

RESEARCH
PAPER

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

Orsolya Vincze^{1,2*}, András Kosztolányi^{1,3}, Zoltán Barta¹, Clemens Küpper⁴, Monif Alrashidi⁵, Juan A. Amat⁶, Araceli Argüelles Ticó⁷, Fiona Burns⁸, John Cavitt⁹, Warren C. Conway¹⁰, Medardo Cruz-López¹¹, Atahualpa Eduardo Desucre-Medrano¹², Natalie dos Remedios¹³, Jordi Figuerola⁶, Daniel Galindo-Espinosa¹⁴, Gabriel E. García-Peña^{15,16}, Salvador Gómez Del Angel¹², Cheri Gratto-Trevor¹⁷, Paul Jönsson¹⁸, Penn Lloyd¹⁹, Tomás Montalvo²⁰, Jorge Enrique Parra⁷, Raya Pruner²¹, Pinjia Que²², Yang Liu²³, Sarah T. Saalfeld²⁴, Rainer Schulz²⁵, Lorenzo Serra²⁶, James J. H. St Clair²⁷, Lynne E. Stenzel²⁸, Michael A. Weston²⁹, Maï Yasué³⁰, Sama Zefania³¹ and Tamás Székely⁷

¹MTA-DE 'Lendület' Behavioural Ecology Research Group, Department of Evolutionary Zoology and Human Biology, University of Debrecen, Debrecen, 4032, Hungary, ²Evolutionary Ecology Group, Hungarian Department of Biology and Ecology, Babeş-Bolyai University, Cluj Napoca, 400006, Romania, ³Department of Ecology, University of Veterinary Medicine Budapest, Budapest, 1077, Hungary, ⁴Institute of Zoology, University of Graz, 8010 Graz, Austria, ⁵Department of Biology, Faculty of Science, University of Ha'il, Ha'il, Saudi Arabia, ⁶Estación Biológica de Doñana (EBD-CSIC), Calle Américo Vespucio s/n, Sevilla 41092, Spain, ⁷Biodiversity Lab, Department of Biology and Biochemistry, University of Bath, Bath BA1 7AY, UK, ⁸The RSPB Centre for Conservation Science, Sandy, Bedfordshire SG19 2DL, UK, ⁹Avian Ecology Laboratory Department of Zoology, Weber State University, Ogden, UT 84408, USA, ¹⁰Department of Natural Resources Management, Texas Tech University, Lubbock, TX 79409, USA, ¹¹Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Cd. México, 04510, México, ¹²Laboratorio de Zoología, Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla 54000, México, ¹³Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK, ¹⁴Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional, Baja California Sur, 23096, México, ¹⁵CESAB – Centre de Synthèse et d'Analyse sur la Biodiversité, Aix-en-Provence Cedex 3, 13857, France, ¹⁶Facultad de Medicina Veterinaria y Zootecnia, Universidad Nacional Autónoma de México, Cd. México 04510, México, ¹⁷Prairie and Northern Wildlife Research Centre, Science and Technology Branch, Environment Canada, Saskatoon, SK S7N 0X4, Canada, ¹⁸Department of Biology, Lund University, Lund, 22362, Sweden, ¹⁹Percy FitzPatrick Institute, DST/NRF Centre of Excellence, University of Cape Town, Rondebosch 7701, South Africa, ²⁰Servei de Vigilància i Control de Plagues Urbanes, Agència de Salut Pública de Barcelona, Barcelona, 08012, Spain, ²¹Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611-0430, USA, ²²Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, College of Life Sciences, Beijing Normal University, Beijing, 100875, China, ²³State Key Laboratory of Biocontrol and College of Ecology and Evolution, Sun Yat-Sen University, Guangzhou 510275, China, ²⁴US Fish and Wildlife Service, Migratory Bird Management, Anchorage, Alaska 99503, USA, ²⁵Schutzstation Wattenmeer Nationalparkhaus, Husum 25813, Germany, ²⁶Istituto Superiore per la Protezione e Ricerca Ambientale (ISPRA), Ozzano dell'Emilia BO, 40064, Italy, ²⁷Centre for Evolutionary Biology, University of Western Australia, Crawley, WA 6009, Australia, ²⁸Point Blue Conservation Science, Petaluma, CA 94954, USA, ²⁹Deakin University, Geelong, Australia, Centre for Integrative Ecology, School of Life and Environmental Sciences, Faculty of Science, Engineering and the Built Environment, Deakin University, Burwood, Vic 3125, Australia, ³⁰Quest University

ABSTRACT

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

Location

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, probably 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.

