar National Parks #398-10/MEF/SG/DGF/DVRN/ SGFF), Falkland Islands (Falkland Islands Government, #R08/2007), Canada (Environment Canada, Agriculture Canada), China (Hebei Forestry Bureau), South-Africa (Cape Nature and SAFRING), Nayarit (#USFWS 23021), Maio (Directorate Geral Ambiente), Tuzla (Turkish Ministry of National Parks, Tuzla Municipality and Governor of Karatas, Mr. E. Karakaya), Germany (Institut für Vogelforschung, "Vogelwarte Helgoland", Wilhelmshaven), Florida (Institutional Animal Care and Use Committee at the University of Florida, project no. E877) and all banding was completed under banding permit #21980 in collaboration with the Florida Fish and Wildlife Conservation Commission, Texcoco (SEMARNAT/SGPA/DGVS/00098/14), Texas (Institutional Animal Care and
Use Committee at Stephen F. Austin State University #TECMW 10-08-07; U.S. Geological Survey Master Banding Permit #23393; Texas Parks and Wildlife Department SPR-0804-009), St Helena (St Helena Government and the BTO, permit number C5326). OV was supported by the European Union and the State of Hungary, co-financed by the European Social Fund in the framework of TÁMOP-4.2.4.A/ 2-11/1-2012-0001 ‘National Excellence Program’ and by the Hungarian Ministry of Human Resources, National Talent Program (NTP-EFÖ-P-15-0043) during the writing of the manuscript. AK was supported by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences. MAW was funded by the Hermon Slade Foundation, BirdLife Australia, M.A. Ingram Trust, and prominent volunteer input from Laura Tan, Kasun Ekanayake, Stephanie Lomas, and Jessica Bywater. MY was funded by NSERC PhD fellowships and a SSHRC research grant. CK was funded by a Marie Curie IEF postdoctoral Fellowship. MCL, DG, GEGP were funded by CONACyT graduate programmes, PQ was funded by United Foundation for Natural Science of National Natural Science Foundation of China and People’s Government of Guangdong Province (No. U0833005) and YL was funded by the open project of State Key Laboratory of Biocontrol, Sun Yat-sen University. We thank Drs. Luis Bala and María de los Ángeles Hernández, for their support and advice during fieldwork in Argentina. Details about support for the study at Ceuta Bay is listed on the website chorlito.org. Madagascar plover fieldwork and molecular sexing were supported by Leverhulme Trust (ID200660763, Ecology and genetics of endemism) and NERC Biomolecular Analysis Facility at the University of Sheffield respectively. JSC was supported by the University of Bath and Falkland Islands Government, and assisted in the field by Neil Dawson, Chris Dodd, Philipp Herrmann and Jacqueline Pearson. JAA was supported by research projects PB95-0110 and CGL2011-24230 from Ministerio de Ciencia e Innovación, Spain, both with EU-ERDF financial support. DGE was funded by the Sonoran Joint Venture (FWS Agreement No. F11AP00052), and by graduate scholarships from the PIFI at Instituto Politécnico Nacional-CICIMAR (20120989) and the Mexican National Council for Science and Technology (CONACYT, No. 99866).
FB was funded by the University of Bath and the RSPB, with support from St Helena National Trust.

CLGT was funded by Environment Canada (Species at Risk), and the Government of Canada’s Interdepartmental Recovery Fund. ZB was supported by a NKFIH grant (grant no. K112527). Financial support: Florida (US Fish and Wildlife Service Panama City Field Office), Germany (Stifterverband für die Deutsche Wissenschaft, Essen), Nayarit (Tides Foundation, Rio Tinto Kennecott, BirdLife International, US Fish and Wildlife Service Region 6, Denker’s Family Foundation and Weber State University). This study is contribution 12319 of Point Blue Conservation Science.

SUPPORTING INFORMATION

Figure S1 Schematic illustration of hypothesis testing.
Table S1 Summary of the data used.
Table S2 Sensitivity analyses.
Appendix S1 Supporting references.

BIOSKETCH

Orsolya Vincze is a PhD candidate at the University of Debrecen. Her research focuses on behavioural ecology and ecophysiology of birds.

REFERENCES


Table 1  Male incubation (binary response variable) in different plover species and populations (n = 5591 individuals). Mixed effects models. \( \chi^2 \) values, degrees of freedom (df) and probability (p) of likelihood ratio tests are given.

