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

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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. 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 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 care (Clutton-Brock 1991; McGraw *et al.*, 2010; Royle *et al.*, 2012; Székely 2014; Bulla *et al.*, 2014). 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 grassland, tropical beaches, salt marshes, sand dunes, semi-deserts, deserts and high altitude mountain lake shores (Piersma & Wiersma 1996). This immense 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).

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

METHODS

Fieldwork

Fieldwork was carried out in 36 breeding populations, 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 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 bellow) 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

Figure S1 for schematic illustration of hypothesis testing).

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 mid-day 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.

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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.

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Table 1 Male incubation (binary response variable) in different plover species and populations (n = 5591 individuals). Mixed effects models. χ2 values, degrees of freedom (df) and probability (p) of likelihood ratio tests are given.

		χ2 (df)	**P**
Model 1	**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	**Fixed term**		
	Time period	64.58 (9)	< 0.0001
	Random terms		
	Population	38.26 (1)	< 0.0001
	Species x time period	36.87 (1)	< 0.0001
Model 3	**Fixed term**		
	Time period	176.43 (9)	< 0.0001
	Random terms		
	Species	11.37 (1)	0.0007
	Population x time period	85.05 (1)	< 0.0001
Model 4	**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.

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.

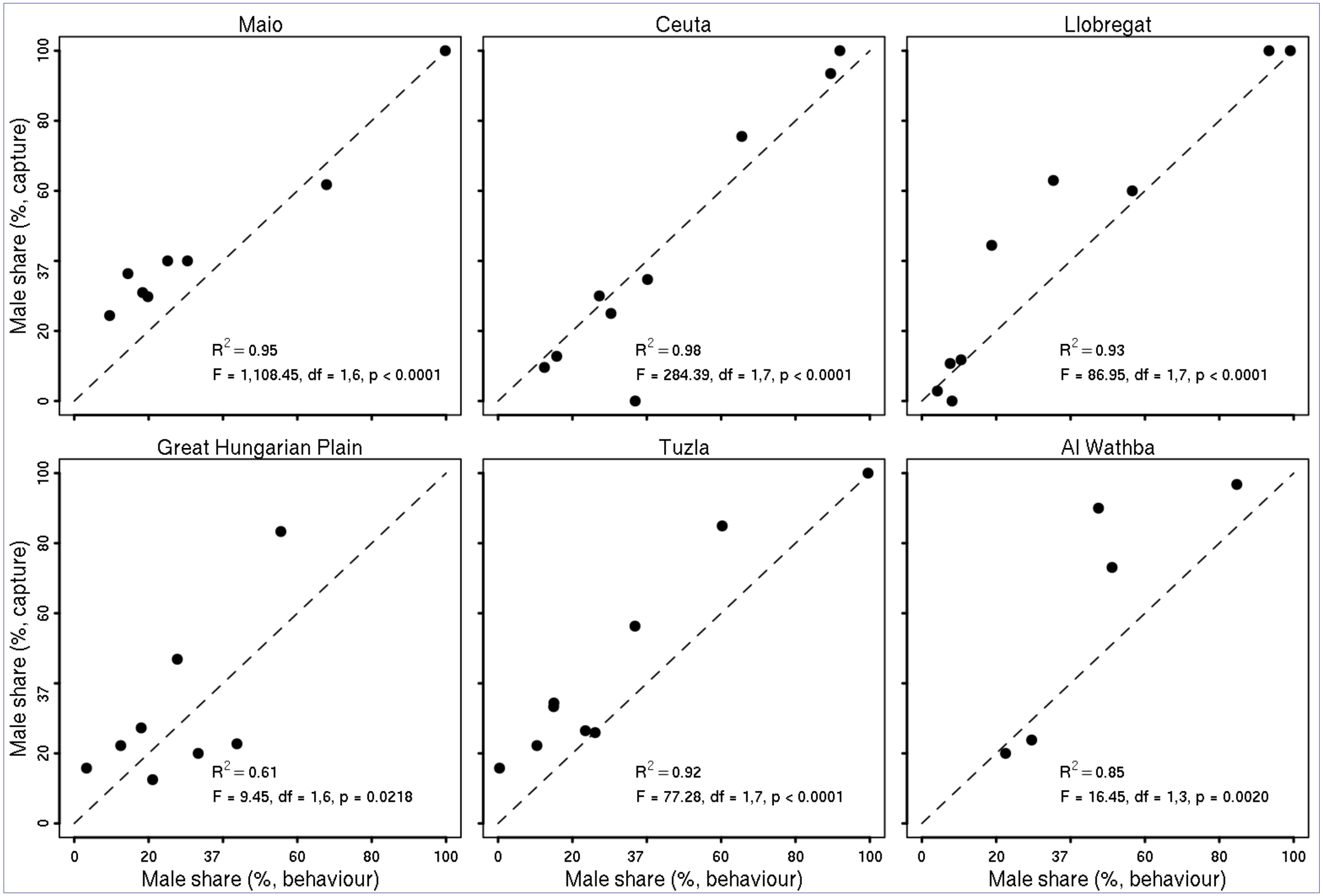
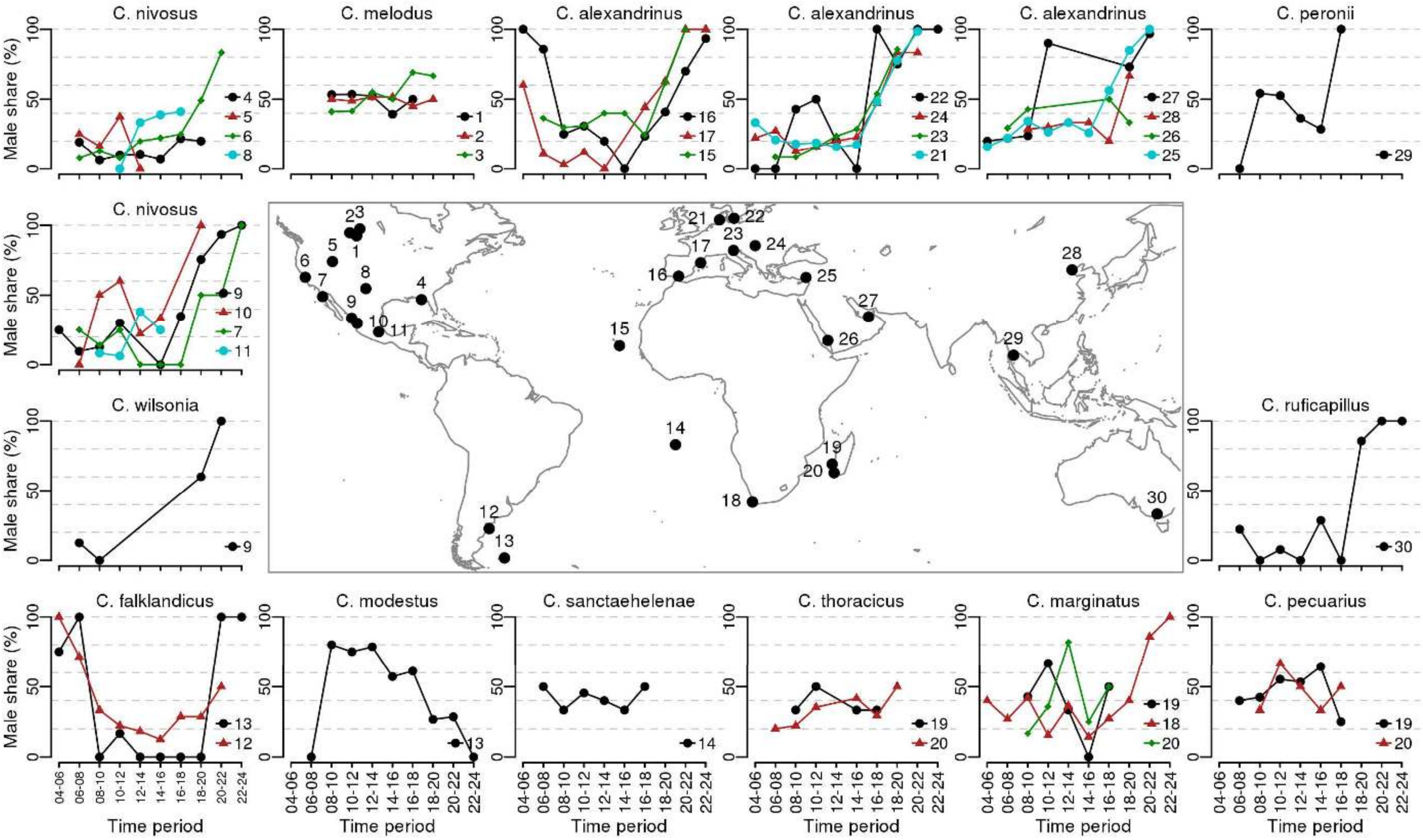

