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# Reduced avian body condition due to global warming has little reproductive or population consequences

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## Abstract

Climate change has strong effects on traits such as phenology and physiology. Studies typically assume that climate-induced trait changes will have consequences for population dynamics, but explicit tests are rare. Body condition reflects energy storage and may directly affect how much can be invested in reproduction and survival. However, the causal pathway by which decreased body condition impacts population dynamics has never been quantified across multiple populations and species. Therefore, we lack a general understanding of the consequences of changes in condition for variables more relevant for conservation, such as population size. Using structural equation modeling, we investigate how temperature-induced changes in body condition affect reproduction, and the subsequent impact on population growth rates of 19 bird species across 80 Dutch sites over a 21-year period. Warmer temperatures were associated with decreased body condition, which led to both decreased and increased reproduction at different sites, cancelling out any overall effect. The indirect effect of temperature on population growth (via body condition and reproduction) only explained within-species variation in the total effects of temperature on population growth. Instead, the direct effect of temperature on population growth (unrelated to condition and reproduction) was the most important pathway underlying the total effects of temperature on population growth, suggesting that unknown variables are mediating this effect. About half of the species are expected to increase under global warming, but this variation was not associated with any species characteristic. Overall, body condition responses to global warming are common, but their consequences on reproduction and subsequently population growth contribute relatively little to the total temperature impacts on population dynamics. Given that warming temperatures have strong effects on population dynamics, understanding the pathways via which temperature impacts population dynamics will be crucial for our ability to predict climate change effects in the future and improve conservation efforts.

Keywords: Birds, body condition, climate change, population dynamics, reproduction, structural equation model

## Introduction

Much of climate change ecology research has focused on the direct effects of climate on trait responses, such as phenology, morphology and physiology. These studies typically assume that climate-induced trait changes will have consequences for reproduction, survival and population dynamics, yet this idea has only more recently begun to be explicitly tested (Jenouvrier et al., 2018, Wilson & Arcese, 2003, McLean et al. 2016). It is now becoming clear that, although changes in physiology or phenology have been found to have significant demographic or population impacts in some species (Wilson and Arcese 2003, Benton et al. 2006, Wright et al. 2009, Ozgul et al. 2010, Plard et al. 2014, Gardner et al. 2016, Youngflesh et al. 2017), this does not always occur (Reed et al. 2013a, Dunn and Møller 2014, Stopher et al. 2014). Such variation can exist because trait changes can affect particular types of demographic or population variables, while other types remain unaffected (Jenouvrier et al. 2018, McLean et al. 2016, Reed et al. 2013, Wilson and Arcese 2003). For instance, Jenouvrier et al. (2018) found that different traits affected either adult survival, breeding success or recruitment. If a trait affects a demographic rate, this does not necessarily lead to population consequences because of, for example, compensatory density dependence in other demographic rates (Reed et al. 2013).

A general understanding of how frequently and in what situations and species a trait response has cascading consequences for populations, and the strength of these impacts, is lacking (Miller-Rushing et al. 2010). As such, we have little ability to predict the outcomes of trait changes, and are unable to identify the particular species that are at most risk of population declines due to climate change (Fewster et al. 2000). Such information is particularly crucial for effective conservation management in light of a rapidly warming world (McDermott and DeGroote 2016).

The different types of responses to changes in climate can be categorised into hierarchical levels, from trait-level responses (phenology or physiology) to demographic- (reproduction or survival) and population- level responses (population size, growth rate or time to extinction) (Nichols and Hines 2002, Miller-Rushing et al. 2010, Jongejans et al. 2010, McLean et al. 2016, van Benthem et al. 2017, Jenouvrier et al. 2018). Under this framework, changes in climate impact the most basal trait level, which in turn can affect demographic rates, and subsequently impact population dynamics. In order for changes in climate to result in an observable population-level response, the effects of climate must flow up through the hierarchical levels (McLean et al. 2016). As climate change is expected to act as a major cause of species extinctions in the near future (Thomas et al. 2004), it is equally important to understand both when trait changes have an effect on population dynamics, and when they do not (van Benthem et al. 2017). By decomposing population responses into relationships among different underlying pathways, we can better understand the mechanisms that drive population decline (Nichols and Hines 2002, Ådahl et al. 2006, McLean et al. 2016).

Despite many trait-level studies assuming that climate-induced changes in traits have strong impacts on population dynamics, there are four feasible mechanisms by which this may not occur (McLean et al. 2016). There would be no change in population dynamics if: (1) the change in trait has little or no impact on any demographic rates, or (2) the change in trait does affect demographic rates but this has little or no impact on population dynamics, or (3) multiple pathways counteract one another and weaken any net population level effects (e.g. decreased survival is compensated for by increased reproduction), and finally (4) multiple climate/environmental variables have counteracting effects that weaken population level effects. These mechanisms have only been explicitly tested in a handful of single species or theoretical studies (Wilson and Arcese 2003, Ådahl et al. 2006, Ozgul et al. 2010), and large-scale comparative studies are very rare (but see McLean et al. 2016). This is in because very few studies have trait, demographic and population level data available on a large number of species.

Understanding the degree of inter- and intra-specific variation can be important for predicting how likely species or populations are to encounter a climate-induced trait change that impacts their population dynamics. Comparative analyses that include both intra- and inter-specific variation are needed to provide some yard-stick for what 'a lot' of intraspecific variation might be (Stevens et al. 2010, Malyshev et al. 2016, McLean et al. 2018). High inter-specific variation (when compared to intra-specific variation) can indicate that certain species with particular characteristics might be more at risk than others. For example, changes in phenology are expected to have more severe consequences for specialist species compared to generalists (Miller-Rushing et al. 2010, Gilman et al. 2010). Alternatively, if responses to trait changes vary substantially among populations of the same species (i.e. high intra-specific variation in trait consequences) but vary little across species, then species characteristics will be of relatively little use for predicting responses. Rather, local characteristics such as habitat type will likely be more effective at predicting which populations are most at risk of changes in population sizes (Stevens et al. 2010, McLean et al. 2018). Broadly speaking, it is important to understand and incorporate both inter- and intra-specific variation when making predictions about global change impacts (Gamfeldt and Källström 2007, Moran et al. 2015), as this informs us how well we can generalize both across population and species.