<table>
<thead>
<tr>
<th>Model</th>
<th>Fixed term</th>
<th>( \chi^2 ) (df)</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model 1</td>
<td>Time period</td>
<td>1017.95 (9)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>Species</td>
<td>9.65 (1)</td>
<td>0.0019</td>
</tr>
<tr>
<td></td>
<td>Population</td>
<td>44.91 (1)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>Nest ID</td>
<td>0.00 (1)</td>
<td>1.0000</td>
</tr>
<tr>
<td>Model 2</td>
<td>Time period</td>
<td>64.58 (9)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>Species</td>
<td>38.26 (1)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>Population x time period</td>
<td>36.87 (1)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Model 3</td>
<td>Time period</td>
<td>176.43 (9)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>Species</td>
<td>11.37 (1)</td>
<td>0.0007</td>
</tr>
<tr>
<td></td>
<td>Population x time period</td>
<td>85.05 (1)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Model 4</td>
<td>Time period</td>
<td>1216.20 (63)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>Mean temperature (°C)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Interaction with time period</td>
<td>84.42 (18)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>Quadratic effect</td>
<td>32.03 (10)</td>
<td>0.0004</td>
</tr>
<tr>
<td></td>
<td>Between-year temperature variation (°C)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Interaction with time period</td>
<td>15.23 (18)</td>
<td>0.6462</td>
</tr>
<tr>
<td></td>
<td>Quadratic effect</td>
<td>2.82 (1)</td>
<td>0.0929</td>
</tr>
<tr>
<td></td>
<td>Linear effect</td>
<td>7.34 (1)</td>
<td>0.0067</td>
</tr>
<tr>
<td></td>
<td>Within-season temperature variation (°C)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Interaction with time period</td>
<td>70.81 (18)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>Quadratic effect</td>
<td>33.68 (10)</td>
<td>0.0002</td>
</tr>
<tr>
<td></td>
<td>Species</td>
<td>14.07 (1)</td>
<td>0.0002</td>
</tr>
<tr>
<td></td>
<td>Population</td>
<td>0.05 (1)</td>
<td>0.8298</td>
</tr>
<tr>
<td></td>
<td>Nest identity</td>
<td>0.00 (1)</td>
<td>1.0000</td>
</tr>
</tbody>
</table>

Footnote: Main effects were tested by removing the main term and all its interactions with other variables. Interaction terms were tested by removing the interaction from full model and comparing the resulting model to the original. Quadratic terms were tested...
by replacing polynomial with linear terms, and comparing the resulting model to the original.
Figure legends

Figure 1. Male share of nest attendance estimated from capture data (%, capture) in relation to male share of nest attendance as obtained from behavioural observations (%, behaviour). Each point represents a 2-hour time period. Dashed lines represent equal estimates by the two methods. Statistics on each panel show the results of a least-squares regression weighted by the number of captures in each time period. $R^2$ represents the coefficient of determination.

Figure 2. Male share of nest attendance (%) calculated from capture data in 36 populations. Each species is plotted on different panel, except Kentish plover and snowy plover which are shown on 3 and 2 panels, respectively. Each line represents a population. Legends refer to location numbers on the map (see Table S1 for population names and exact coordinates).

Figure 3. Daily changes in predicted probability of male care (i.e. capture) in relation to (a) mean temperature, (b) between-year variation and (c) within-season variation. Each panel shows a different time period (see panel title for time period). Dashed lines represent 95% confidence intervals. Predictions are based on minimal model 4 from which the non-significant interaction and quadratic terms for between-year variation were removed (Table 1).

Figure 4. Predicted probability of male care (i.e. male capture) throughout the day under different climate scenarios. Each panel shows a climate scenario where the candidate temperature variable (i.e. shown by the main title of each sub-graph) takes three values (i.e., 2.5% quantile, median, 97.5% quantile), while the other two temperature variables are set to their median. Predictions are based on minimal model 4 from which the non-significant interaction and quadratic terms for between-year variation were removed (Table 1).
Figure 1.
Figure 2.
Figure 3 (a)

Mean temperature (°C)

Probability of male care

04-06 06-08 08-10 10-12 12-14

14-16 16-18 18-20 20-22 22-24
Figure 3 (b)

- Probability of male care
- Between-year temperature variation

- Four panels: 04-06, 06-08, 08-10, 10-12, 12-14, 14-16, 16-18, 18-20, 20-22, 22-24
Figure 3 (c)
Figure 4.
Figure S1. Schematic presentation of how the effect of each variable was tested. All derived models (i.e. shown by arrowheads) were compared to the model from which they originate (i.e. shown by the base of the arrows). Models were compared using likelihood ratio statistics.
**Table S1** Summary of parental care data from different populations of plovers *Charadrius* spp. Sexing method refers to molecular sexing (M), plumage and/or other morphometric measurements or behaviour based (P). Numbers in square brackets in the Population column refer to the localities on the map in Figure 2. See Appendix S1 for references cited here.