*Correspondence: Orsolya Vincze, Department of
Evolutionary Zoology and Human Biology, University of
Debrecen, Debrecen 4032, Hungary.
E-mail: orsolya.vincze@vocs.unideb.hu

Keywords

Climate, environmental stochasticity, global change, parental care,
parental cooperation, seasonal environment.

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, and 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 the behavioural responses of animals to climate change, 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 that 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 that 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.*, 2016). 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 shortage. 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; Tököllyi *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 2 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 those that are optimal for 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). However, if the

environmental conditions 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 workload. Incubation in most bird species is provided by one parent only, typically the female. In the rare cases 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 temperature (stochasticity). The latter is expected, since high inter-annual environmental fluctuations increase the probability of extreme events (Easterling *et al.*, 2000). Additionally, we test the effect of environmental change within the breeding season (seasonality). We predict an increased male share in highly seasonal environments, since seasonality restricts breeding time and re-mating opportunities, thus increasing the value of the current brood relative to future broods. Under such a scenario, higher levels of cooperation between the parents are 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, 1975). Birds in the tropics generally have a slower pace of life, as reflected by a lower reproductive rate, smaller clutch sizes, higher survival, slower development and extended post-natal parental provisioning (Martin, 1996; Russell *et al.*, 2004) requiring males to perform an elevated share of parental care.

In this study we use data from 36 plover populations. Plovers (*Charadrius* spp.) are ground-nesting shorebirds with a body mass ranging from approximately 20 g to 50 g. Although the ancestor of this monophyletic group probably 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-elevation 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 two to four eggs in poorly insulated scrapes. Incubation is usually carried out by both parents, although the extent of involvement of males 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.*, 2010).

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 55° N and 52° S latitude, and between 145° E and 121° W longitude). To examine how climate influences incubation behaviour, we used the space-for-time substitution approach, a powerful ecological method (Pickett, 1989), to infer temporal trends from spatial data. 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 1 to 16 breeding seasons per population (see Table S1 in the Supporting Information). Parents were captured on their nest while incubating, using funnel traps, noose mats, box traps or bownet traps (see Székely *et al.*, 2008 for general methodology; specific references are 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 3 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-h time periods following previous analyses of incubation patterns in small plovers (Alrashidi *et al.*,

2011; Vincze *et al.*, 2013). Records between 00:00 h and 04:00 h were not included in data analyses, since we lacked such data from most populations. To estimate the division of parental care between the sexes, we used the sex of the incubating parent as binary response variable in statistical models. A total of 5591 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 the male share estimated from capture data with the 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-h time period. Based on behavioural observations, *male share* (% , *behaviour*) was calculated as the percentage of the total time the nest was incubated by either parent in a given 2-h time period that was incubated by males. The relationship between capture-based and behavioural observation-based estimates of male share was analysed using linear regressions for the six populations separately, where each 2-h time period represented a datum. These data points were weighted by the number of captures in each 2-h time period, since the precision of the estimate of male share (% , *capture*) is expected to increase with the total number of individuals captured in a given time period. In addition, to test whether the association between capture-based and behavioural observation-based male share is similar across populations we constructed a pooled mixed-effects model. This model included male share (% , *behaviour*) as a dependent variable, male share (% , *capture*) as a fixed covariate, population as random factor, and a random intercept and random slope for male share (% , *capture*), i.e. 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 ($0.5^\circ \times 0.5^\circ$). 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 experienced by the plovers 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 years of data collection in each population. Note that although results presented are based on 20 years of climate data, 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.

1. *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.
2. *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.
3. *Within-season temperature variation* was obtained in two steps. First, we calculated the average temperature of each breeding season month 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, Tököllyi *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 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 correlations). 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 division of care and environmental data. To account for 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; 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-h windows between 04:00 h and 24:00 h). 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 nonlinear 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 IDs (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 $\times$ time period interaction in addition to the terms in Model 1, while in Model 3 the population $\times$ 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 with the original using likelihood ratio statistics (Table S3).

To test whether phylogenetic relatedness influenced our results, the above models were repeated using Bayesian Markov chain Monte Carlo generalized linear mixed models, including a correlational structure based on the species-level phylogenetic tree of the 12 *Charadrius* species studied here (model description and calculation of the 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, the 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/fac#predconf> (last accessed 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 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.