Changes in physiology (e.g. body condition, mass or size) are trait level responses which, although being coined as one of the major responses to climate across the globe (Gardner et al. 2011, Villar and Naya 2018), are much less studied compared to phenological traits. Previous studies have generally found that hotter temperatures have been associated with decreased body condition in both juvenile and adult birds(Garant et al. 2004, Van Buskirk et al. 2010, du Plessis et al. 2012, Aubry et al. 2013, Gardner et al. 2016, McLean et al. 2018).

Very little is known about the consequences of *climate-induced changes* in body condition. Some studies have found that decreased adult body mass results in reduced survival and reproduction, perhaps as a consequence of foraging conditions (Harding et al. 2011, Aubry et al. 2013, Paquette et al. 2014, Gardner et al. 2016). However, as average temperatures increase, having less fat insulation against the cold might be beneficial in birds as being heavier can increase energy expenditure (Covas et al. 2002, Quillfeldt et al. 2006, Brodin et al. 2017), raise predation risk (through the need to feed more and also increased fat content; Covas et al. 2002, Rogers 2015), and impact flight performance (Senar et al. 2002). Changes in temperature may not have such strong effects on smaller individuals because they are able to dump heat more efficiently due to a larger surface area-volume ratio (Gardner et al. 2011). However, this could also apply to decreased body condition (rather than just body size). For instance, decreased fat storage would change an individual's surface area-volume ratio by decreasing their volume. If this is the case, lower body condition could be advantageous and actually lead to higher reproduction or survival under warmer conditions as they may be able to dump heat more effectively. Moreover, studies that specifically investigate the full pathway of whether climate-induced changes in body condition or mass affect demographic rates and whether this in turn results in population consequences have been limited to a couple of single species studies (Ozgul et al. 2010, van Benthem et al. 2017). Consequently, broader comparative studies are needed for improving understanding on this topic and to determine the generality of patterns across populations and species.

Here, we determine what the consequences of temperature-induced changes in body condition are on demography and population dynamics of 19 common small passerines using 21 years of field data collected from 80 sites across the Netherlands. Body condition is calculated as mass corrected for size, therefore providing an indication of the amount of fat and protein reserves (Labocha and Hayes 2012). We use structural equation modeling, a path analysis technique that can model and quantify cascading effects, but does not require demographic data on all vital rates; meaning that we can utilize data on many more species than conventional demographic modeling approaches can (discussed by McLean et al. 2016). We have previously shown that warming typically leads to reduced body condition in these species (McLean et al. 2018). Now, we quantify the direct effects that temperature-induced changes in body condition have on reproductive success, and their subsequent indirect effects on the population growth rate. We then determine the intra- and inter-specific variation at each level of the hierarchy. Specifically, we ask: (1) how much the focal pathway (i.e. temperature -> body condition -> reproduction -> population growth) contributes to the total change in reproduction or population growth with temperature, (2) can trait sensitivity to temperature predict demographic or population sensitivity to temperature, and (3) which types of species or habitats are most at risk of flow-on effects from temperature-induced changes in body condition?

## Materials and Methods

### Bird data

Body mass, body size and reproduction data were collected as part of the Dutch Constant Effort Site (CES) program, which covers 80 sites across the Netherlands, spanning 21 years (1994-2014; see Appendix 1 Fig S1 for map). The CES-project follows a standardised protocol where birds are captured using mist nets from the 13th April until the 13th August every year (Robinson et al. 2009). Most sites were sampled 12 times per year (range 9-12). Captured birds are ringed and morphometric measurements taken, including body mass (grams) and wing length (maximum chord measurement; Svensson 1992). The sex and age-class (juvenile or adult) are classified based on plumage (wherever possible). For all species we consider juveniles to be less than one year old and born in the year of capture.

Independent annual population growth rates were calculated using abundance count data from the Dutch Breeding Bird Monitoring Program (BMP) which has been running since 1984. This bird counting methodology uses fixed study plot territory mapping, a bird counting methodology that produces reliable estimates of total bird abundance compared to point/transect counts, and makes year-to-year comparisons possible at the site level (Van Turnhout et al. 2010). Study plots are visited 5-10 times per year, with every visit covering the whole plot. We calculated the weighted mean abundance for each of the CES sites by averaging the 5 closest BMP sites that had the same habitat type (typically within a 15km radius of the CES sites). Mean abundance values were weighted by the inverse of the spatial distance (closer sites had a higher influence on the mean abundance value). We note that close overlap in population measures for the BMP and CES programs exists (van der Jeugd et al. 2007). There was a correlation of 0.45 (95%CI 0.43, 0.48, $p<0.001$) when comparing the counts of the closest BMP sites to the count of adults captured in mist nets from the CES data. This suggests that the count data from BMP sites matches the abundance estimates from the CES sites adequately.

### Climatic data

Daily temperature records over the study period were taken from 37 weather stations across the Netherlands (Royal Netherlands Meteorological Institute). Each CES-location was matched with the closest weather station (mean distance 17 km, range 1.9-32.6 km; see Appendix 1 Table S2). In a previous paper (McLean et al. 2018), we performed climate window analyses for each species to find the time period during which mean temperature explained the most variation in body condition (R package *climwin*; Bailey and van de Pol 2016). This time period was found to be from early May to mid-July (spring-early summer) for the majority of species (Appendix 1 Table S3). Because we are interested in how temperature-induced changes in body condition affects demographic and population rates, we use the same spring temperature periods that were found to affect body condition to explain variation in reproductive success and population growth rates.

