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

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ABSTRACT

Aim Parental care improves offspring survival and therefore has a major impact on reproductive success. It is increasingly recognised that coordinated bi-parental care is necessary to ensure offspring survival in hostile environments, but little is known about the influence of environmental fluctuation on parental cooperation. Assessing the impacts of environmental stochasticity, however, is essential for understanding how populations will respond to climate change and increasing frequencies of extreme weather events associated with the latter. Here we investigate the influence of environmental stochasticity on biparental incubation in a cosmopolitan ground nesting avian genus.

Location Global

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

Results We show that both average ambient temperature and its fluctuations influence parental cooperation during incubation. Male care relative to female care increases with both mean ambient temperature and temperature stochasticity. Local climatic conditions explain within-species population differences in parental cooperation, likely reflecting phenotypic plasticity of behaviour.

Main conclusions The degree of flexibility in parental cooperation is likely to mediate the impacts of climate change on the demography and reproductive behaviour of wild animal populations.

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-histories (e.g. earlier spring and/or later autumn migration, earlier breeding), changes in geographical ranges and physiology, as well as population trends (Walther *et al.*, 2002; 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 respond behaviourally to altered climate is surprisingly limited, making it impossible to predict the extent to which behavioural plasticity may mitigate the effects of climate change.

Investigations of the impacts of climate change on populations often only focus on average temperature changes (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 (Thompson *et al.*, 2013; Vasseur *et al.*, 2014; IPCC, 2014; Lawson *et al.,* 2015). Climate change, although often associated with increased environmental averages, also results in increased environmental uncertainty and variability (Thompson *et al.*, 2013; Vasseur *et al.*, 2014; Lawson *et al.*, 2015). Such 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 behaviourally, and how such plasticity might mitigate the impacts of climate change. We investigate parental behaviour, a major contributor to reproductive success in a wide range of taxa, as a function of average climatic conditions, as well as of between-year and within-season variation (stochasticity and seasonality). Given its role in buffering offspring against environmental conditions, parental behaviour could represent an important link between climate change and its impacts on populations.

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 care (Clutton-Brock, 1991; McGraw *et al.*, 2010; Royle *et al.*, 2012; Székely, 2014; Bulla *et al.*, in press). 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 in terms of time and energy invested by parents, and its benefits in terms of 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: for example, the need for care particularly increases in extremely cold or hot climates, or during times of resource shortages. Parental protection and provisioning substantially improve offspring survival under such 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 effects 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 optimum for embryonic development by turning and warming or cooling the eggs in cold or hot conditions, respectively (Deeming, 2002; Alrashidi *et al.*, 2011; Vincze *et al.*, 2013; 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 relatively poorly buffered against extreme temperatures given the conductive nest substrate, the minimal insulating material and the lack of shade (Webb, 1987; Deeming, 2002; Alrashidi *et al.*, 2011).

In environments with ambient temperatures close to optimal embryonic development (35-39°C: Webb, 1987), one parent may provide sufficient incubation in the absence of other constraints (Deeming, 2002; Alrashidi *et al.*, 2011; Vincze *et al.*, 2013). If the environmental conditions, however, deviate from the optimal in either direction, increased parental effort is expected. This increase could be achieved by both parents or by either of the two parents increasing their work load. Incubation in most bird species is provided by one parent only, typically the female. In the rare case when both parents incubate, one of them often shoulders most of the work and the second parent provides less care, leaving the latter with the greatest potential to enhance parental effort if needed (Auer *et al.*, 2007). In plovers, females usually incubate during the day, while males are responsible for night-time incubation when conditions are often more benign (Vincze *et al.,* 2013, Ekanayake *et al.* 2015). Consequently, we expect males' share relative to females' to increase under harsh ambient conditions, such as high or low average temperatures or high inter-annual fluctuations of temperatures (stochasticity). The latter is expected, since high inter-annual environmental fluctuations increases the probability of extreme events (Easterling *et al.*, 2000). Additionally, we test the effect of within-breeding season environmental change (seasonality). We predict increased male share in highly seasonal environments, since seasonality restricts breeding time and remating opportunities, thus increasing the value of current relative to future broods. Under such a scenario higher levels of cooperation between the parents is expected, as observed in late-season broods in Kentish plovers (e.g. Székely & Cuthill, 2000). Note however, that extended parental care is predicted for both sexes under constant environmental circumstances (low seasonality) too, as part of the tropical life-history syndrome (Wilson, 1985). Birds in the tropics generally have slower pace of life, as reflected by lower reproductive rate, smaller clutch sizes, higher survival, slower development and extended postnatal parental provisioning (Martin, 1996, Russell et al., 2004) requiring an elevated male share of parental care.

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. Although the ancestor of this monophyletic group likely evolved in temperate or cold climates of the Northern hemisphere (dos Remedios *et al.,* 2015), they now breed on all continents except Antarctica, in habitats as varied as arctic tundra, temperate grassland, tropical beaches, salt marshes, sand dunes, semi-deserts, deserts and high altitude mountain lake shores (Piersma & Wiersma, 1996). This broad variation in breeding environment provides an excellent opportunity to conduct a geographically large-scale study, capturing a substantial range of global ecological diversity. Plovers usually lay 2-4 eggs in uninsulated scrapes. Incubation is usually carried out by both parents, although the extent of male involvement in incubation is highly variable among species and populations (Vincze *et al.*, 2013). In addition, the share of incubation by each sex may vary throughout the day: in most species males tend to incubate at night, whereas females carry out most of the daytime incubation (Vincze *et al.*, 2013; but see St Clair *et al.*, 2010a). Chicks are precocial and nidifugous, and often either the male or the female parent provides post-hatch care alone, while the other parent might 'desert' and become polygamous (Kosztolányi *et al.*, 2006).

Here we investigate how climate influences parental behaviour using an extensive dataset on parental care that covers temperate and tropical habitats in both the northern and southern hemispheres (between 55ºN to

52ºS latitude, and between 145ºE to 121ºW longitude). To examine how climate influences incubation behaviour, we used the space-for-time substitution approach to infer temporal trends from spatial data, a powerful method in ecology (Pickett, 1989). First, we establish how the division of incubation behaviour varies across species, populations and time of day. Second, we test whether ambient temperature and fluctuations in temperature influence the division of care between males and females. Third, we investigate how the change in climate can influence parental cooperation.

METHODS

Fieldwork

Fieldwork was carried out in 36 breeding populations of 12 plover species, and ranged from one to 16 breeding seasons per population (Table S1). Parents were captured on their nest using funnel traps, noose mats, box traps or bownet traps while incubating (see Székely *et al.*, 2008 for general methodology, and specific references in Table S1). For each captured bird we recorded the time of capture and sex of the captured 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 incubation-sharing patterns are least stable around the egg-laying (e.g. delayed onset of incubation) and egg-hatching periods (e.g. desertion around hatching), we only included nests that had been incubated for at least three days and for no 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 0000h and 0400h 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 estimated from capture data with male share estimated from 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. Additionally, to test whether the association between capture-based and behavioural observation-based male share is similar across populations we constructed a pooled mixed effect model. This model included male share (%, behaviour) as dependent variable, male share (%, capture) as fixed covariate and male share (%, capture) by population random intercept and slope term, with each population having a unique intercept and slope. In the latter model the significance of the random slope term was assessed by replacing this with a random intercept term and comparing the two models using likelihood ratio statistics. The model was weighted by the number of captures in each 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, inclusive; this seemed sufficient to represent the ambient temperatures the plovers experienced in our study given that the longest population dataset spanned 16 years (Table S1). 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 of climate data prior to (and including) the last year of field data collection. These models yielded highly consistent results (see 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 in two steps. First, standard deviation of average temperature of each month of the breeding season was calculated over the 20 years; second, these monthly standard deviations were averaged for each population. (iii) Within-season temperature variation was obtained in two steps. First, we calculated the average temperature of each breeding season months over the 20 year period. Second we calculated 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). To test whether collinearity exists in models containing all three temperature variables, we calculated variance inflation factors (VIFs) for a simple model without quadratic terms and interactions (cf. model 4 below), 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). All VIFs for climate variables were below 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 (but see below for analyses incorporating species level phylogeny). We used the sex of parents (1-male and 0-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 0400h and 2400h). The three temperature variables were standardised, using the "scale" function implemented in R, to ease model fitting and comparison of 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 initially tested for the effects of laying date, we excluded this variable from further models because it did not influence the sex of the parent captured.