RESULTS

Consistency between captures and behavioural observations

Capture-based behavioural estimates reflect the division of parental care in plovers, since capture-based estimates of male share were good predictors of male share obtained by behavioural observations (Fig. S1, $R^2 = 0.61\text{--}0.97$, $n = 6$ populations). In the model that incorporated data from all six of these populations the random slope term was not significant [χ^2 (d.f.) = 0.41 (2), $P = 0.8154$], indicating a similar slope between behaviour- and capture-based estimates of male share across populations. Taken together, these results suggest that male share estimated on the basis of capture data gives congruent estimates of care division to those based on 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 *Charadrius melodus*, males and females spent comparable times on incubation throughout the day (Fig. 1). On the other hand, incubation sharing followed a diurnal pattern in species such as *Charadrius alexandrinus*, *Charadrius ruficapillus* and *Charadrius modestus* (Fig. 1). Furthermore, there were considerable differences in daily patterns of incubation among the different populations of the same species (Fig. 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). The male share of incubation generally increased with mean ambient temperature. This effect, however, was dependent on the time of day, as indicated by the significant interaction between time period and mean ambient temperature. For example, during daylight hours (08:00–20:00 h) the male share of incubation increased with mean ambient temperature, though the increase was nonlinear and varied depending on the time window (Fig. 2a).

Temperature fluctuations also predicted incubation (Fig. 2b,c). Between-year variation tended to have a linear influence on daily shifts: male share of incubation increased with

Table 1 Male incubation (binary response variable) in different plover species and populations ($n = 5591$ individuals)

		χ^2 (d.f.)	P
Model 1	Sex ~ Time period + (1 Species) + (1 Population) + (1 Nest ID)		
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 Nest ID)		
Fixed term	Time period	64.58 (9)	< 0.0001
Random terms	Population	38.26 (1)	< 0.0001
	Species $\times$ time period	36.87 (1)	< 0.0001
Model 3	Sex ~ Time period		
	+ (1 Species) + (1 Population) + (1 Population:Time period) + (1 Nest ID)		
Fixed term	Time period	176.43 (9)	< 0.0001
Random terms	Species	11.37 (1)	0.0007
	Population $\times$ 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 Nest ID)		
Fixed terms	Time period	1216.20 (63)	< 0.0001
	Mean temperature ($^{\circ}\text{C}$)		
	Interaction with time period	84.42 (18)	< 0.0001
	Quadratic effect	32.03 (10)	0.0004
	Between-year temperature variation ($^{\circ}\text{C}$)		
	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 ($^{\circ}\text{C}$)		
	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 ID	0.00 (1)	1.0000

Mixed-effects models. χ^2 values, degrees of freedom (d.f.) and probability (P) of likelihood ratio tests are given.

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 the full model and comparing the resulting model with the original. Quadratic terms were tested by replacing polynomial (marked with “poly”) with linear terms, and comparing the resulting model with the original (see Table S2 for full details of the testing procedures).

variation in temperature between years and this effect was similar throughout the day (Fig. 2b). Within-season temperature variation also predicted shifts in the daily routines of males relative to females: with increasing change in temperature during the breeding season, male share generally decreased between 06:00 h and 16:00 h. The effect of within-season temperature variation, however, was strongly nonlinear early in the morning and in the evening (Fig. 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 temperature this happened at the expense of a lowered share of care during the early morning hours (Fig. 3a,b). Furthermore, with increasing within-season temperature range, the male share of incubation decreases until the afternoon (Fig. 3c).

DISCUSSION

Three major insights have emerged from our study regarding the effects of climate on parental behaviour. First, the