### Calculation of Response Variables

#### *Body Condition*

Body condition was calculated by correcting body mass for wing length (a measure of structural size), while accounting for the confounding effects of age (adult or juvenile), sex (if identifiable for that species), time of day and date of capture (both non-linear) and the random intercept individual ID (to account for any non-independence due to recaptures of individuals). Consequently, our measure of body condition can be considered as a measure of body fat (Balbontín et al. 2012, Labocha and Hayes 2012, Gardner et al. 2016), or whether an individual's weight is above or below average given their size and other characteristics. When investigating the effects of climate on body condition, wing length is generally thought to be the best single linear predictor of structural size for passerines (Gosler et al. 1998, Gardner et al. 2009). Although wing length has been found to be affected by climate (for example, Collins et al. 2017), we found no overall change in wing length over the length of the study (only 6 out of 46 species showed any significant changes, with varying directions), suggesting that our measure of body condition was not affected by any climate-induced changes in wing length (see Appendix 1 Table S4). However, three species which have temperature-induced changes in body condition did show increases in wing length over time (the Eurasian wren, common blackbird and dunnock) so these species may need to be interpreted with caution. Body condition was calculated such that a body condition of 0 reflects an individual's mass as average given its other characteristics. To make changes in condition comparable across species, we converted body condition residuals to a percentage of the species' mean weight. For example, if two birds had a body condition that was 2 grams above the mean for their population, but one birds was from a 10 and the other from a 100 gram species , then these individuals would have a body condition respectively 20% and 2% larger than the average for their size. Next, we calculated the mean and the standard error of the body condition percentages for each site and year per species to match the format of other variables (see below). We previously found no different patterns among males and females (McLean et al. 2018), and henceforth they are grouped in all analyses.

### *Reproductive success*

As an index of per capita reproduction, the proportion of juveniles caught at each site per year was calculated from the numbers of captured birds (Du Feu and McMeeking 1991, Peach et al. 1996, Nur et al. 2000). Sample size was used to weight the proportion of juveniles caught at each site per year in the SEM analysis.

### *Population growth rate*

We calculated the population growth rate (r) at a given site (s) and year (t) from the change in abundance (n) between years:

$$\mathrm{r}_{\mathrm{s,t}} = \log\left(\frac{n_{s,t+1} + c_s}{n_{s,t} + c_s}\right)$$

The constant *c* reflects a small term that was included in the formula in order to account for situations when no territories were found at a site in a given year, and was set to the mean number of territories at that site across all years multiplied by 0.01. We calculated a measure of sample size to weight population growth in the SEM analysis based on how confident we were in the estimate (See Appendix S1 for details).

## Statistical Analyses

We conducted our analyses on 19  passerine species that were previously found to have temperature effects on body condition (McLean et al. 2018). For each species there were data from on average 3690 (range 40-26257) birds, 33 sites (range 7-50) and 18 years (range 9-20). This amounted to a total sample size of 3,106 site-by-year estimates across all 19 species that served as input for the statistical analysis described below.

### *Structural Equation Modeling*

Structural equation modeling is a regression-based approach to evaluating causal linkages among variables in a single multivariate network. It is ideal for our analysis as variables can function as both predictors and responses within a single model, and therefore can identify indirect effects. SEMs translate a path diagram (i.e., box-and-arrow diagram indicating directed linkages) into a set of linear equations that are evaluated independently (Grace 2006a). We constructed a single structural equation model (SEM) using the R-package *piecewiseSEM* (Lefcheck 2016), software that allows for the inclusion of response variables that are not normally distributed, as well as random effects that account for non-independence in the data.

Following McLean et al. (2016), our SEM has one focal (or indirect) pathway which flows from temperature to body condition and on to reproductive success, then onto population growth rate (see Fig 2 for full path diagram). Temperature also has a direct pathway to the variables reproduction and population growth, which allows us to evaluate whether any temperature related changes are due to changes in the focal paths, or instead, via some other unmeasured trait. Importantly, temperature may not be the causal mechanism and could be a proxy for some other variable that is also changing over time (Iler et al. 2017). We decided to leave out the pathway connecting body condition directly to population growth rate *a priori* so that the model did not become 'saturated' also known as a 'just-identified' model, where all uniquely estimable parameters are utilised (Pugesek et al. 2003, Grace 2006a). The normal model fit statistics cannot be calculated for a saturated SEM as the model as it will always result in a perfect fit to the empirical data, and therefore the plausibility of the model cannot be confirmed (Pugesek et al. 2003).

We included all species in one SEM so that we could determine the overall trends for common passerines as well as compare intra- versus inter-specific variability (See Appendix 1 for SEM structure and R code). Random intercept and slope terms with a hierarchical structure of sites nested within species were included in each pathway to allow the strength of pathways to vary among sites and species and address non-independence of observations made on different sites of the same species (we assume that a site which is good for species A is not necessarily good for species B). We used the random slope coefficients from the mixed SEM as estimates of the species and site effect sizes. These estimates can be thought of as sensitivity values (e.g. how strongly body condition is affected by a change in temperature) (McLean et al. 2018). The variable body condition was weighted by the inverse of the standard error such that estimates with larger standard errors contributed less, upweighting samples with higher precision. Likewise, population growth and the proportion of juveniles (i.e. reproductive success) were weighted by sample size (See Appendix S1 for details). Population growth rate and body condition were modelled using Gaussian error-distributions, while reproductive success had binomial error distributions and logit link functions. The final SEM did include many parameters (k=26), yet we still had 113 observations per parameter, which is generally considered an appropriate number for accurate estimates even with a high number of random groups.