<table>
<thead>
<tr>
<th>Species</th>
<th>Population</th>
<th>Coordinates</th>
<th>Years of data collection</th>
<th>Number of captures</th>
<th>% male captures</th>
<th>Sexing method</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. alexandrinus</em></td>
<td>Maio Island (Cape Verde) [15]</td>
<td>15°09'N, 23°13'W</td>
<td>2007-2010</td>
<td>244</td>
<td>40.57</td>
<td>M, P</td>
<td>Székely T., A.A. Tico &amp; A. Kosztolányi unpubl data</td>
</tr>
<tr>
<td><em>C. alexandrinus</em></td>
<td>Farasan Islands (Saudi Arabia) [26]</td>
<td>16°48'N, 41°53'E</td>
<td>2008-2009, 2011</td>
<td>45</td>
<td>35.56</td>
<td>P</td>
<td>AlRashidi et al., 2011</td>
</tr>
<tr>
<td><em>C. alexandrinus</em></td>
<td>Al Wathba Wetland (United Arab Emirates) [27]</td>
<td>24°16'N, 54°36'E</td>
<td>2005-2006</td>
<td>175</td>
<td>48.00</td>
<td>P</td>
<td>Kosztolányi et al., 2009, AlRashidi et al., 2010</td>
</tr>
<tr>
<td><em>C. alexandrinus</em></td>
<td>Fuente de Piedra Lake (Spain) [16]</td>
<td>37°06'N, 04°45'W</td>
<td>1991-1996</td>
<td>174</td>
<td>49.43</td>
<td>P</td>
<td>Fraga &amp; Amat (1996), Amat &amp; Masero 2004</td>
</tr>
<tr>
<td><em>C. alexandrinus</em></td>
<td>Bohai Bay (China) [28]</td>
<td>39°05'N, 118°12'E</td>
<td>2012</td>
<td>38</td>
<td>31.58</td>
<td>M, P</td>
<td>Que, P. &amp; Y. Liu unpubl. data</td>
</tr>
<tr>
<td><em>C. alexandrinus</em></td>
<td>Lagoon of Venice and Po Delta (Italy) [23]</td>
<td>45°10'N, 12°24'E</td>
<td>1993-1995</td>
<td>157</td>
<td>45.86</td>
<td>P</td>
<td>Serra, L. unpubl. data</td>
</tr>
<tr>
<td><em>C. falklandicus</em></td>
<td>Sea Lion Island (Falklands) [13]</td>
<td>51°41'S, 59°10'W</td>
<td>2005-2008</td>
<td>63</td>
<td>42.86</td>
<td>M, P</td>
<td>St Clair et al., 2010a</td>
</tr>
<tr>
<td><em>C. marginatus</em></td>
<td>Cape Peninsula (South Africa) [18]</td>
<td>34°08'W, 18°20'E</td>
<td>1999-2003</td>
<td>162</td>
<td>32.72</td>
<td>P</td>
<td>Lloyd, P. unpubl. data</td>
</tr>
<tr>
<td>Species</td>
<td>Location</td>
<td>Coordinates</td>
<td>Years</td>
<td>N</td>
<td>Sex</td>
<td>References</td>
<td></td>
</tr>
<tr>
<td>---------------</td>
<td>---------------------------------------------</td>
<td>-----------------</td>
<td>----------------</td>
<td>-----</td>
<td>-----</td>
<td>------------------------------------------------------------------</td>
<td></td>
</tr>
<tr>
<td>C. melodus</td>
<td>Saskatchewan Coteau (Canada) [1]</td>
<td>49°44'N, 105°23'W</td>
<td>2002-2006</td>
<td>139</td>
<td>P</td>
<td>Cohen &amp; Gratto-Trevor 2011; Gratto-Trevor 2011</td>
<td></td>
</tr>
<tr>
<td>C. modestus</td>
<td>Sea Lion Island (Falklands) [13]</td>
<td>51°41'S, 59°10'W</td>
<td>2005-2008</td>
<td>99</td>
<td>M, P</td>
<td>St Clair et al., 2010a, St Clair et al., 2010b</td>
<td></td>
</tr>
<tr>
<td>C. nivosus</td>
<td>Ceuta Bay (Mexico) [9]</td>
<td>29°44'N, 85°06'W</td>
<td>2008-2010</td>
<td>300</td>
<td>P</td>
<td>Pruner, R. unpubl. data</td>
<td></td>
</tr>
<tr>
<td>C. nivosus</td>
<td>San Quintin Bay (Mexico) [7]</td>
<td>30°40'N, 116°0'W</td>
<td>2012</td>
<td>45</td>
<td>P</td>
<td>Galindo-Espinosa, D. unpubl. data</td>
<td></td>
</tr>
<tr>
<td>C. ruficapillus</td>
<td>Altona Saltworks (Australia) [29]</td>
<td>37°53'S, 144°47'E</td>
<td>2008-2012</td>
<td>71</td>
<td>P</td>
<td>Lomas et al., 2014, Weston, M.A. unpubl. data</td>
<td></td>
</tr>
</tbody>
</table>