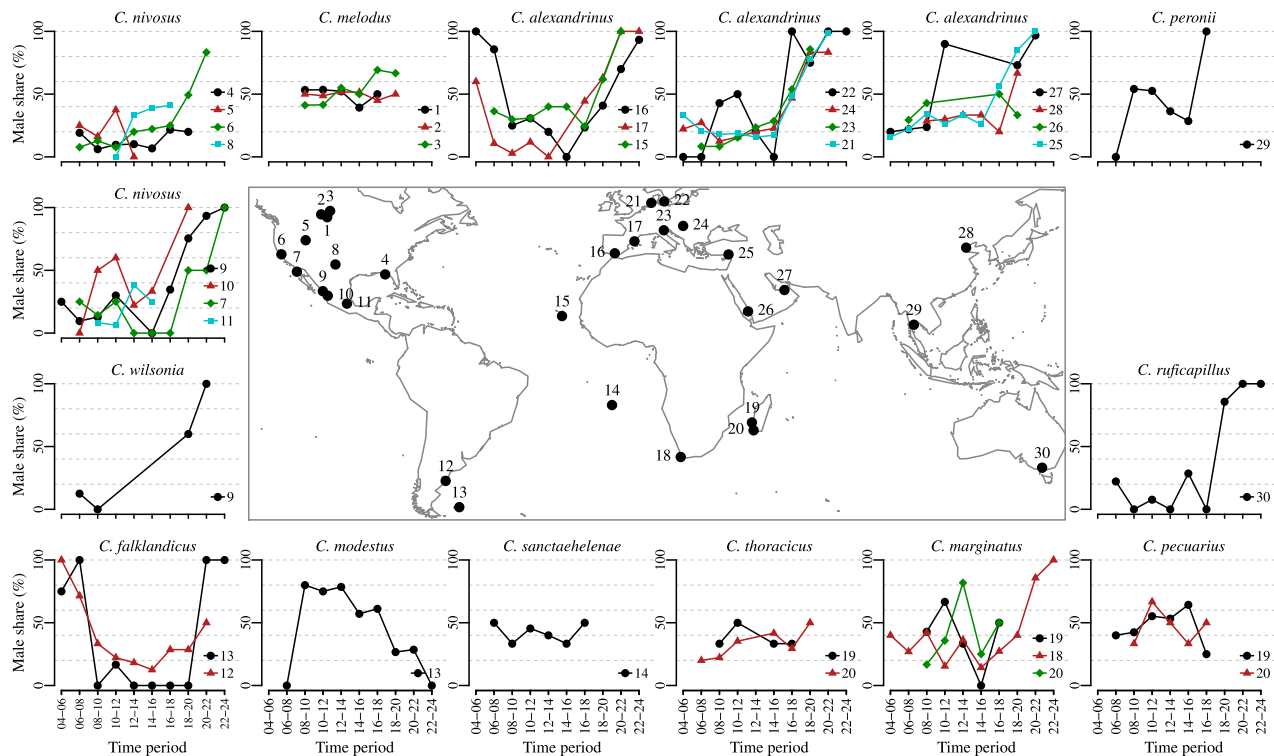


Figure 1 Male share of nest attendance (%) calculated from capture data in 36 populations. Each species is plotted in a different panel, except Kentish plover (*Charadrius alexandrinus*) and snowy plover (*Charadrius nivosus*) which are shown on three and two panels, respectively. Each line represents a population. Legends refer to location numbers on the map (see Table S1 for population names and exact coordinates, and Appendix S1 for references).

contribution of males to parental care was strongly influenced by ambient temperature. Second, temperature effects on behaviour varied with time of the day: not only did overall care division change with changing environmental conditions, but the daily routine of care division was also affected. Specifically, the share of parental care carried out by males 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, geographical variation in the division of care 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 the division of care 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 climatic 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 a greater frequency of extreme events (Vasseur *et al.*, 2014; IPCC, 2014; Lawson *et al.*, 2015), our findings suggest that patterns of parental care will shift in the near future in biparental species. Such shifts may include greater diurnal care 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