The rules of path coefficients (Grace 2006b) tell us that the total change in population growth rate from a small change in temperature is the product of each of the underlying relationships between temperature, trait and demography (McLean et al. 2018).

$$\frac{dPop}{dTemp} = \frac{dCond}{dTemp} * \frac{\partial Repro}{\partial \mathrm{Cond}} * \frac{\partial \mathrm{Pop}}{\partial \mathrm{Repro}} + \frac{\partial Repro}{\partial \mathrm{Temp}} * \frac{\partial \mathrm{Pop}}{\partial \mathrm{Repro}} \qquad eq.\ 1$$

$$+\frac{\partial \mathrm{Pop}}{\partial \mathrm{Temp}}$$

Where, we use '$\partial'$ and 'd' to distinguish partial and full regression coefficients, respectively. The top line of equation 1 gives the indirect effect via the focal pathway (i.e. via body condition and reproduction), while the second line shows the indirect effect via reproduction alone, and the third line the direct effects via other unknown traits or demographic rates. Similarly, the total effect of temperature on reproductive success is calculated as:

$$\frac{\mathrm{dRepro}}{\mathrm{dTemp}} = \frac{\mathrm{dCond}}{\mathrm{dTemp}} * \frac{\partial \mathrm{Repro}}{\partial \mathrm{Cond}} \qquad \textit{eq. 2}$$

$$+\frac{\partial \mathrm{Repro}}{\partial \mathrm{Temp}}$$

Here, the top line of equation 2 gives the indirect effect of temperature via body condition, while the second line gives the direct effect unrelated to condition.

Because the slope estimates with reproductive success as the response variable were on the logit scale, and therefore nonlinear, we calculated a linear approximation in order to calculate the combined pathways. The linear approximation was calculated as the first derivative of the logistic regression equation at the mean predictor-value at each site (or species) on the absolute (back-transformed) scale (see Appendix 1 Fig S2 for details).

### *Intra- and inter-specific analysis*

We used the amount of intra- versus inter-specific variation in relationships as a measure to determine whether there was relatively higher intra-specific variation (Blanck and Lamouroux 2006, Rubolini et al. 2007, Stevens et al. 2010). For each pathway, we compared the ratio of the among-species variance (variance component for the random slopes at the 'species' level in above models) to the total variance (the sum of the within-species variance –estimated by the variance in the random slope at the 'site' level— and the among-species slope variance; see Appendix 1 for details). A value closer to one would indicate there would be relatively more among-species variation compared to within-species variation, suggesting that intra-specific responses are fairly consistent. Conversely, if there is a lot of within-species variance relative to among-species variance the ratio is expected to be closer to zero. This ratio can also be interpreted as the intra-class correlation coefficient (ICC;i.e. the similarity between the responses of populations of the same species; Snijders 2011).

### *Comparative Analyses*

In order to determine how important each underlying pathway was in contributing to the total climate induced change in population growth (or reproduction) among sites and species, we quantified the $R^2$ values within and between species. The $R^2_{between}$ value was calculated as the $R^2$ of a model that included all species and site data, while the $R^2_{within}$ value was calculated as the average $R^2$ across all species from models that analysed each species separately.

To address the question, "does trait sensitivity to temperature predict demographic or population sensitivity to temperature?", we investigated how well body condition sensitivity explained variation in total pathways (i.e. temperatures overall effect on population, and on reproductive success) across species and sites. To distinguish whether any association between trait sensitivity and population or demographic sensitivity was due to within- or between-species associations we used a within-subject centring approach (van de Pol and Wright 2009). We fitted a linear model with the total change in population or reproduction due to temperature ($dPop/dTemp$ or $dRepro/dTemp$) as the response variable and included two fixed effects: (1) within-species centred values of body condition sensitivity to temperature ($x_{ij} - \overline{x_j}$ where $i$ refers to sites, $j$ to species and $x$ to the site slope coefficients of body condition over temperature ($\frac{dCond}{dTemp}$); essentially eliminating any between-species variation), and (2) the species' mean body condition sensitivities to temperature ($\overline{x_j}$ where different sites for the same species are all given the same $\overline{x_j}$ value; expressing only the between-species variation).

*Species characteristics*

To determine which species or populations might be at most risk of flow-on effects from temperature-induced changes in body condition, we tested whether a number of different site and species characteristics (e.g. wet/dry habitat type, life expectancy) could explain variation among sites and species in path estimates (Table 1; See Appendix 1 for descriptions and calculations of characteristics). Because the relationship between body condition and reproduction did not differ across species (i.e. the % variance explained by the random slope term was 0), but only across sites within species, we only considered site characteristics for this pathway. We identified a number of *a priori* hypotheses about which species and site characteristics might be important (Table 1). This list is not exhaustive and each hypothesis could of course be tested in much greater detail than done here, for instance, we only check whether the densities of two predators (Eurasian sparrowhawks *Accipiter nisus* and Northern goshawks *Accipiter gentilis*) impact these relationships, while owls or mammals could be equally important. Some of our *a priori* hypotheses predicted the sign or direction of path estimates across species. For instance, in sites with high predator densities being lighter might mean less time spent foraging in order to avoid predators and improve flying and energy expenditure which may increase reproductive success (Lima 1986). However, most hypotheses did not predict the sign of the relationship, but only suggested the strength of effects.

We first tested the hypotheses that only suggested the strength of effects (rather than the direction of the relationship) individually to determine if they were of any predictive ability. We took the absolute slope estimates for every site and included them as the response variable in a simple linear regression, the hypothesised characteristic as the fixed term and species and site as random intercept terms. If a characteristic was identified as explaining some variation (confidence intervals did not cross zero) then we next tested whether it could also predict the direction (i.e. non-absolute slope estimates).

Using a model selection approach, the total effects of temperature on reproduction and of temperature on population growth (rather than the individual pathways) were then tested to see whether the directional characteristics that were found to be important for individual pathways were also able to explain variation in the total pathways. Models were selected on the basis of the AICc, and model weights were calculated as a measure of the relative importance of each model in the model set (Burnham and Anderson 2002).