We built four mixed effects models (Table S3). First, to test how division of care 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 ID's (*Model 1*). Next, to test whether the daily pattern of incubation differed between plover species and populations, we built two models: in *Model 2* we included the species x time period interaction in addition to the terms in *Model 1*, while in *Model 3* the population x time period interaction was included in addition to the terms in *Model 1*. Finally, to investigate the effects of ambient temperature, and its fluctuations between years and within-seasons, *Model 4* 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 each of the 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 (Table S3).

To test whether phylogenetic relatedness influenced our results, the above models were repeated using Bayesian MCMCglmms, including a correlational structure based on the species level phylogenetic tree of the 12 *Charadrius* species studied here (model description and calculation of phylogenetic signal are given in Appendix S2). The results of the latter models provided qualitatively similar results to the mixed modelling framework (Table S4). Moreover, phylogenetic signal of the investigated trait in these models was low (0.10 – 0.12), while removing the phylogenetic relatedness from the models had only a slight influence on model fit (Table S4).

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). Predicted values and 95% confidence intervals based on the fixed-effects were calculated by the method outlined at http://glmm.wikidot.com/faq#predconf (last accessed at: 30 June 2016).

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 S3, M4.5), 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 ten 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.

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 good predictors of male share obtained by behavioural observations (Figure S1, $R^2 = 0.61$ - 0.97, n = 6 populations). In the model that incorporated data from all six of these populations the random slope term was not significant (χ^2 (df) = 0.41 (2), p=0.8154), indicating a similar slope between behaviour and capture based male share estimates across populations. Taken together, these results suggest that male share estimated based on capture data gives congruent estimates of care division to behavioural observations across populations, validating our methodology.

Incubation routines in different populations

Incubation sharing differed between plover species and populations (Models 2 and 3, Table 1, see also Table S4). On the one hand, in species such as *C. melodus,* males and females spent comparable time on incubation throughout the day (Figure 1). On the other hand, incubation sharing followed a diurnal pattern in species such as *C. alexandrinus, ruficapillus* and *modestus* (Figure 1). Furthermore, there were considerable differences in daily patterns of incubation among the different populations of the same species (Figure 1).

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, see also Table S4). 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 (0800 - 2000 h) the male share of incubation increased with mean ambient temperature, though the increase was non-linear and varied depending on the time window (Figure 2a).

Temperature fluctuations also predicted incubation (Figure 2b,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 2b). Within-season temperature variation also predicted shifts in daily routines of males relative to females: with increasing change in temperature during the breeding season, male share generally decreased between 0600 h and 1600 h. The effect of within-season temperature variation was however strongly non-linear early in the morning and in the evening (Figure 2c).

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 3a,b). Furthermore, with increasing within-season temperature range, male share in incubation decreases until afternoon (Figure 3c).

DISCUSSION

Three major insights have emerged from our study regarding the effects of the climate 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: 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, since population effects were reduced or diminished after controlling for climatic effects. The latter suggests that different plover populations respond in similar ways to ambient environment, reflecting phenotypic plasticity in behaviour.

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 a counter-example). 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 (at least in habitats with higher temperatures) 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 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 (Deeming, 2002; Reid *et al.*, 2002). 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). The latter 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). Note however that the lack of flexibility in parental provisioning could result in even sharper effects on population resilience, due to the inability of such species to compensate for environmental change. Given that male *Charadrius* spp. plovers are generally more ornamented than females, and that the more brightly coloured males may be more detectable to diurnal, visually foraging egg predators, diurnal male care in at least some species may result in compromised nest crypsis (Ekanayake *et al.*, 2015). Thus, the prevailing predator environment may also constrain the degree of male care.

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 diversity in daily routines of care to variation in the environment. Our results imply that the behavioural response to temperature changed during the day; in particular, behaviour around mid-day seemed to be most influenced. This suggests that breeding routines are driven by the need to buffer the embryo against extremely hot temperatures in hot environments, whilst in colder climates this period offers flexibility, given that the warmer midday may represent a time when incubation is least critical to embryonic development and survival (Weston & Elgar, 2005). These results should 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 species varied with between-population differences in climatic conditions. Local adaptation is unlikely since many plover species show low genetic differentiation (Küpper *et al.*, 2012, Eberhart-Phillips et al., 2015) with individual plovers able to move large geographic distances and therefore potentially providing parental care in different climatic conditions to those in which they received it (Stenzel et al. 1994). This may explain why 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 actual environmental conditions 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), or by the use of nest cover, used by many species considered by this study, and which reduces the influence of prevailing temperatures on those experienced by eggs (Lomas *et al.*, 2014).

Our results indicate highly significant relationships between environmental stochasticity, seasonality, parental care division and its daily routines, but the theoretical bases of these relationships are not well understood (Klug *et al.*, 2012). Previous theoretical analyses of care and life history traits pointed out that environmental unpredictability can have complex and counter-intuitive influences on care provisioning (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.

Using parental care data from an exceptionally wide geographic range, we have shown that cooperation during incubation, a major component of parental care in birds, is significantly related to mean and variation of ambient 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 evolution.

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SUPPORTING INFORMATION

Supplementary acknowledgments

Table S1 Summary of the data used.

Appendix S1 Supporting references.

Table S2 Sensitivity analyses.

Table S3 Detailed description of hypothesis testing.

Appendix S2 Description of Bayesian modelling framework.

Table S4 Results of the Bayesian models.

BIOSKETCH

Orsolya Vincze is a PhD candidate at the University of Debrecen. Her research focuses on behavioural ecology and ecophysiology of birds. All authors share an interest in the evolutionary ecology, behaviour and conservation of plovers.