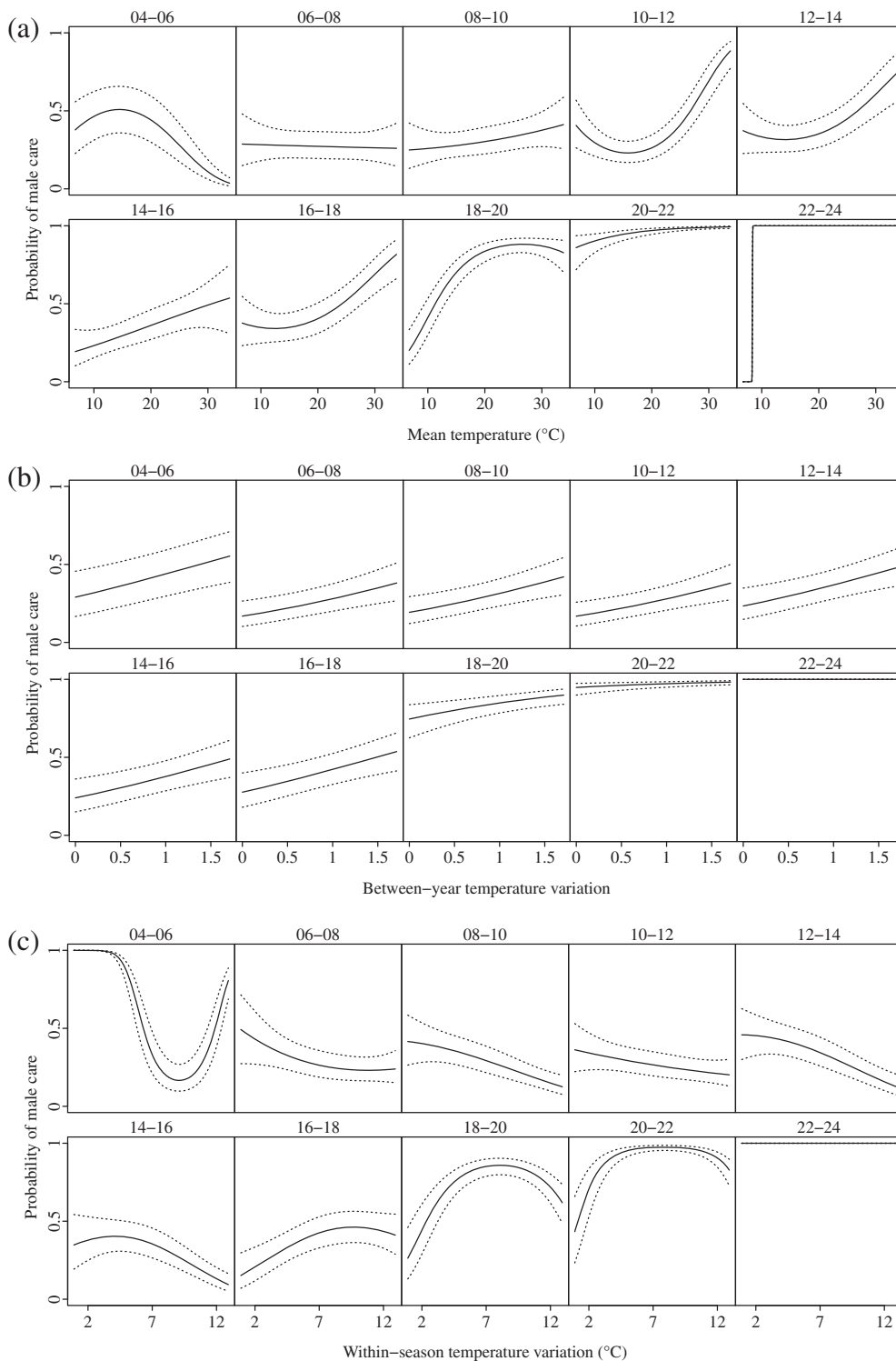


Figure 2 Daily changes in predicted probability of male care (i.e. capture) in relation to (a) mean temperature, (b) between-year variation, and (c) within-season variation. Each panel shows a different time period; see the panel title for time period. Dashed lines represent 95% confidence intervals. Predictions are based on minimal Model 4 from which the non-significant interaction and quadratic terms for between-year variation were removed (Table 1). The standardized temperature variables (see Methods) were converted back to the original scale on the figures.

other activities (Deeming, 2002; Reid *et al.*, 2002). For instance, a greater share of care by a given sex may constrain its foraging time, or may reduce its ability to attract further mates or provision other broods, and 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

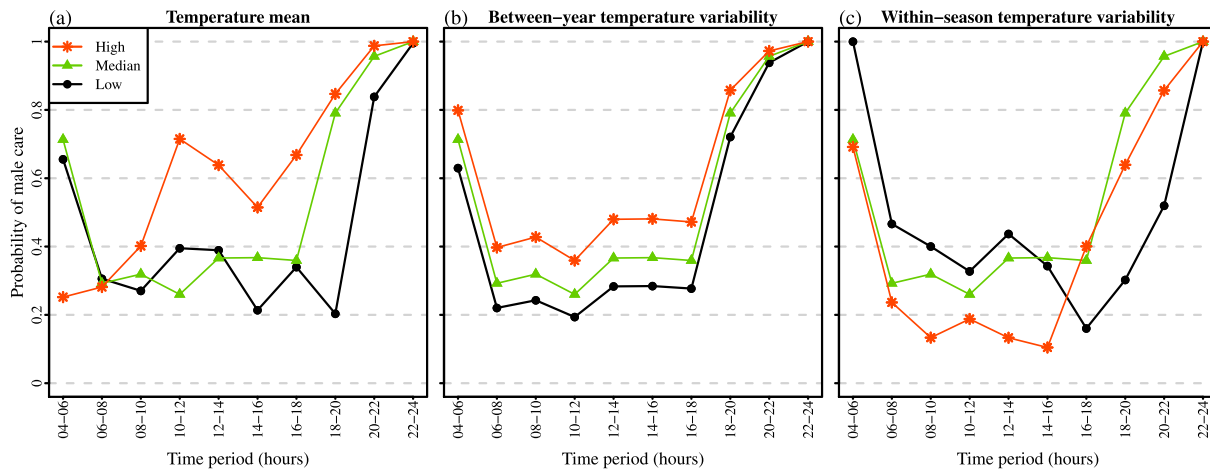


Figure 3 Predicted probability of male care (i.e. male capture) throughout the day under different climate scenarios. Each panel shows a climate scenario where the candidate temperature variable (i.e. shown by the main title of each sub-graph) takes three values (i.e. 2.5% quantile, median, 97.5% quantile), 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).