## Results

We tested the model fit of the SEM by the test of directional separation (Lefcheck 2016) and found that the model represents the data well, suggesting that no important paths were missing (P=0.184, Fisher C=3.39, df=2).

Body condition decreased on average by 0.23% per ˚C (95%CI: -0.36, -0.10; Fig 2a). However, we found high between-species variation for the direct effects of temperature on body condition (ICC = 40%), suggesting that some species were more sensitive than others and that sites within a species responded quite similarly (illustrated for Eurasian wren in Fig 1a). This means that, although there is some variation across different populations, there appear to be reasonably species-specific responses in body condition to changing temperatures (i.e. a strong species signal).

The association between body condition and reproductive success differed substantially across sites within a species. Site slopes ranged from negative to positive effects (illustrated for Eurasian wrens in Fig 1b), such that on average each species showed no association between body condition and reproduction, and there was no overall effect across all species (Fig 2b; slope= -0.001% juveniles per 1% change in adult condition, 95%CI: -0.009, 0.006). Indeed, the ICC was 0% (Fig 2b), indicating that among-species variance was limited compared to the high amount of within-species variances in sensitivities. The direct effect of temperature on reproduction, unrelated to body condition, differed among both species and sites (ICC=19%). Across all species there was a weak positive trend, although the confidence intervals just crossed zero (Fig 2d; slope= 0.008% juveniles per ˚C, 95%CI: -0.005, 0.022).

The association between reproduction and population growth rate was consistent among-species, but differed mostly within-species (Fig 2c; ICC<0.1%). On average, there was a non-significant positive trend suggesting that increased reproduction leads to increased population growth rate (slope across all species= 0.1577 growth rate per % juveniles, 95%CI: -0.0514, 0.3668). In the case of the direct effect of temperature on growth rate, individual species showed strong relationships, with around half having negative effects, and the other half positive effects, essentially cancelling out any overall effect (Fig 2e; slope across all species= 0.0133 growth rate per ˚C, 95%CI: -0.0592, 0.0858). Indeed, the among-species variation was very high (ICC=69%) suggesting that temperature impacts population growth (unrelated to body condition and proportion of juveniles) in very species-specific ways.

### How important is the focal pathway in contributing to the total change in reproduction or population growth with temperature?

The total effect of temperature on the population growth rate (i.e. all pathways combined) differed among-species, such that roughly half increased population growth rates with warmer temperatures, while the other half decreased or showed no change (Fig 2h). Population growth rates increased on average by 0.008 per °C across all species and sites. The total effect of temperature on reproduction showed that the proportion of juveniles increased by 0.006% per °C across all species and sites, but there was substantial variation in responses across sites (Fig 2g).

The focal path (i.e. the temperature -> body condition -> reproduction -> population growth rate pathway) explained within-species trends, but was not related to how species' responded on average. The focal path explained little variation among-species in the total effects of temperature on population growth (Fig 3a) or reproduction (Fig 3d), suggesting that it was of little importance in contributing to total changes for individual species. However, the focal pathway did explain some variation within-species (across sites; 28% and 18% for population growth rate and reproduction, respectively), such that sites which showed stronger decreases in population growth rate from temperature due to the focal pathway also showed stronger decreases in total.

The non-focal reproduction pathway (temperature -> reproduction -> population growth rate) which was unrelated to body condition, explained substantially more variation among sites in the total effects of temperature on population growth compared to the focal pathway (81% variance explained; Fig 3c). Furthermore, the non-focal direct pathways between temperature and both reproduction (Fig 3e) and population growth rates (Fig 3b) contributed most strongly to the overall sensitivities to temperature across species (i.e. the total effects of temperature on reproduction and population growth were well predicted by the direct pathway, unrelated to body condition). Given the strong importance of the direct pathway in these trends, it suggests that both body condition and reproduction are of relatively little importance for determining temperature-impacts on population growth rate. Instead, these direct effects are likely mediated by other unmeasured traits or demographic rates.

**Does trait sensitivity to temperature predict demographic or population sensitivity to temperature?**

Temperature sensitivity in body condition predicted growth rate sensitivity but not sensitivity in reproductive success. We found a positive association between sensitivity in body condition to temperature and total sensitivity in population growth to temperature across sites and species (slope= 0.087, 95%CI: 0.067, 0.107). This relationship was solely due to among-species variation, such that species that showed stronger declines in body condition with warmer temperatures, also showed stronger declines in population growth with temperature (Fig 4a, the red between-species slope = 0.131, 95%CI: 0.107, 0.154). Conversely, sensitivities of sites within a species were not related to population sensitivity (Fig 4a, the red between-species slope = 0.001, 95%CI: -0.032, 0.034).

Sensitivity in body condition to temperature was not associated with sensitivity in reproduction to temperature (Fig 4b; between-species slope = 0.008, 95%CI: -0.008, 0.024; within-species slope = 0.002, 95%CI: -0.019, 0.023). Therefore, trait-level sensitivity to temperature does not predict demographic level sensitivity to temperature.

**Are certain types of species or sites more at risk of stronger relationships among levels?**

We found a number of site and species characteristics that could explain variation in path estimates (Table 1). Firstly, we found that in sites with high predator densities, decreased body condition tended to have negative consequences on reproduction. While in sites with no, or very low densities of predators, decreased body condition tended to be associated with improved reproduction. Two characteristics could explain variation in the strength of the direct effects of temperature on reproduction. Sites with high population densities showed stronger changes in reproduction with temperature (i.e. absolute slope estimates), but population density was unable to explain any variation in the sign or direction of the relationship between temperature and reproduction. Opposite to what was predicted, we found that more short-lived species had stronger associations between temperature and reproduction, but that life expectancy could not explain the sign of such trends.

The strength of density dependence (calculated as the linear regression of population growth rate ($r_t$) over the population size in year t) was the only characteristic that was able to explain some variation among species and sites in their association between reproduction and population. Opposite to what was expected, we found that species with stronger density dependence actually had stronger and more positive associations between reproduction and population growth. No characteristics were found to explain the variation in the association between temperature and population growth.