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

		χ2 (df)	**P**
Model 1	**Sex ~ Time period + (1|Species)+(1|Population)+(1|NestID)**		
	Fixed term		
	Time period	1017.95 (9)	< 0.0001
	Random terms		
	Species	9.65 (1)	0.0019
	Population	44.91 (1)	< 0.0001
	Nest ID	0.00 (1)	1.000
Model 2	**Sex ~ Time period** **+ (1|Species) + (1|Species:Time period) + (1|Population) + (1|NestID)**		
	Fixed term		
	Time period	64.58 (9)	< 0.0001
	Random terms		
	Population	38.26 (1)	< 0.0001
	Species × time period	36.87 (1)	< 0.0001
Model 3	**Sex ~ Time period** **+ (1|Species) + (1|Population) + (1|Population:Time period)** **+ (1|NestID)**		
	Fixed term		
	Time period	176.43 (9)	< 0.0001
	Random terms		
	Species	11.37 (1)	0.0007
	Population × time period	85.05 (1)	< 0.0001
Model 4	**Sex ~ Time period** **+ poly(Mean temperature,2)** **+ poly(Between−year temperature variation,2)** **+ poly(Within−season temperature variation,2** **+ Time period:poly(Mean temperature,2)** **+ Time period:poly(Between−year temperature variation,2)** **+ Time period:poly(Within−season temperature variation,2)** **+ (1|Species) + (1|Population) + (1|NestID)**		
	Fixed terms		
	Time period	1216.20 (63)	< 0.0001
	Mean temperature (°C)		
	Interaction with time period	84.42 (18)	< 0.0001

	Quadratic effect	32.03 (10)	0.0004
	Between-year temperature variation (°C)		
	Interaction with time period	15.23 (18)	0.6462
	Quadratic effect	2.82 (1)	0.0929
	Linear effect	7.34 (1)	0.0067
	Within-season temperature variation (°C)		
	Interaction with time period	70.81 (18)	< 0.0001
	Quadratic effect	33.68 (10)	0.0002
	Random terms		
	Species	14.07 (1)	0.0002
	Population	0.05 (1)	0.8298
	Nest identity	0.00 (1)	1.0000

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 (see Table S2 for full details of the testing procedures).

Figure legends

Figure 1. Male share of nest attendance (%) calculated from capture data in 36 populations. Each species is plotted on different panel, except Kentish plover (*Charadrius alexandrinus*) and snowy plover (*Charadrius nivosus*) 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, and Appendix S1 for references).

Figure 2 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 3. 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

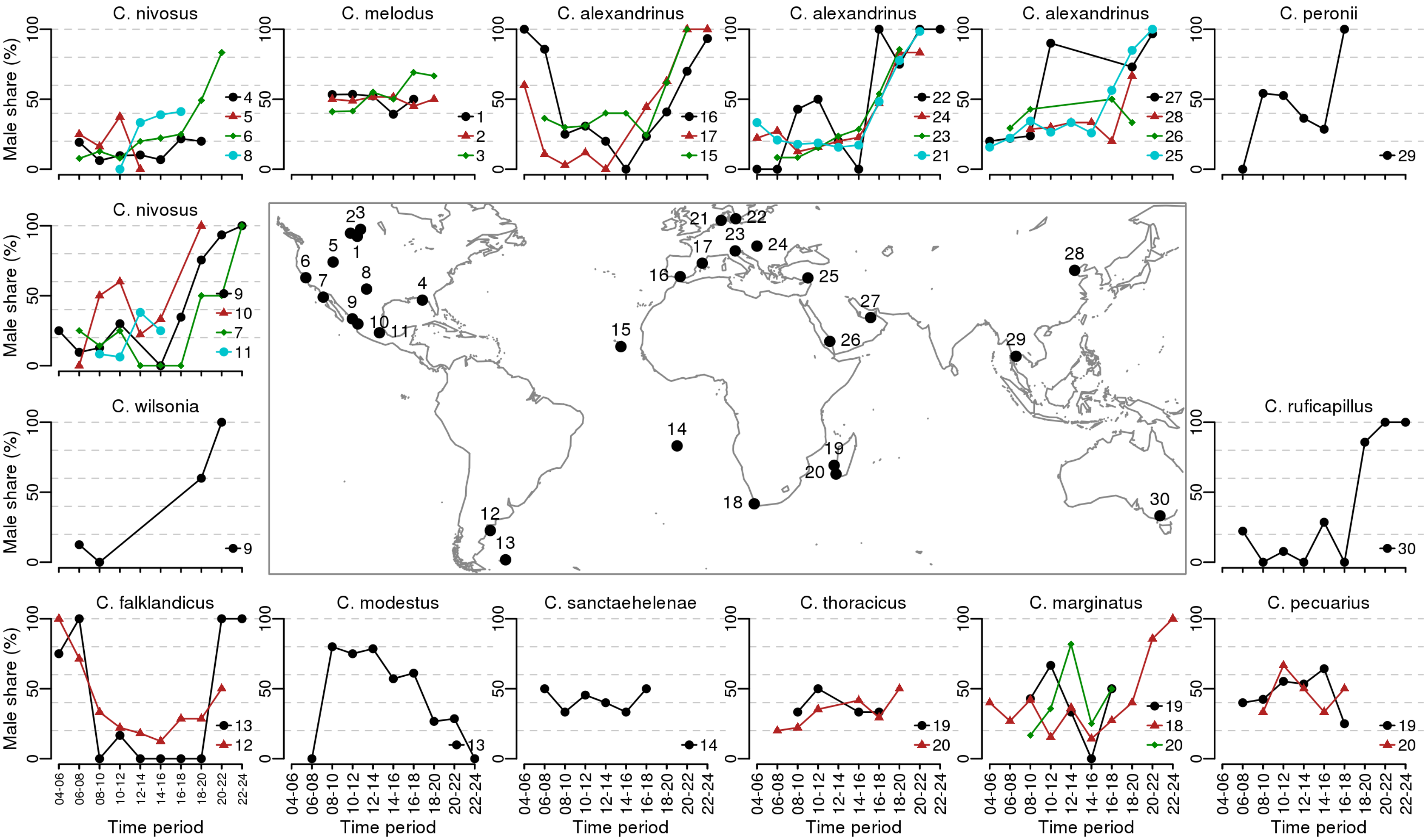
C. nivosus
C. melodus
C. alexandrinus
C. alexandrinus
C. alexandrinus
C. peronii
C. nivosus
C. wilsonia
C. ruficapillus
C. falklandicus
C. modestus
C. sanctaehelenae
C. thoracicus
C. marginatus
C. pecuarius
Male share (%)
0
50
100
Time period
04-06
06-08
08-10
10-12
12-14
14-16
16-18
18-20
20-22
22-24
4
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Figure 2 (a)