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 affected. 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, 2006). 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 the contribution to care by males correlates with other aspects of breeding systems (e.g. 0% male care is 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 patterns of brood care, frequency of polygamy and extra-pair paternity may vary in relation to environmental fluctuations (e.g. in temperature, 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 also 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 geographical distances and therefore potentially provide 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 (Alrashidi *et al.*, 2011; Vincze *et al.*, 2013). Another consequence of the observed flexibility in parental behaviour is that these populations might be able to cope effectively 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, which reduces the influence of prevailing temperatures on the temperature experienced by the eggs (Lomas *et al.*, 2014).

Our results indicate highly significant relationships between environmental stochasticity, seasonality, the division of parental care 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 present-day 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 geographical range, we have shown that cooperation during incubation, a major component of parental care in birds, is significantly related to the mean and variation of ambient temperature. 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 to build 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 history. In addition, we encourage the development of theoretical models investigating the influence of environmental fluctuations on the evolution of parental care and breeding systems.

ACKNOWLEDGEMENTS

This work was supported by the Hungarian Eötvös Scholarship (MÁEÖ2016_15/76740 to O.V.), János Bolyai Research Scholarship of the Hungarian Academy of Sciences (to A.K.), by the NERC Biomolecular Analysis Facility (MGF184, NBAF933, NBAF547) and NKFIH grants (K112527, K112670, K116310). Funding of laboratory and fieldwork, as well as permits, are detailed in the Supporting Information (Acknowledgements S1).

REFERENCES

- Alrashidi, M., Kosztolányi, A., Shobrak, M., Küpper, C. & Székely, T. (2011) Parental cooperation in an extreme hot environment: natural behaviour and experimental evidence. *Animal Behaviour*, **82**, 235–243.
- Auer, S.K., Bassar, R.D. & Martin, T.E. (2007) Biparental incubation in the chestnut-vented tit-babbler *Parus subcaeruleus*: mates devote equal time, but males keep eggs warmer. *Journal of Avian Biology*, **38**, 278–283.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48.
- Bonsall, M.B. & Klug, H. (2011) The evolution of parental care in stochastic environments. *Journal of Evolutionary Biology*, **24**, 645–655.
- Both, C. & Visser, M.E. (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, **411**, 296–298.
- Botero, C.A. & Rubenstein, D.R. (2012) Fluctuating environments, sexual selection and the evolution of flexible mate choice in birds. *PLoS One*, **7**, e32311.
- Botero, C.A., Boogert, N.J., Vehrencamp, S.L. & Lovette, I.J. (2009) Climatic patterns predict the elaboration of song displays in mockingbirds. *Current Biology*, **19**, 1151–1155.
- Bradshaw, W.E. & Holzapfel, C.M. (2006) Evolutionary response to rapid climate change. *Science*, **312**, 1477–1478.
- Bulla, M., Valcu, M., Dokter, A.M. *et al.* (2016) Unexpected diversity in socially synchronized rhythms of shorebirds. *Nature*, **540**, 109–113.
- Chambers, L.E., Gibbs, H., Weston, M.A. & Ehmke, G.C. (2008) Spatial and temporal variation in the breeding of masked lapwings (*Vanellus miles*) in Australia. *Emu*, **108**, 115–124.
- Clutton-Brock, T.H. (1991) *The evolution of parental care*. Princeton University Press, Princeton, NJ.
- Deeming, C. (2002) *Avian incubation: behaviour, environment and evolution*. Oxford University Press, Oxford.
- Dewar, R.E. & Richard, A.F. (2007) Evolution in the hyper-variable environment of Madagascar. *Proceedings of the National Academy of Sciences USA*, **104**, 13723–13727.
- Dos Remedios, N., Lee, P.L., Burke, T., Székely, T. & Küpper, C. (2015) North or south? Phylogenetic and biogeographic origins of a globally distributed avian clade. *Molecular Phylogenetics and Evolution*, **89**, 151–159.
- Dunn, P.O. & Winkler, D.W. (2010) Effects of climate change on timing of breeding and reproductive success in birds. *Effects of climate change on birds* (ed. by A.P. Møller, W. Fiedler and P. Berthold), pp. 113–128. Oxford University Press, Oxford.
- Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. (2000) Climate extremes: observations, modeling, and impacts. *Science*, **289**, 2068–2074.
- Eberhart-Phillips, L.J., Hoffman, J.I., Brede, E.G., Zefania, S., Kamrad, M., Székely, T. & Bruford, M.W. (2015) Contrasting genetic diversity and population structure among three sympatric Madagascan shorebirds: parallels with rarity, endemism, and dispersal propensity. *Ecology and Evolution*, **5**, 997–1010.
- Ekanayake, K.B., Weston, M.A., Nimmo, D.G., Maguire, G.S., Endler, J.A. & Küpper, C. (2015) The bright incubate at night: sexual dichromatism and adaptive incubation division in an open-nesting shorebird. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20143026.
- Fraga, R.M. & Amat, J.A. (1996) Breeding biology of a Kentish plover (*Charadrius alexandrinus*) population in an inland saline lake. *Ardeola*, **43**, 69–85.
- Gonzalez, J.C.T., Sheldon, B.C. & Tobias, J.A. (2013) Environmental stability and the evolution of cooperative breeding in hornbills. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20131297.
- Gratto-Trevor, C.L. (2011) Ageing and sexing the piping plover *Charadrius melodius*. *Wader Study Group Bulletin*, **118**, 118–122.
- Houston, A.I. & McNamara, J.M. (1999) *Models of adaptive behaviour: an approach based on state*. Cambridge University Press, Cambridge.
- IPCC (2014) Climate change 2014: impact adaptation and vulnerability. AR5, Working Group II (WGII AR5). Available at: <http://ipcc-wg2.gov/AR5/> (accessed 10 July 2014).