Predator density explained little variation in the total effect of temperature on reproduction (slope= -0.016 [95%CI: -0.121, 0.089]). Similarly, neither predator density (slope= -0.017 [-0.048, 0.013]) nor density dependence (slope= -0.001 [-0.008, 0.009]) could explain the total effect of temperature on population growth.

## Discussion

We have found that temperature-induced declines in adult body condition have complex within- and between-species consequences on demography and population dynamics in 19 common passerines in the Netherlands. In general, warmer temperatures were associated with decreased body condition, which in turn was associated with both decreased and increased reproductive success of individual populations (sites), such that any overall effect was essentially cancelled out. There was a slight, but nonsignificant, positive association between reproduction and population growth that was consistent across almost all species and sites. However, body condition and reproduction were of relatively little importance for determining the total effects of temperature on populations. Instead, the direct pathway (unrelated to body condition and reproduction) was the most important pathway underlying the total effects of temperature on population growth, suggesting that other unknown traits or demographic rates are mediating the population response to warmer temperatures. Several species and site characteristics were identified that could explain variation among species and sites in individual path relationships, but these were of little predictive use for determining overall responses to increased temperatures.

### Temperature-induced declines in body condition have some consequences, but are not the main driver of overall temperature affects

There was no clear pathway linking temperature-induced changes in body condition to demography, and subsequently to population growth rate. For instance, the focal pathway (temperature -> body condition -> reproduction -> population growth) only explained relatively little of the within-species variation in the total effects of temperature on the population growth rate. This suggests that the strong effects of temperature on body condition and their subsequent effects on reproduction are carrying through to the population growth rate, but does not influence a species' overall vulnerability to temperature much, only how populations within a species might respond. Given that the focal path explained 28% of the within-species variation in the total effect of temperature on population growth, but could not explain any between-species variance, the focal path might be important for predicting which populations within a species will be at more risk, especially for those species that are declining strongly with warming temperatures such as the short-toed treecreeper (*Certhia brachydactyla*) and Eurasian blackcap (*Sylvia atricapilla*).

The focal pathway contributed little to overall changes in reproduction and population growth from warming temperatures for two reasons. Firstly, decreased body condition increased reproductive success in some sites but decreased it in others, such that on average there was no overall effect for individual species. Intra-specific variation such as this has been suggested to reduce the effects of climate change on species by buffering, or stabilising, the overall impact (termed portfolio effects; Gamfeldt et al. 2005, Oney et al. 2013, Malyshev et al. 2016, Abbott et al. 2017). Therefore, given the high intra-specific variation, portfolio effects could have a role in dampening the consequences of body condition on reproduction. Secondly, although different species differed markedly in their population growth sensitivity to temperature, the focal pathway only explained some variation for individual sites within a species. Half of the 19 species increased their population growth rates with warmer temperatures, while the other half either decreased or showed no changes. Given these highly species-specific responses to temperature, our ability to make general predictions of population change based on the focal pathway are limited (Malyshev et al. 2016). Overall, the common assumption that climate-induced changes in body condition will have strong impacts on population dynamics is only weakly met in our study.

By using a structural equation modeling framework, we were able to decompose the contributions of different pathways and identify missing pathways. The direct temperature to reproduction pathway was most important for determining overall responses in reproduction, suggesting that temperature-induced changes in reproduction were most likely mediated by an unmeasured temperature-dependent trait other than body condition. We previously found the timing of egg laying to be strongly impacted by spring temperature (similar time periods to those used here based on body condition), and that it had a positive effect on reproductive success in common bird species in the United Kingdom (McLean et al. 2016). Additionally, the match-mismatch of breeding time with the timing of the food peak has also been shown to affect breeding success (Visser et al. 1998). The direct pathway between temperature and population growth rate was also strong for most species in this study. This suggests that these effects are also mediated by some unknown traits (e.g. phenology) and demographic rates (e.g. juvenile or adult survival; (Grosbois and Thompson 2005)). The decomposition of effects into direct and indirect pathways is critical for determining such patterns and would not have been possible to distinguish using traditional regression techniques (Grace 2008). Moreover, the existence of multiple important pathways could be identified even though not all relevant traits were measured, which helps guide future research.

Given the fact that trait-level sensitivity to temperature does not predict demographic level sensitivity to temperature, and that the focal pathway explained little of the variation in the total population responses to temperature (Fig 3a), we may be missing an important pathway from body condition to population growth. This missing pathway could be acting via different underlying mechanisms than those looked at here (e.g. survival), or some other environmental variable correlated with temperature is causing the population change (e.g. due to shared temporal trends). In our SEM analyses, we could not include a direct pathway from body condition to population growth rate to test whether body condition affected population growth rate via another demographic rate than reproduction (e.g. survival), as this additional parameter would have saturated the model. However, a post-hoc comparison showed that (i) most species and sites did not have a strong association between population growth rate and body condition in general (Appendix 2), and (ii) the sensitivity of population growth rate to temperature was not well explained by the simple regression slopes of population growth over body condition (between-species slope = -0.04, 95%CI: -0.1, 0.005l; Appendix 2). This tentatively suggests that any effects of body condition working via other demographic mechanisms will be of little importance. However, we note that potential counteracting effects between demographic rates could disguise such a relationship, for example, if increased survival is compensated for by decreased reproduction. Consequently, an important next step would be to identify species for which sufficient demographic data is available to estimate both the focal body condition pathway via reproduction as well as via other demographic pathways (survival, immigration and emigration), and their subsequent impacts on population dynamics.