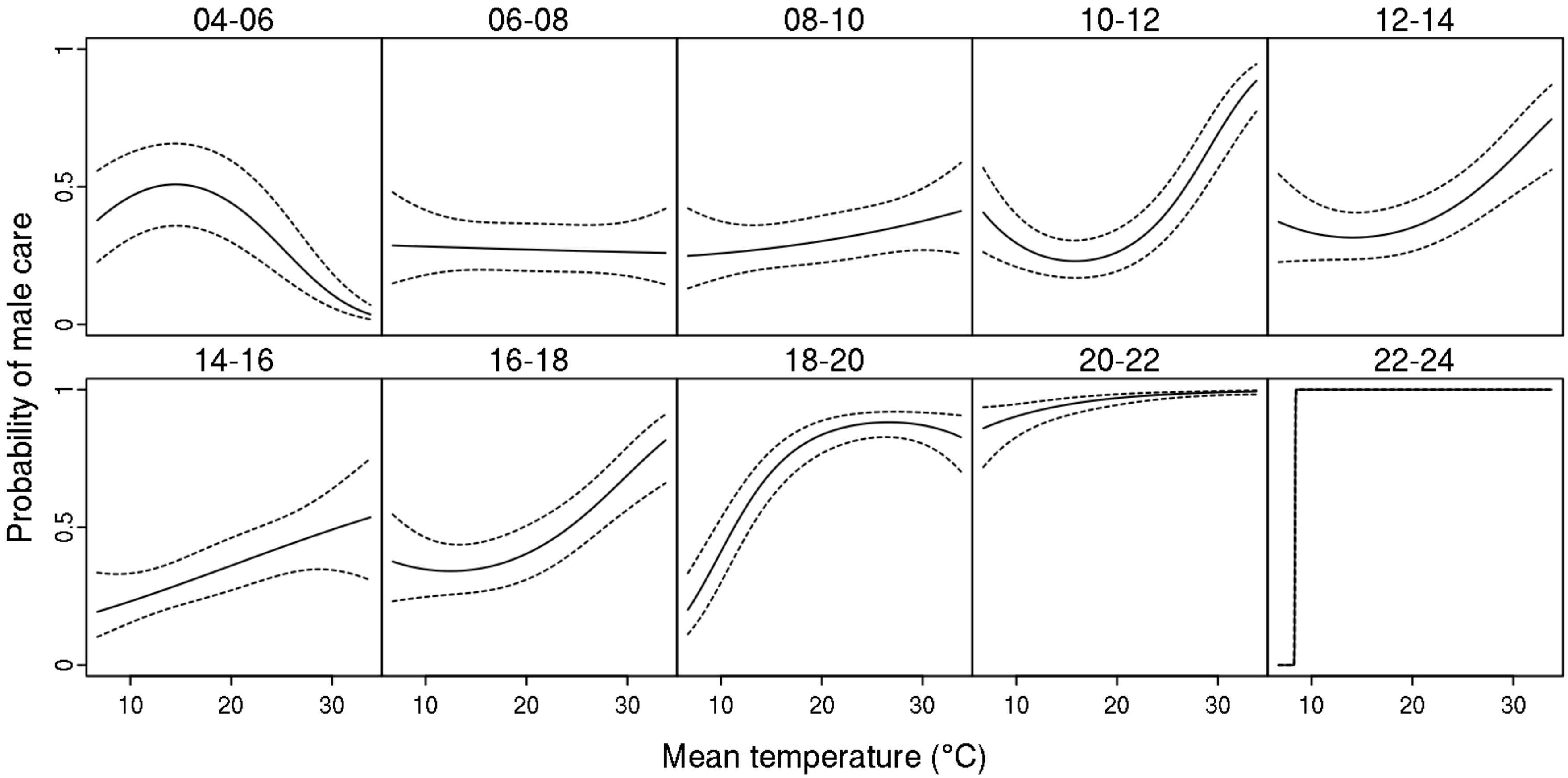

04-06
06-08
08-10
10-12
12-14
14-16
16-18
18-20
20-22
22-24
Probability of male care
0
0.5
1
10
20
30
Mean temperature (°C)

Figure 2 (b)

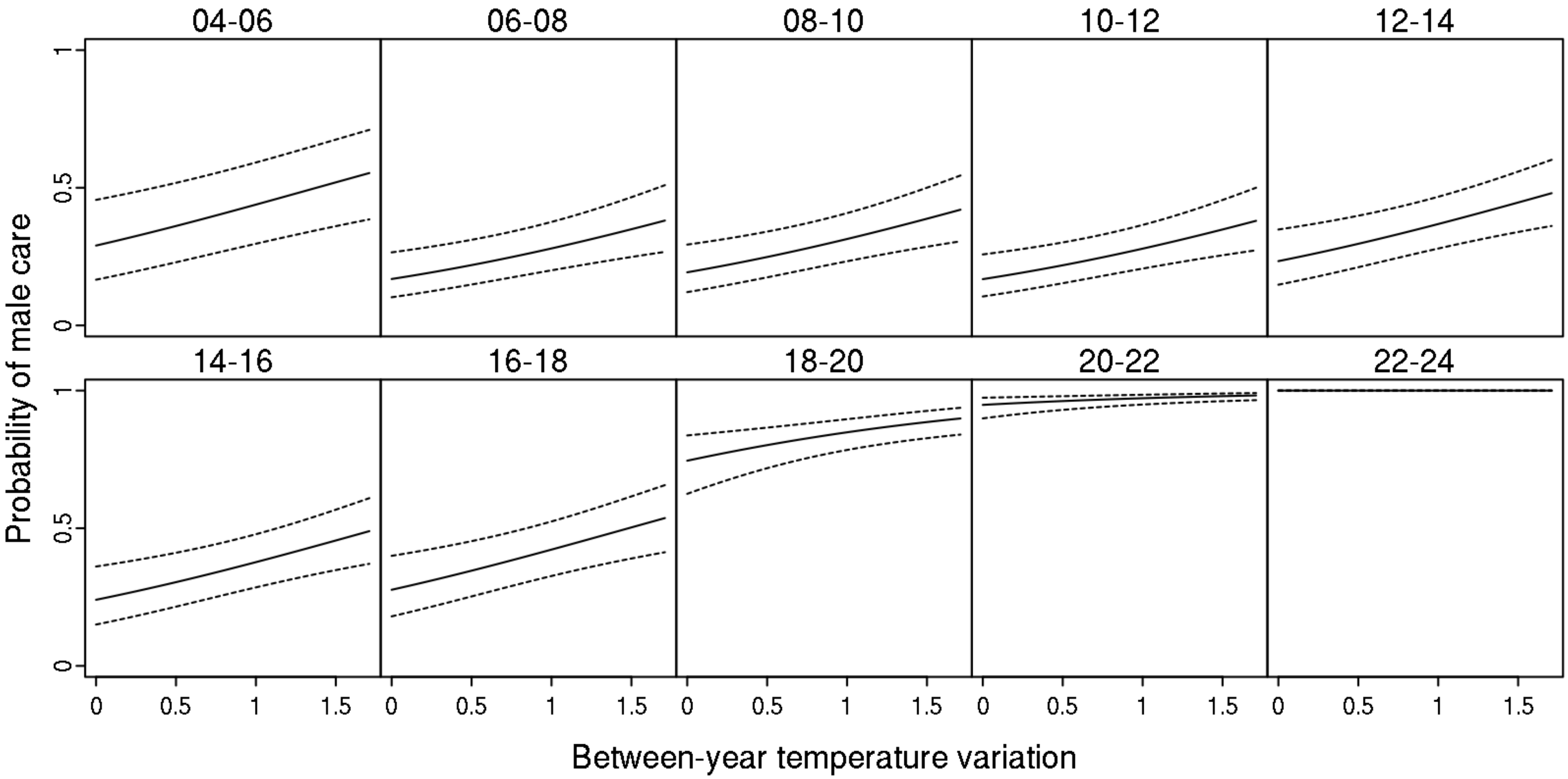

04-06
06-08
08-10
10-12
12-14
14-16
16-18
18-20
20-22
22-24
Probability of male care
0
0.5
1
0
0.5
1
1.5
Between-year temperature variation

Figure 2 (c)