- Jetz, W. & Rubenstein, D.R. (2011) Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Current Biology*, **21**, 72–78.
- Klug, H., Alonzo, S.H. & Bonsall, M.B. (2012) Theoretical foundations of parental care. *The evolution of parental care* (ed. by N.J. Royle, P.T. Smiseth and M. Kölliker), pp. 21–39. Oxford University Press, Oxford.
- Kosztolányi, A., Székely, T., Cuthill, I.C., Yilmaz, K.T. & Berberoglu, S. (2006) Ecological constraints on breeding system evolution: the influence of habitat on brood desertion in Kentish plover. *Journal of Animal Ecology*, **75**, 257–265.
- Küpper, C., Edwards, S.V., Kosztolányi, A., Alrashidi, M., Burke, T., Herrmann, P., Argüelles-Tico, A., Amat, J.A., Amezian, M., Rocha, A., Hötker, H., Ivanov, A., Chernicko, J. & Székely, T. (2012) High gene flow on a continental scale in the polyandrous Kentish plover *Charadrius alexandrinus*. *Molecular Ecology*, **21**, 5864–5879.
- Lawson, C.R., Vindenes, Y., Bailey, L. & Pol, M. (2015) Environmental variation and population responses to global change. *Ecology Letters*, **7**, 724–736.
- Liker, A., Freckleton, R.P. & Székely, T. (2013) The evolution of sex roles in birds is related to adult sex ratio. *Nature Communications*, **4**, 1587.
- Lips, K.R. (2001) Reproductive trade-offs and bet-hedging in *Hyla calypsa*, a Neotropical treefrog. *Oecologia*, **128**, 509–518.
- Lomas, S.C., Whisson, D.A., Maguire, G.S., Tan, L.X., Guay, P.J. & Weston, M.A. (2014) The influence of cover on nesting red-capped plovers: a trade-off between thermoregulation and predation risk? *Victorian Naturalist*, **131**, 115–127.
- McGraw, L., Székely, T. & Young, L.J. (2010) Pair bonds and parental behaviour. *Social behaviour: genes, ecology and evolution* (ed. by T. Székely, A. Moore and J. Komdeur), pp. 271–301. Cambridge University Press, Cambridge.
- Martin, T.E. (1996) Life history evolution in tropical and south temperate birds: what do we really know? *Journal of Avian Biology*, **27**, 263–272.
- Mitchell, T.D. & Jones, P.D. (2005) An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *International Journal of Climatology*, **25**, 693–712.
- Parra, J.E., Beltrán, M., Zefania, S., Dos Remedios, N. & Székely, T. (2014) Experimental assessment of mating opportunities in three shorebird species. *Animal Behaviour*, **90**, 83–90.
- Pickett, S.T.A. (1989) Space-for-time substitution as an alternative to long-term studies. *Long-term studies in ecology: approaches and alternatives* (ed. by G.E. Likens), pp. 110–135. Springer, New York.
- Piersma, T. & Wiersma, P. (1996) Family Charadriidae (plovers). *Handbook of the birds of the world*, Vol. 3, (ed. by J. del Hoyo, A. Elliott and J. Sargatal), pp. 384–442. Lynx Editions, Barcelona.
- R Core Team (2014) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org/>.
- Reid, J.M., Monaghan, P. & Ruxton, G.D. (2002) Males matter: the occurrence and consequences of male incubation in starlings (*Sturnus vulgaris*). *Behavioral Ecology and Sociobiology*, **51**, 255–261.
- Royle, N.J., Smiseth, P.T. & Kölliker, M. (2012) *The evolution of parental care*. Oxford University Press, Oxford.
- Rubenstein, D.R. & Lovette, I.J. (2007) Temporal environmental variability drives the evolution of cooperative breeding in birds. *Current Biology*, **17**, 1414–1419.
- Russell, E.M., Yom-Tov, Y. & Geffen, E. (2004) Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. *Behavioral Ecology*, **15**, 831–838.
- Searcy, W.E. & Yasukawa, K. (1995) *Polygyny and sexual selection in red-winged blackbirds*. Princeton University Press, Princeton, NJ.
- St Clair, J.J.H., Küpper, C., Herrmann, P., Woods, R.W. & Székely, T. (2010) Unusual incubation sex-roles in the rufous-chested dotterel *Charadrius modestus*. *Ibis*, **152**, 402–404.
- Stenzel, L.E., Warriner, J.C., Warriner, J.S., Wilson, K.S., Bidstrup, F.C. & Page, G.W. (1994) Long-distance breeding dispersal of snowy plovers in western North America. *Journal of Animal Ecology*, **63**, 887–902.
- Székely, T. (2014) Sexual conflict between parents: offspring desertion and asymmetrical parental care. *Cold Spring Harbor Perspectives in Biology*, **6**, a017665.
- Székely, T. & Cuthill, I.C. (2000) Trade-off between mating opportunities and parental care: brood desertion by female Kentish plovers. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 2087–2092.
- Székely, T., Kosztolányi, A. & Küpper, C. (2008) Practical guide for investigating breeding ecology of Kentish plovers *Charadrius alexandrinus*. Version 3. Unpublished report, University of Bath. Available at: http://www.bath.ac.uk/biosci/biodiversity-lab/pdfs/KP_Field_Guide_v3.pdf (accessed 23 July 2014).
- Székely, T., Remeš, V., Freckleton, R.P. & Liker, A. (2013) Why care? Inferring the evolution of complex social behaviour. *Journal of Evolutionary Biology*, **26**, 1381–1391.
- Thompson, R.M., Beardall, J., Beringer, J., Grace, M. & Sardina, P. (2013) Means and extremes: building variability into community-level climate change experiments. *Ecology Letters*, **16**, 799–806.
- Tököllyi, J., McNamara, J.M., Houston, A.I. & Barta, Z. (2012) Timing of avian reproduction in unpredictable environments. *Evolutionary Ecology*, **26**, 25–42.
- Tököllyi, J., Schmidt, J. & Barta, Z. (2014) Climate and mammalian life histories. *Biological Journal of the Linnean Society*, **111**, 719–736.
- Vasseur, D.A., DeLong, J.P., Gilbertet, B., Greig, H.S., Harley, C.D., McCann, K.S., Savage, V., Tunney, T.D. & O'Connor, M.I. (2014) Increased temperature variation