Despite the complexity of the consequences of temperature-induced changes in body condition, some insights into the possible mechanisms underlying condition fluctuations can be made. Firstly, if decreased body condition was a direct negative effect from poorer foraging conditions or physiological stress in warmer weather, then species or populations with the largest mass loss would be expected to have negative consequences on reproduction or population dynamics (Harding et al. 2011). This may be the case in our study given that (1) species which had stronger decreases in body condition per degree also showed stronger decreases in population growth rate per degree, and (2) sites with more predators experienced more negative effects of declining body condition on reproduction. Although some studies suggest lower mass can improve predator avoidance through improved flight capabilities and predator avoidance (Covas et al. 2002, Rogers 2015), others show that lower condition can impact return latency to nests after exposure to predators (Wallin 1987, Winkler 1992). However, we also found that temperature-induced low body condition led to improved reproduction in roughly half of populations across all species. If decreased body condition provided some advantage, for example, through lowered energy expenditure (Covas et al. 2002, Quillfeldt et al. 2006) or improved flight performance (Senar et al. 2002) a positive relationship between body condition and demography or population growth would be expected. Lastly, it is unlikely that decreasing body condition under warmer conditions is an adaptation. If it was an adaptation to ‘keep up’ with the climate, one would expect to see negative consequences in those populations which had no change or increased body condition (Croll et al. 1991, Chevin et al. 2010), which wasn’t the case in our study. Perhaps the consequences are so variable because the impact of changes in body condition may depend on various factors and mechanism, leading to highly idiosyncratic climate responses.

### Which types of species or habitats are more at risk of flow-on effects?

Given that the consequences of climate-induced changes in traits on demography and population dynamics are not always consistent across species and even sites, the key challenge is then to understand in what situations we can predict when these effects are likely to play an important role. Some species’ population growth rates were more sensitive to warmer temperatures than others, as direct population growth responses to temperature were highly species-specific and variable, ranging from strong decreases to increases with warmer weather. These strong species signals have two key implications: that certain species with particular characteristics might be more at risk from global warming than others, and that population- or location-specific features (e.g. presence of climate refuges, habitat type or quality, predation pressures) have relatively little influence on these relationships. Although we were able to identify several species and site characteristics that helped to explain variation in individual pathways, we were unable to identify any species characteristics (density dependence, life expectancy, migration) or site characteristics (wet/dry habitat type, population density) that explained these striking population growth responses to temperature. Of course, changes in the population size within any individual species, taxon or geographic region may have any number of possible explanations, from the size of feeding ranges (Sandvik and Erikstad 2008) to position within the distribution range (Meller et al. 2018) or warm/cold adapted species (Parmesan and Yohe 2003). Thus, many more case studies are needed to improve our ability to reliably predict such flow-on effects under future climate change.

Perhaps the most surprising result we found was that decreased body condition did not have a consistent effect on reproductive success on species. Associations between body condition and reproductive success have been previously found in a range of taxa (Chastel et al. 1995, Naef-Daenzer et al. 2001, Masello and Quillfeldt 2003, Quillfeldt et al. 2006, Ozgul et al. 2010, Aubry et al. 2013, Paquette et al. 2014), although most are are not explored in the context of climate variability. We were unable to account for certain factors that could provide further insight into the trends found here. For instance, the effects of body condition on reproduction might actually change over the breeding season, a scale at which we were unable to focus on. Indeed, our measure of body condition was fairly coarse given it was the average body condition over the breeding season of the population per year per species, essentially providing a measure of the condition of the population. Quillfeldt *et al.* (2006) found that only high adult body mass before egg laying was important for reproduction. After egg laying, adults tend to lose mass because they do not need to be buffered against unpredictable food supply (as food is usually plentiful at the time that chicks hatch). It could also be possible that changes in reproduction could impact the body condition of adults, but we did not look into this different causal pathway. Future studies with more fine-scale individual level data are needed to investigate such possibilities.

Given each response variable in the model was measured in different years, sites and species, it was expected that the overall $R^2$ values from the model would be relatively low (Fig 2). This is further enhanced because many intrinsic factors (e.g. density dependence, age-structures) and extrinsic factors (e.g. micro-climate, habitat, which could conceivably help to explain the variation), were not available to be included in our multi-species model. Noise from such confounding processes would be expected to reduce the explanatory power of the relationship between variables (Møller and Jennions 2002). In such cases, the estimated strength of such relationships (as measured by the regression coefficient) should remain unbiased, but their associated uncertainty will increase (Hutcheon et al. 2010). Population growth rates had the lowest amount of variation explained (4%), but also would be most likely to be influenced by many other unexamined traits. Additionally, measurement accuracy, "randomness" caused by unpredictable changes, and evolutionary history of species and populations can all considerably limit how much variation can be explained (Møller and Jennions 2002). Considering these above points, the amount of variation explained in reproductive success was remarkably high (33%). This suggests that temperature impacts on reproductive success via yet unknown traits are very important.

### Methodological issues with large scale hierarchical models

There are considerable challenges involved with 'matching up' so many response variables that are sampled and calculated in differing ways. We could not take into account transient individuals (i.e. individuals that are not residents but are passing through sites) for any response variable. We used abundance count data from the BMP scheme and matched these sites as best as possible (based on distance and habitat type) to the CES locations. Some abundance estimates might not have been as representative of the CES sites as others, however, the counts based on the CES and BMP data were reasonably strongly correlated and the fact that most species and populations had positive relationships between reproduction and the population growth rate suggests that our measures are meaningful and that we have sufficient statistical power.

Here, we assumed that the relationships were linear (an assumption common throughout the field). However, future work should seek to determine the importance of thresholds or changes in climatic variance within such path relationships (Lawson et al. 2015). For instance, if changes of body condition past some key value result in different effects on reproductive success (i.e. nonlinear relationship between the two) then the mean would not be representative of the entire population.