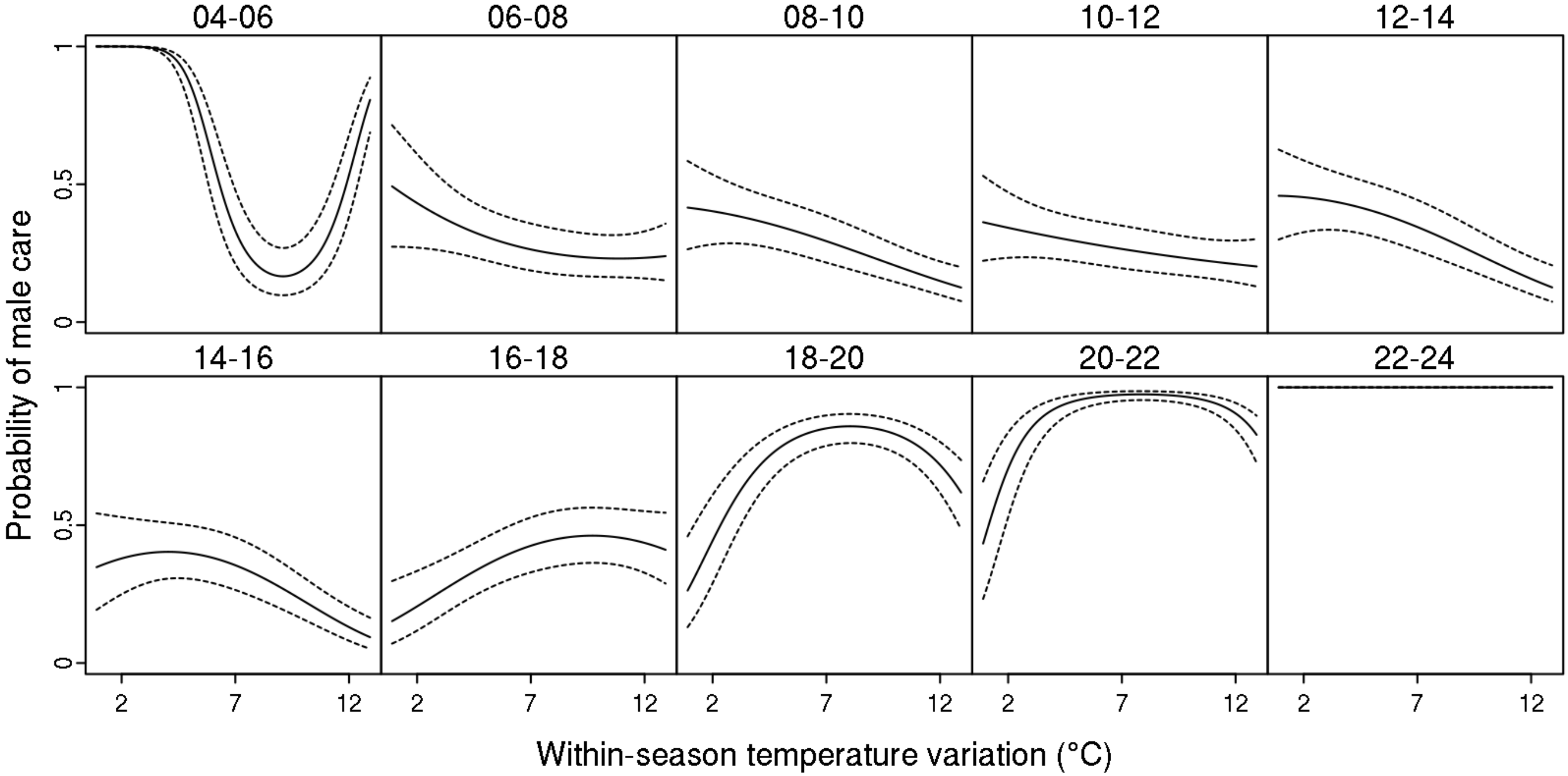
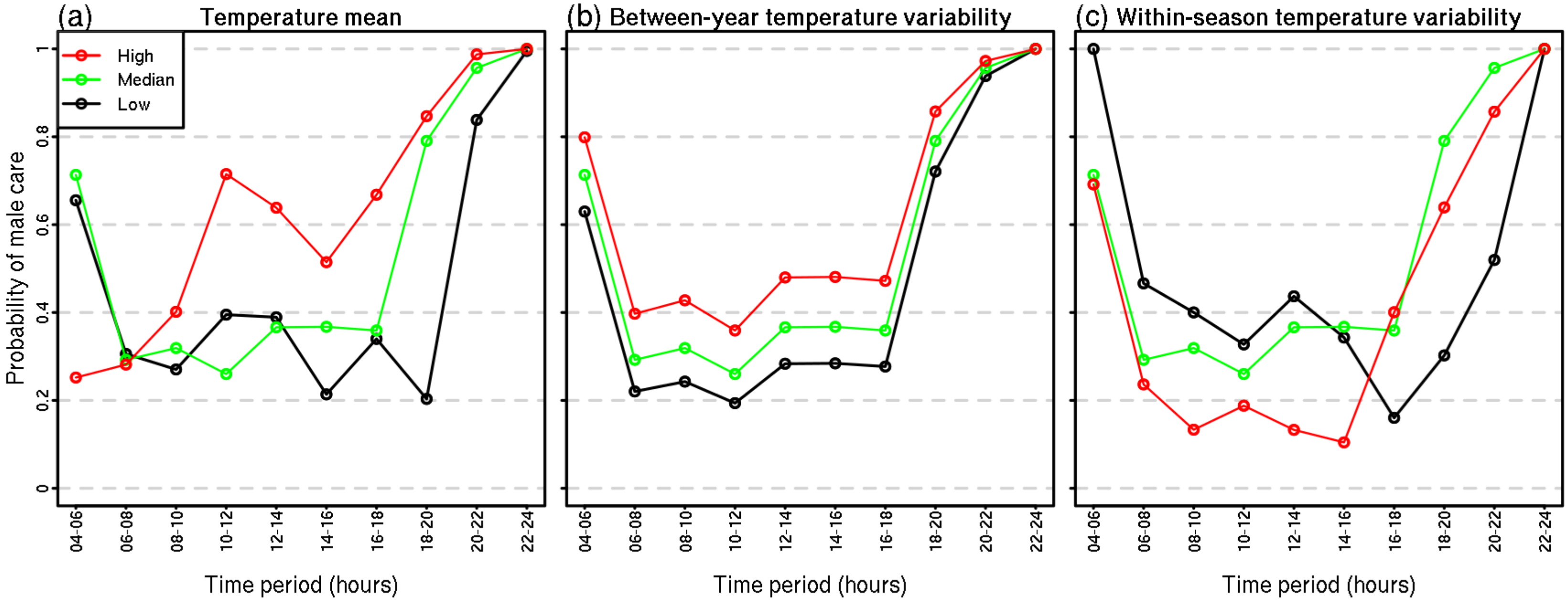

04-06
06-08
08-10
10-12
12-14
14-16
16-18
18-20
20-22
22-24
Probability of male care
0
0.5
1
2
7
12
Within-season temperature variation (°C)

Figure 3.


(a)
Temperature mean
(b)
Between-year temperature variability
(c)
Within-season temperature variability
High
Median
Low
Probability of male care
0
0.2
0.4
0.6
0.8
1
04-06
06-08
08-10
10-12
12-14
14-16
16-18
18-20
20-22
22-24
Time period (hours)

SUPPORTING INFORMATION

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Figure S1 Male share of nest attendance estimated from behavioural observations (%, behaviour) in relation to male share of nest attendance as obtained from capture data (%, capture). Each point represents a 2-hour time period. Dashed lines indicate perfect agreement between 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.