Maio
Ceuta
Llobregat
Great Hungarian Plain
Tuzla
Al Wathba
Male share (%, capture)
Male share (%, behaviour)
0
20
37
60
80
100
$R^2 = 0.95$
F = 1,108.45, df = 1,6, p < 0.0001
$R^2 = 0.98$
F = 284.39, df = 1,7, p < 0.0001
$R^2 = 0.93$
F = 86.95, df = 1,7, p < 0.0001
$R^2 = 0.61$
F = 9.45, df = 1,6, p = 0.0218
$R^2 = 0.92$
F = 77.28, df = 1,7, p < 0.0001
$R^2 = 0.85$
F = 16.45, df = 1,3, p = 0.0020

Figure 2.


C. nivosus
4
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C. melodus
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C. alexandrinus
16
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C. alexandrinus
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C. alexandrinus
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26
25
C. peronii
29
C. nivosus
9
10
7
11
C. wilsonia
9
C. ruficapillus
30
C. falklandicus
13
12
C. modestus
13
C. sanctaehelenae
14
C. thoracicus
19
20
C. marginatus
19
18
20
C. pecuarius
19
20
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
1
2
3
4
5
6
7
8
9
10
11
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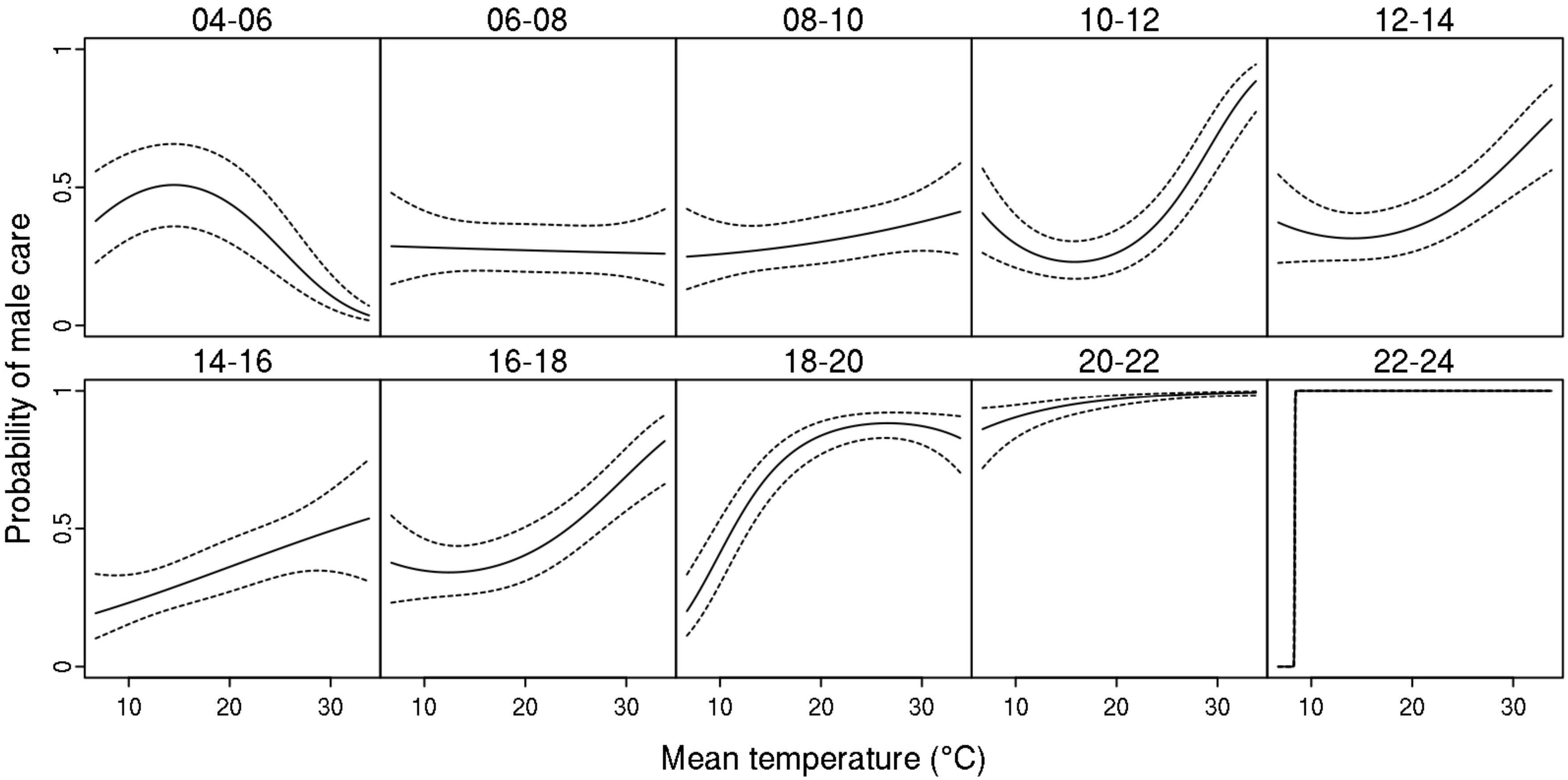
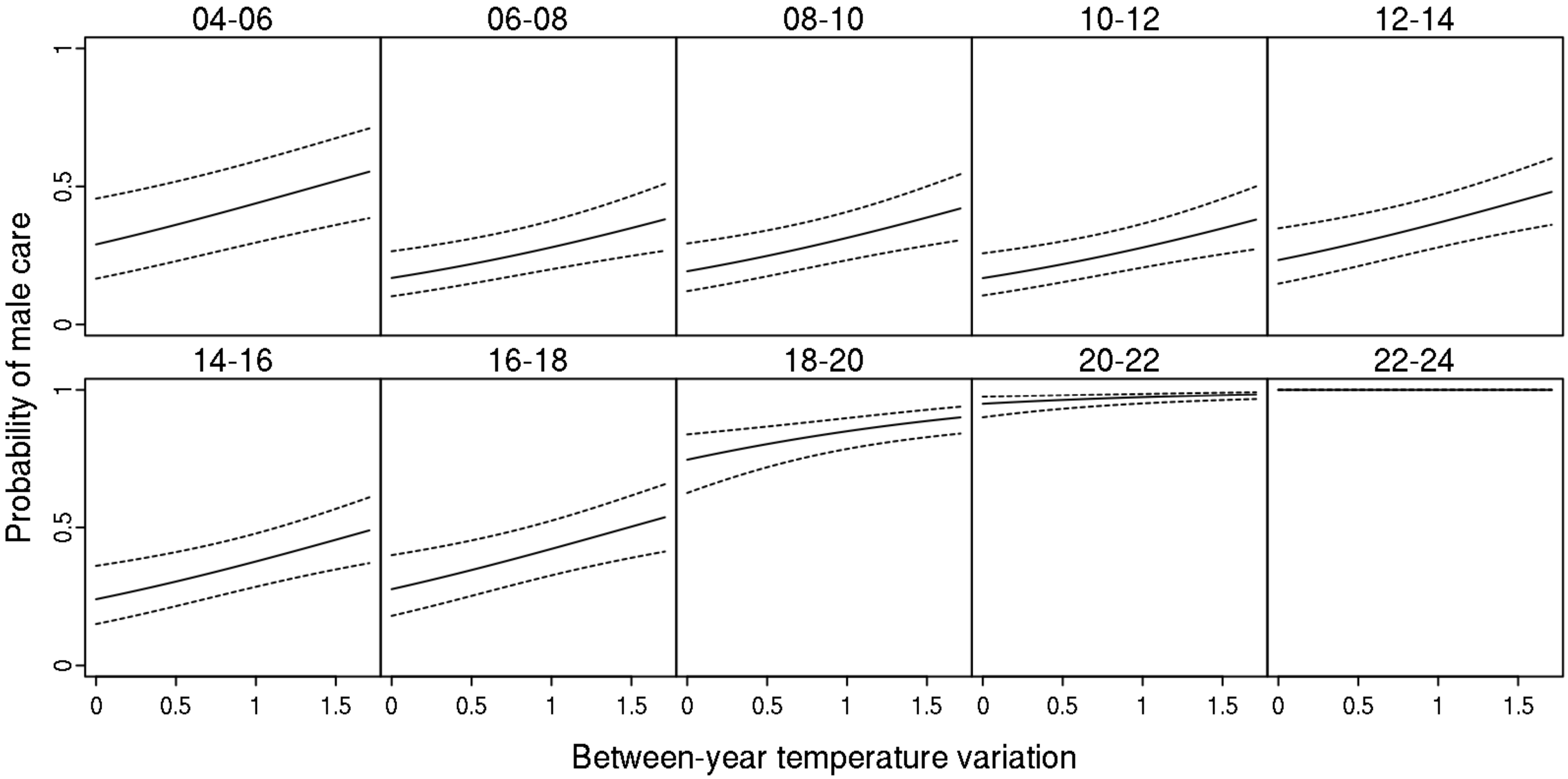
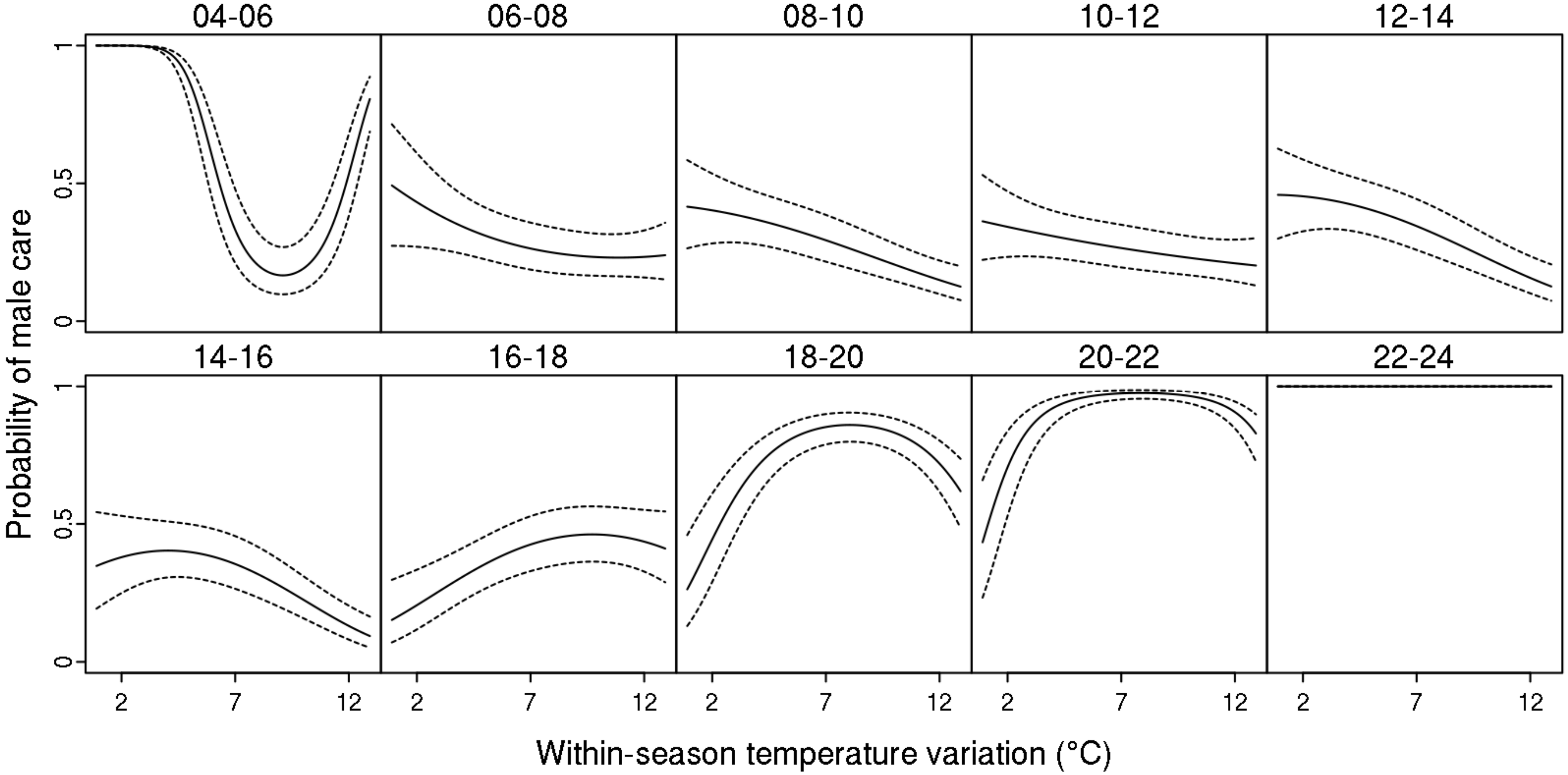
676 **Figure 3 (a)**