**Footnote:** Molecular sexing markers: P2P8, Z-002B and Calex-31 (Griffiths et al., 1998, Dawson 2007, Küpper et al., 2007)
Table S2. Sensitivity analyses for the length of the time period on which the calculation of the three climate variables was based on.

<table>
<thead>
<tr>
<th>Model 4</th>
<th>Fixed terms</th>
<th>5 years</th>
<th></th>
<th>10 years</th>
<th></th>
<th>15 years</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Time period</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mean temperature (°C)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Interaction with time period</td>
<td>79.96 (18)</td>
<td>&lt; 0.0001</td>
<td>77.28 (18)</td>
<td>&lt; 0.0001</td>
<td>85.49 (18)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>Quadratic effect</td>
<td>32.93 (10)</td>
<td>0.0003</td>
<td>32.76 (10)</td>
<td>0.0003</td>
<td>33.26 (10)</td>
<td>0.0002</td>
</tr>
<tr>
<td></td>
<td>Between-season temperature variation (°C)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Interaction with time period</td>
<td>37.86 (18)</td>
<td>0.0040</td>
<td>23.35 (18)</td>
<td>0.1777</td>
<td>15.76 (18)</td>
<td>0.6091</td>
</tr>
<tr>
<td></td>
<td>Quadratic effect</td>
<td>16.32 (10) *</td>
<td>0.0907</td>
<td>1.52 (1)</td>
<td>0.2173</td>
<td>1.22 (1)</td>
<td>0.2690</td>
</tr>
<tr>
<td></td>
<td>Linear effect</td>
<td>6.19 (2) *</td>
<td>0.0452</td>
<td>4.67 (1)</td>
<td>0.0307</td>
<td>6.03 (1)</td>
<td>0.0140</td>
</tr>
<tr>
<td></td>
<td>Within-season temperature variation (°C)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Interaction with time period</td>
<td>40.71 (18)</td>
<td>0.0017</td>
<td>32.57 (18)</td>
<td>0.0188</td>
<td>70.65 (18)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>Quadratic effect</td>
<td>23.97 (10)</td>
<td>0.0077</td>
<td>32.76 (10)</td>
<td>0.0003</td>
<td>29.36 (10)</td>
<td>0.0011</td>
</tr>
<tr>
<td></td>
<td>Random terms</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Species</td>
<td>16.40 (1)</td>
<td>&lt; 0.0001</td>
<td>14.49 (1)</td>
<td>0.0001</td>
<td>14.46 (1)</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>Population</td>
<td>0.22 (1)</td>
<td>0.6367</td>
<td>0.60 (1)</td>
<td>0.4400</td>
<td>0.07 (1)</td>
<td>0.7919</td>
</tr>
<tr>
<td></td>
<td>Nest identity</td>
<td>0.00 (1)</td>
<td>0.9984</td>
<td>0.00 (1)</td>
<td>1.0000</td>
<td>0.00 (1)</td>
<td>1.0000</td>
</tr>
</tbody>
</table>

*Interaction with time period retained in model (similarly to the other two temperature variables) due to its significant effect.
**Appendix S1.** Supplementary references for Table S1