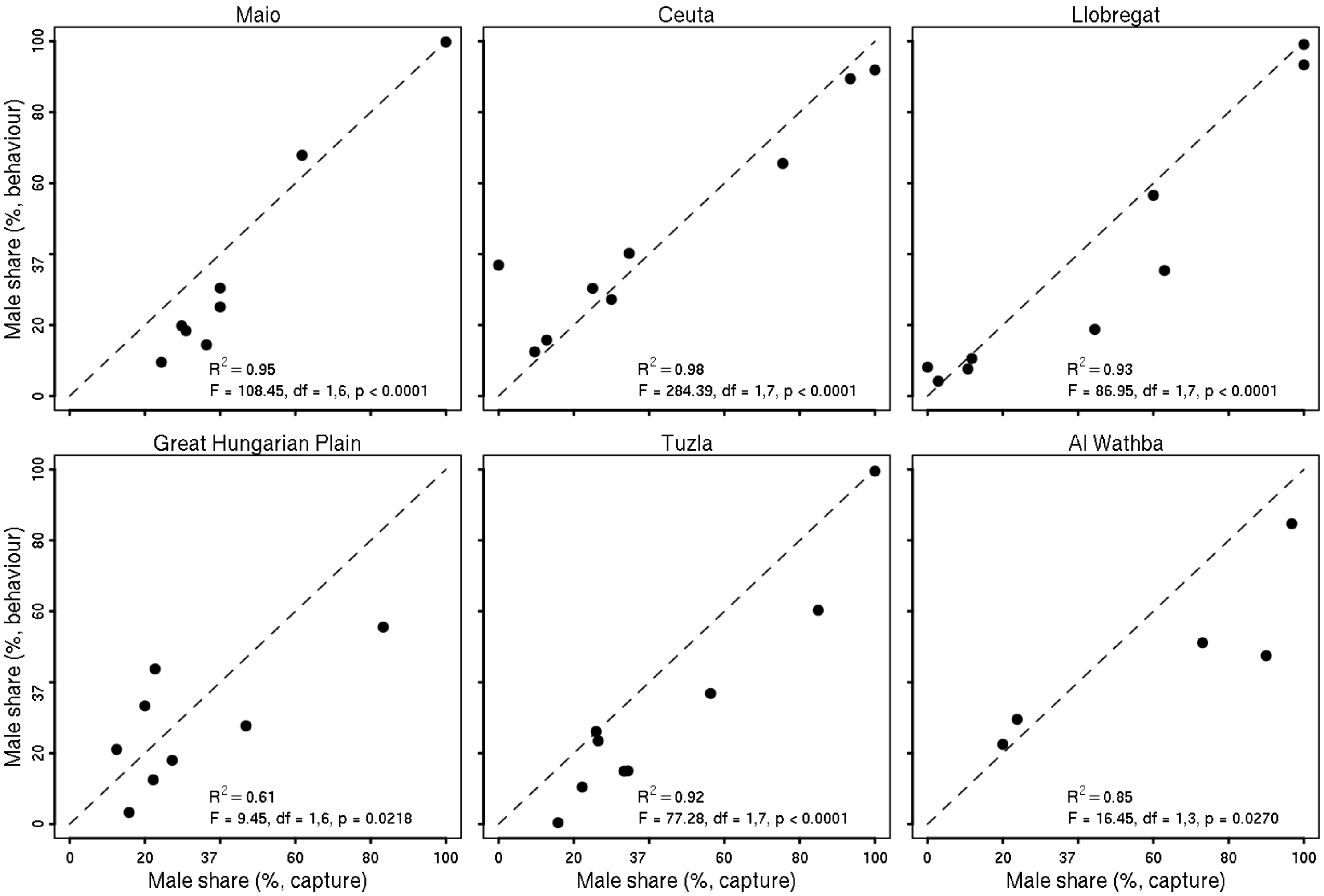

Table S1 Summary of parental care data from different populations of plovers *Charadrius spp.* Sexing method refers to molecular sexing (M), plumage and/or other morphometric measurements or behaviour based (P). Numbers in square brackets in the 'Population' column refer to the localities on the map in Figure 2. See Appendix S1 for references cited here.

Species	**Population**	**Coordinates**	**Years of data collection**	**Number of captures**	**% male captures**	**Sexing method**	**References**
C. alexandrinus	Maio Island (Cape Verde) [15]	15º09'N, 23º13'W	2007−2010	244	40.57	M, P	Székely T., A.A. Tico & A. Kosztolányi unpubl data
C. alexandrinus	Farasan Islands (Saudi Arabia) [26]	16º48'N, 41º53'E	2008−2009, 2011	45	35.56	P	AlRashidi *et al.*, 2011
C. alexandrinus	Al Wathba Wetland (United Arab Emirates) [27]	24º16'N, 54º36'E	2005−2006	175	48.00	P	Kosztolányi *et al.*, 2009, AlRashidi *et al.*, 2010
C. alexandrinus	Tuzla Lake (Turkey) [25]	36º42'N, 35º03'E	1996−2000, 2004	604	46.19	P	Kosztolányi & Székely 2002
C. alexandrinus	Fuente de Piedra Lake (Spain) [16]	37º06'N, 04º45'W	1991−1996	174	49.43	P	Fraga & Amat (1996), Amat & Masero 2004
C. alexandrinus	Bohai Bay (China) [28]	39º05'N, 118º12'E	2012	38	31.58	M, P	Que, P. & Y. Liu unpubl. data
C. alexandrinus	Llobregat Delta (Spain) [17]	41º18'N, 02º08'E	1994−1995, 1998, 2000−2008	173	41.71	P	Figuerola & Cerdà 1998
C. alexandrinus	Lagoon of Venice and Po Delta (Italy) [23]	45º10'N, 12º24'E	1993−1995	157	45.86	P	Serra, L. unpubl. data
C. alexandrinus	Great Hungarian Plain (Hungary) [24]	46º40'N, 19º10'E	1988−1994	186	39.25	P	Székely & Lessells 1993, Székely *et al.*, 1994
C. alexandrinus	Schleswig−Holstein (Germany) [21]	54º45'N, 08º01'E	1989−1998, 2001−2002, 2004−2005	530	44.34	P	Schulz, R. unpubl. data
C. alexandrinus	Falsterbo Peninsula (Sweden) [22]	55º15'N, 12º34'E	1981−1988, 1990−1991, 1993−1994, 1996	44	47.73	P	Jönsson, P. unpubl. data
C. falklandicus	Sea Lion Island (Falklands) [13]	51º41'S, 59º10'W	2005−2008	63	42.86	M, P	St Clair *et al.*, 2010b
C. falklandicus	Peninsula Valdés (Argentina) [12]	42º30'S, 63º56'W	2006−2007	62	36.51	M, P	García−Peña 2009
C. marginatus	Cape Peninsula (South Africa) [18]	34º08'S, 18º20'E	1999−2003	162	32.72	P	Lloyd, P. unpubl. data
C. marginatus	Lake Tsimanampetsotsa (Madagascar) [20]	24º48'S, 43º49'E	2005−2006, 2011−2012	41	43.90	M	Zefania, S, J. Parra & T. Székely unpubl. data
C. marginatus	Andavadoaka saltmarsh (Madagascar) [19]	22º04'S, 43º14'E	2010−2012	48	43.75	M	Zefania, S, J. Parra & T. Székely unpubl. data
C. melodus	Saskatchewan Coteau (Canada) [1]	49º44'N, 105º23'W	2002−2006	139	49.64	P	Cohen & Gratto−Trevor 2011; Gratto−Trevor 2011