677 **Figure 3 (b)**

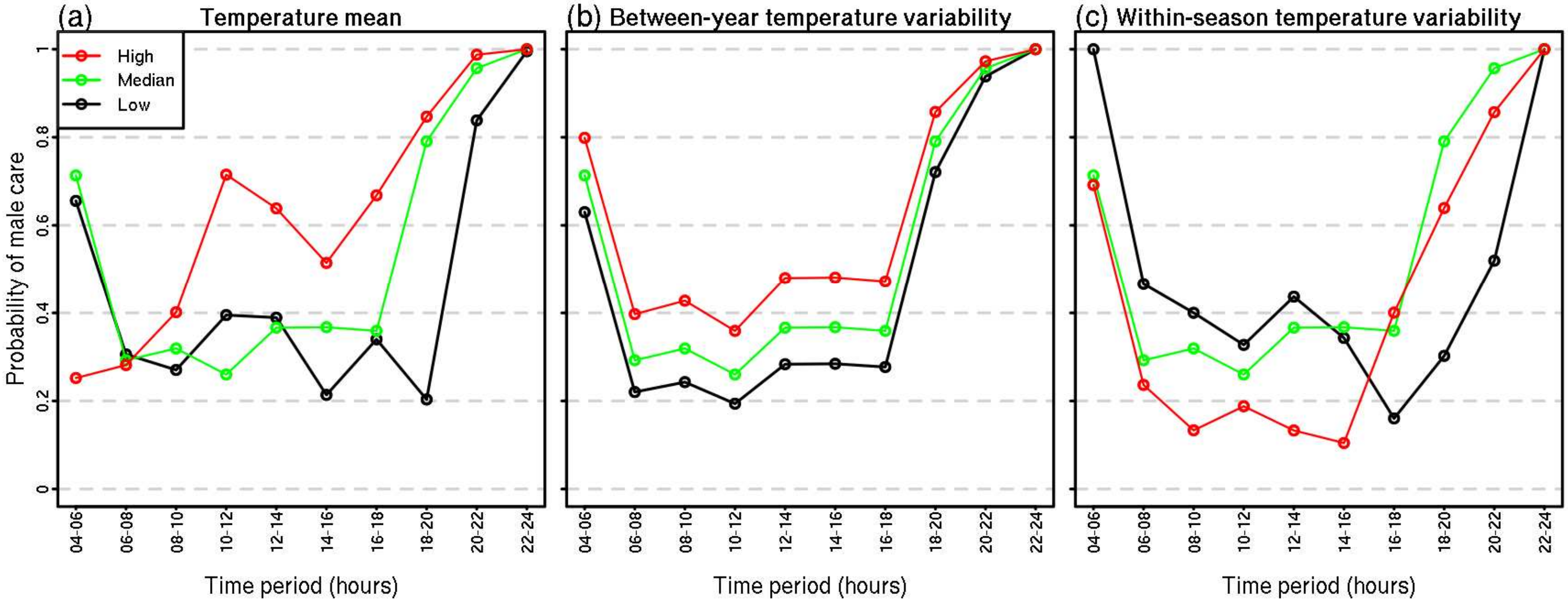


678 **Figure 3 (c)**



679

Figure 4.