- poses a greater risk to species than climate warming. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20132612.
- Vincze, O., Székely, T., Küpper, C., Alrashidi, M., Amat, J.A., Ticó, A.A., Burgas, D., Burke, T., Cavitt, J., Figuerola, J., Shobrak, M., Montalvo, T. & Kosztolányi, A. (2013) Local environment but not genetic differentiation influences biparental care in ten plover populations. *PLoS One*, **8**, e60998.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Webb, D.R. (1987) Thermal tolerance of avian embryos: a review. *Condor*, **89**, 874–898.
- Webb, J.N., Székely, T., Houston, A.I. & McNamara, J.M. (2002) A theoretical analysis of the energetic costs and consequences of parental care decisions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **357**, 331–340.
- Weston, M.A. & Elgar, M.A. (2006) Parental care in hooded plovers (*Thinornis rubricollis*). *Emu*, **105**, 283–292.
- Wilson, E. (1975) *Sociobiology: the new synthesis*. Harvard University Press, Cambridge, MA.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Table S1 Summary of the data used.

Table S2 Sensitivity analyses.

Table S3 Detailed description of hypothesis testing.

Table S4 Results of the Bayesian models.

Appendix S1 Supporting references.

Appendix S2 Description of Bayesian modelling framework.

Acknowledgements S1 Supplementary acknowledgements: funding of laboratory and fieldwork; permits.

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.

Editor: Richard Field