C. melodus	Saskatchewan Diefenbaker (Canada) [2]	50º43'N, 107º30'W	2002−2007	268	49.44	P	Cohen & Gratto−Trevor 2011; Gratto−Trevor 2011
C. melodus	Saskatchewan Quill (Canada) [3]	51º55'N, 104º22'W	2002−2006	176	49.15	P	Cohen & Gratto−Trevor 2011; Gratto−Trevor 2011
C. modestus	Sea Lion Island (Falklands) [13]	51º41'S, 59º10'W	2005−2008	99	55.56	M, P	St Clair *et al.*, 2010a, St Clair *et al.*, 2010b
C. nivosus	Texcoco (Mexico) [11]	19º30'N, 98º29'W	2009−2012	57	21.05	P	DeSucre−Medrano, A. E. & S. Gomez del Angel unpubl. data
C. nivosus	Nayarit (Mexico) [10]	22º16'N, 105º12'W	2010−2012	44	40.91	P	Villar, C. & J. Cavitt unpubl. data
C. nivosus	Ceuta Bay (Mexico) [9]	23º54'N, 106º57'W	2006−2012	451	48.12	M, P	Küpper, C. & M. Cruz−López unpubl. data
C. nivosus	Florida (USA) [4]	29º44'N, 85º06'W	2008−2010	300	10.33		Pruner, R. unpubl. data
C. nivosus	San Quintin Bay (Mexico) [7]	30º40'N, 116º0'W	2012	45	19.57	P	Galindo−Espinosa, D. unpubl. data
C. nivosus	Texas (USA) [8]	33º12'N, 102º30'W	1999−2000, 2008−2009	127	33.86	M, P	Saalfeld *et al.*, 2011
C. nivosus	Monterey Bay (USA) [6]	36º45'N, 121º25'W	1984−1999	581	18.93	P	Warriner *et al.*, 1986, Stenzel *et al.*, 2011
C. nivosus	Great Salt Lake (USA) [5]	41º41'N, 112º55'W	2007−2010	80	22.50	P	Cavitt *et al.*, 2008, Hall & Cavitt 2012
C. pecuarius	Lake Tsimanampetsotsa (Madagascar) [20]	24º48'S, 43º49'E	2005, 2007, 2012	37	43.24	M	Zefania, S., J. Parra & T. Székely unpubl. data
C. pecuarius	Andavadoaka saltmarsh (Madagascar) [19]	22º04'S, 43º14'E	2010, 2012	118	49.15	M	Zefania, S., J. Parra & T. Székely unpubl. data
C. peronii	Prachuap Khiri Khan (Thailand) [29]	12º00'N, 99º53'E	2004−2005	65	46.97	P	Yasué & Dearden 2006a,b, 2007a,b
C. ruficapillus	Altona (Cheetham) Saltworks (Australia) [30]	37º53'S, 144º47'E	2008−2012	71	36.62	P	Lomas *et al.*, 2014, Weston, M.A. unpubl. data
C. sanctaehelenae	St. Helena Island (St. Helena) [14]	15º58'S, 05º43'W	2004, 2007−2009	48	41.67	M, P	Burns *et al.*, 2013
C. thoracicus	Lake Tsimanampetsotsa (Madagascar) [20]	24º48'S, 43º49'E	2004−2009, 2011−2012	93	31.18	M	Zefania, S, J. Parra & T. Székely unpubl. data
C. thoracicus	Andavadoaka saltmarsh (Madagascar) [19]	22º04'S, 43º14'E	2010	19	31.58	M	Zefania, S, J. Parra & T. Székely unpubl. data
C. wilsonia	Ceuta Bay (Mexico) [9]	23º54'N, 106º57'W	2009, 2012	27	37.04	P	Küpper, C. & M. Cruz−López unpubl. data

Footnote: Molecular sexing markers: P2P8, Z−002B and Calex−31 (Griffiths *et al.*, 1998, Dawson, 2007, Küpper *et al.*, 2007)

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Table S2. Sensitivity analyses for the length of the time period on which the calculation of the three climate variables was based on. χ2 values, degrees of freedom (df) and probability (p) of likelihood ratio tests are given.

Model 4		5 years		10 years		15 years	
	Fixed terms	**χ2 (df)**	**P**	**χ2 (df)**	**P**	**χ2 (df)**	**P**
	Time period	1214.40 (63)	< 0.0001	1219.2 (63)	< 0.0001	1217.70 (63)	< 0.0001
	<u>Mean temperature (°C)</u>						
	Interaction with time period	79.96 (18)	< 0.0001	77.28 (18)	< 0.0001	85.49 (18)	< 0.0001
	Quadratic effect	32.93 (10)	0.0003	32.76 (10)	0.0003	33.26 (10)	0.0002
	<u>Between−year temperature variation (°C)</u>						
	Interaction with time period	37.86 (18)	0.0040	23.35 (18)	0.1777	15.76 (18)	0.6091
	Quadratic effect	16.32 (10) *	0.0907	1.52 (1)	0.2173	1.22 (1)	0.2690
	Linear effect	6.19 (2) *	0.0452	4.67 (1)	0.0307	6.03 (1)	0.0140
	<u>Within−season temperature variation (°C)</u>						
	Interaction with time period	40.71 (18)	0.0017	32.57 (18)	0.0188	70.65 (18)	< 0.0001
	Quadratic effect	23.97 (10)	0.0077	32.76 (10)	0.0003	29.36 (10)	0.0011
	Random terms						
	Species	16.40 (1)	< 0.0001	14.49 (1)	0.0001	14.46 (1)	0.0001
	Population	0.22 (1)	0.6367	0.60 (1)	0.4400	0.07 (1)	0.7919
	Nest identity	0.00 (1)	0.9984	0.00 (1)	1.0000	0.00 (1)	1.0000

*Interaction with time period was retained in the model (similarly to the other two temperature variables) due to its significant effect.

Table S3. Description of how the effect of each variable was tested. Models were obtained from the initial model shown in bold (i.e. m0). The effect of each variable was obtained by comparing the initial model with the derived one using likelihood ratio statistics. Model identity is given for each derived model, while the 'Test' column speciefies the two models compared when testing each effect.

	Variable tested	**Test**	**Model**	**Model description**
Model 1	**Initial model**		**M1.0**	**Sex ~ Time period + (1|Species) + (1|Population) + (1|NestID)**
	Time period	M1.0 - M1.1	M1.1	− Time period
	Species	M1.0 - M1.2	M1.2	− (1|Species)
	Population	M1.0 - M1.3	M1.3	− (1|Population)
	Nest ID	M1.0 - M1.4	M1.4	− (1|NestID)
Model 2	**Initial model**		**M2_0**	**Sex ~ Time period + (1|Species) + (1|Population) + (1|Species:Time period) + (1|NestID)**
	Time period	M2.0 − M2.1	M2.1	− Time period
	Population	M2.0 − M2.2	M2.2	− (1|Population)
	Species × time period	M2.0 − M2.3	M2.3	− (1|Species:Time period)
Model 3	**Initial model**		**M3.0**	**Sex ~ Time period + (1|Species) + (1|Population) + (1|Population:Time period) + (1|NestID)**
	Time period	M3.0 − M3.1	M3.1	− Time period
	Species	M3.0 − M3.2	M3.2	− (1|Species)
	Population × time period	M3.0 − M3.3	M3.3	− (1|Population:Time period)
Model 4	**Initial model**		**M4.0**	**Sex ~ Time period + poly(Mean temperature, 2) + poly(Between−year temperature variation, 2) + poly(Within−season temperature variation, 2) + Time period:poly(Mean temperature, 2) + Time period:poly(Between−year temperature variation, 2)**