(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

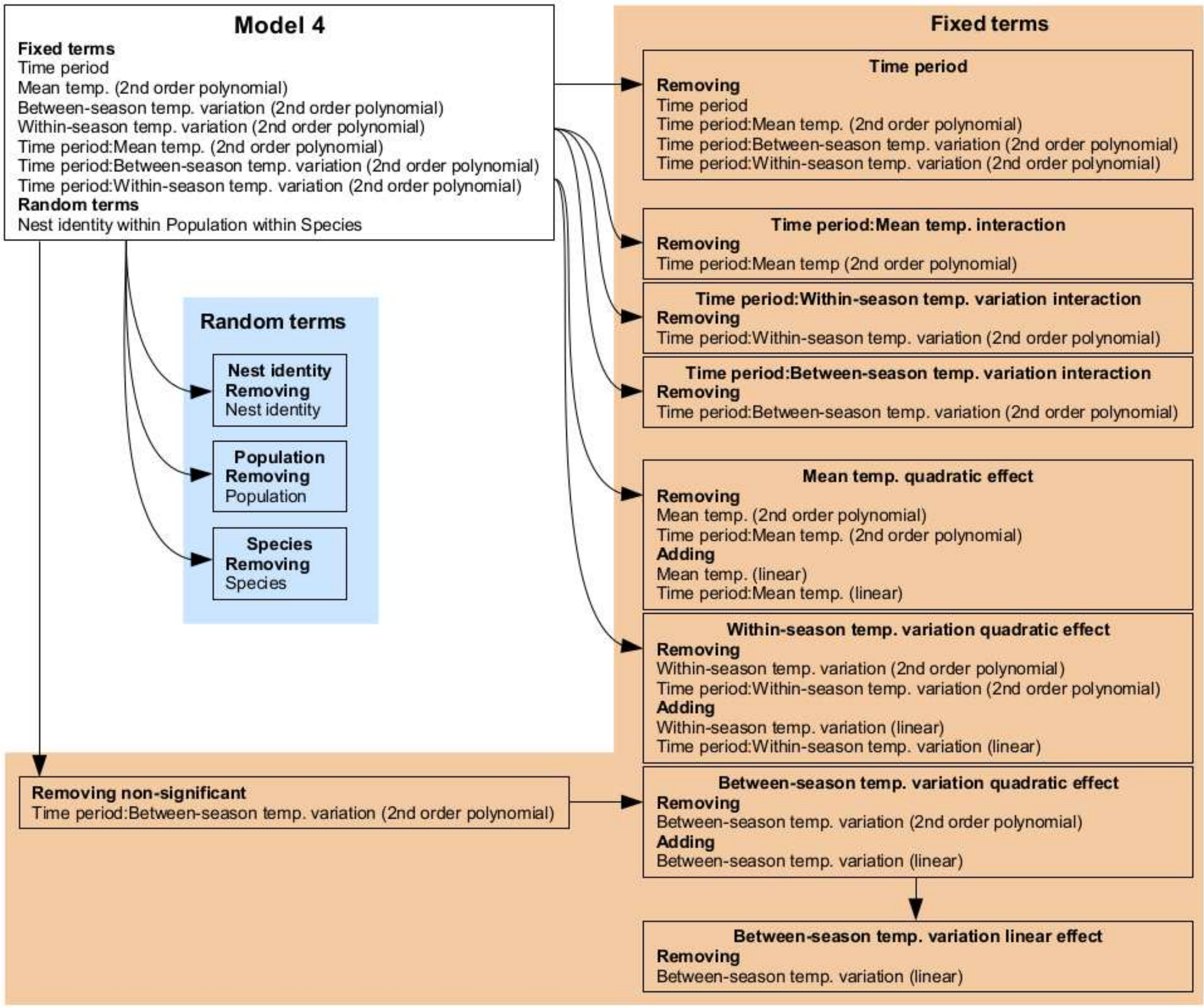


Figure S1. Schematic presentation of how the effect of each variable was tested. All derived models (i.e. shown by arrowheads) were compared to the model from which they originate (i.e. shown by the base of the arrows). Models were compared using likelihood ratio statistics.

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.

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.*, 2010a
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	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	P, M	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 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	P, M	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, M	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)

Table S2. Sensitivity analyses for the length of the time period on which the calculation of the three climate variables was based on.

Model 4	**Fixed terms**	5 years		10 years		15 years	
	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-season 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 retained in model (similarly to the other two temperature variables) due to its significant effect.

Appendix S1. Supplementary references for Table S1

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