				+ Time period:poly(Within−season temperature variation, 2) + (1|Species) + (1|Population) + (1|NestID)
	Time period	M4.0 – M4.1	M4.1	− Time period − Time period:poly(Mean temperature, 2) − Time period:poly(Within−season temperature variation, 2) − Time period:poly(Between−year temperature variation, 2)
	<u>Mean temperature (°C)</u>			
	Interaction with time period	M4.0 – M4.2	M4.2	− Time period:poly(Mean temperature, 2)
	Quadratic effect	M4.0 – M4.3	M4.3	− poly(Mean temperature, 2) − Time period:poly(Mean temperature, 2) + Mean temperature + Time period:Mean temperature
	<u>Between−year temperature variation (°C)</u>			
	Interaction with time period	M4.0 – M4.4	M4.4	− Time period:poly(Between−year temperature variation, 2)
	Quadratic effect	M4.4 − M4.5[*]	M4.5	− poly(Between−year temperature variation, 2) + Between−year temperature variation
	Linear effect	M4.5 − M4.6[**]	M4.6	− Between−year temperature variation
	<u>Within−season temperature variation (°C)</u>			
	Interaction with time period	M4.0 – M4.7	M4.7	− Time period:poly(Within−season temperature variation, 2)
	Quadratic effect	M4.0 – M4.8	M4.8	− poly(Within−season temperature variation, 2) − Time period:poly(Within−season temperature variation, 2) + Within−season temperature variation + Time period:Within−season temperature variation
	Species	M4.0 – M4.9	M4.9	− (1|Species)
	Population	M4.0 – M4.10	M4.10	− (1|Population)
	Nest identity	M4.0 – M4.11	M4.11	− (1|NestID)

[*] Interaction effect was not significant, therefore we compared M4.5 to the model without interaction (M4.4) instead of the initial model (M4.0).

[**] Neither interaction, nor quadratic effects were significant, therefore we compared M4.6 to the model without interaction and quadratic effect (M4.5) instead of the initial model (M4.0).

Appendix S2. Description of the Bayesian modelling framework.

To test how phylogenetic relatedness might influence our results we we constructed Bayesian MCMCglmm models implemented in R package 'MCMCglmm' with categorical trait distribution (Hadfield 2010). The phylogenetic tree was obtained from Dos Remedios et al. (2015). Since prior information about parameter distribution was not available, we used non-informative priors. All models were run for 101,000 times with a burn-in of 1,000 and a thinning interval of 10. Fixed and random effects in the initial, as well as in derived models were identical to the modelling framework presented in Table S2, except in the case of mixed models, m5 and m6 for Model 4: these models were derived from the initial model (m0) and their DIC values were compared to the initial models'. Phylogenetic effect was tested by removing the phylogeny regarding the the Species random term, while keeping the latter random term in the model. Species effect was tested by removing phylogeny information and the Species random term. Phylogenetic signal, as reflected by Pagel's λ was calculated for all four initial models, following Wilson *et al.*, 2010.

Prior specifications are given bellow, where *n* stands for the number of fixed parameters estimated in each of the models, Phylogeny is a phylogenetic tree representing the evolutionary history of the 12 *Charadrius* species included in this study. Number of G structure elements in the prior was modified according to the number of random factors in each model.

```
Prior = list(   R = list(V = n, fix = 1),
                G = list(  G1 = list(V = 1, nu = 1, alpha.mu = 0, alpha.V = 1000),
                           G2 = list(V = 1, nu = 1, alpha.mu = 0, alpha.V = 1000),
                           G3 = list(V = 1, nu = 1, alpha.mu = 0, alpha.V = 1000)),
                B = list(mu = rep(0, n), V = diag(n) * (1 + pi^2/3)))
inv.phylo <- inverseA(Phylogeny, nodes = "TIPS", scale = TRUE)

Model_1 <- MCMCglmm(Sex ~ Time period,
                random = ~ Species + Population + NestID,
                family = 'categorical',
                ginverse = list(Species = inv.phylo$Ainv),
                prior = Prior, nitt = 101000, burnin = 1000, thin = 10)
```

```
Model_2 <- MCMCglmm(Sex ~ Time period,
                random = ~ Species:Time period + Population + NestID,
                family = 'categorical',
                prior = Prior, nitt = 101000, burnin = 1000, thin = 10)

Model_3 <- MCMCglmm(Sex ~ Time period,
                     random = ~ Species + Population:Time period + NestID, family='categorical',
                     ginverse = list(Species = inv.phylo$Ainv),
                     prior = Prior, nitt = 101000, burnin = 1000, thin = 10)

Model_4 <- MCMCglmm(Sex ~ Time period
                     + poly(Mean temperature, 2)
                     + poly(Between-year temperature variation, 2)
                     + poly(Within-season temperature variation, 2)
                     + Time period:poly(Mean temperature, 2)
                     + Time period:poly(Between-year temperature variation, 2)
                     + Time period:poly(Within-season temperature variation, 2),
                     random = ~ Species + Population + NestID,
                     family = 'categorical',
                     ginverse = list(Species = inv.phylo$Ainv),
                     prior = Prior, nitt = 101000, burnin = 1000, thin = 10)

Pagel's λ <- Model$VCV[, "Species"]/(Model$VCV[, "Species"] + Model$VCV[, "units"] + pi^2/3)
```

References

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Table S4. Results of MCMCglmms explaining variation in male incubation (binary response variable) in different plover species and populations (n = 5591 individuals). Initial models include species, population and nest ID as random factors, as well as a correlational matrix between species, according to their phylogenetic history. All variables were tested by removing them from the initial model and comparing the derived model to the initial one using Deviance Information Criteria (DIC). Note that model 2 was not controlled for phylogeny, as this was not permitted by the model set up. All Δ_{DIC} shows the DIC difference of the derived model compared to the initial one. Positive Δ_{DIC} values indicate a worse fit of the derived model compared to the global models, while negative values indicate the opposite.

		DIC	**Δ_{DIC}**
Model 1	Sex ~ Time period, random = ~ Species + Population + NestID	5139.97	
	Fixed term		
	Time period	6052.2	912.23
	Random terms		
	Species	5144.01	4.04
	Population	5198.18	58.21
	Nest ID	5140.12	0.15
	Phylogeny	5141.92	1.96
	λ = 0.14 (95% HPD interval 0.00-0.32)		
Model 2	Sex ~ Time period, random = ~ Time period:Species + Population + NestID	5020.15	
	Fixed term		
	Time period	6040.62	1020.46
	Random terms		
	Population	5070.51	50.36
	Species x time period	5141.74	121.59
Model 3	Sex ~ Time period, random = ~ Species + Time period:Population + NestID	4942.95	
	Fixed term		
	Time period	5997.86	1048.07

	Random terms		
	Species	4935.61	− 6.76
	Population x time period	5140.15	217.17
	Phylogeny	4942.25	− 1.09
	λ = 0.10 (95% HPD interval 0.00-0.30)		
Model 4	Sex ~ Time period + poly(Mean temperature, 2) + poly(Between−year temperature variation, 2) + poly(Within−season temperature variation, 2) + Time period:poly(Mean temperature, 2) + Time period:poly(Between−year temperature variation, 2) + Time period:poly(Within−season temperature variation, 2), random = ~ Species + Population + NestID	5045.83	
	Fixed terms		
	Time period	6050.89	1005.05
	Mean temperature (°C)		
	Interaction with time period	5090.31	44.48
	Quadratic effect	5066.16	20.33
	Between−year temperature variation (°C)		
	Interaction with time period	5048.69	2.86
	Quadratic effect	5054.32	8.48
	Within−season temperature variation (°C)		
	Interaction with time period	5074.61	28.78
	Quadratic effect	5061.96	16.13
	Random terms		
	Species	5047.73	1.89
	Population	5049.35	3.52
	Nest identity	5045.97	0.14
	Phylogeny	5047.65	1.82
	λ = 0.19 (95% HPD interval 0.03-0.39)		