Measurement error in the explanatory variable (whether climate, trait or demographic rate) can lead to underestimated strengths of relationships, such that they appear to be weaker than they truly are (regression dilution; Hutcheon et al. 2010). Because we used a piecewise SEM (a necessity due to the differing distributions and weightings in our SEM), this means that the propagation of error surrounding the average measures of body condition and reproduction per site per year are not taken into account and the path estimates might be underestimated. More methodological work is needed to account for uncertainty propagation in such models..

## Conclusions

When a trait is climate sensitive it is tempting to assume, as most studies do implicitly or explicitly, that this will have demographic and/or population consequences. When studies show that both a trait and population growth rate (or a demographic rate) are climate sensitivity, it is even more tempting to assume that this trait sensitivity has population consequences. Our study shows that climate change ecology is not that simple, and our SEM analysis specifically allows us to quantify the contribution of different pathways, thereby gaining novel mechanistic insights. Shifting from naive univariate analysis to the type of multivariate path analysis conducted in this study will be particularly important if many organisms will have multiple traits being affected by climate change, which may be likely. Detailed long-term studies that have measured a suite of traits may be particularly useful to investigate which traits may the key mediators of climate change impacts (Jenouvrier et al. 2018).

Furthermore, additional large-scale studies on the consequences of climate-induced body condition changes are now needed to determine whether our results hold more general across a broader range of taxa and regions. Additionally, future studies should aim to provide evidence that long-term, intensive, individually-based studies provide similar estimates of at least some path coefficients. Finally, because species showed strong species-specific responses in population dynamics to temperature that ranged from positive to negative, it is now vital to identify life-history characteristics that can predict those species that are more sensitive to warmer temperatures. This will potentially be of great value to biodiversity conservation because practitioners could use species characteristics to prioritize conservation efforts to those more at risk of declining population sizes, something of particular importance for species lacking in data.

## Data accessibility

The data will be made available from the Dryad Digital Repository.

## Supporting Information

Appendix 1 – Additional details on methodology

Appendix 2 – Additional details for results

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## Authors’ Contributions

NM and MvdP conceived the ideas and, in consultation with HvdJ, CVT and JL designed the analysis; HvdJ and CVT provided the avian data; NM analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## Figure Legends

**Figure 1** Fitted species and site responses for the Eurasian Wren for (a) the responses of body condition to temperature, (b) reproductive success to body condition, and (c) population growth rate to reproductive success. Each black line shows the path estimate for a different site, while the red line shows the overall species response.

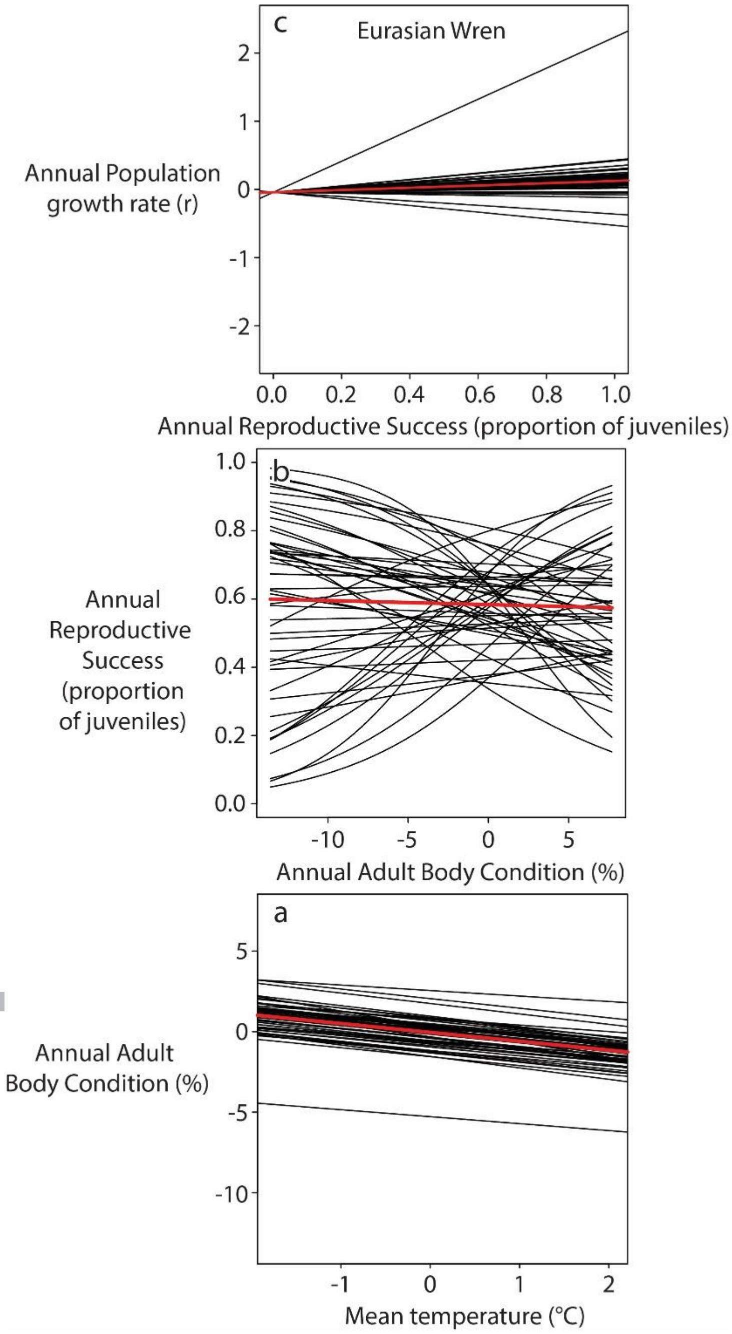


**Figure 2** Decomposition of pathways in the structural equation model by which temperature-driven changes in body condition affect reproductive success and population growth rate in 19 bird species across 80 sites over a 21 year period (n=3,106). Panel (i) ‘Underlying Relationships’ displays the graphical model used in the structural equation analysis carried out on all species. The model includes the indirect effects of temperature on population growth rate via body condition and reproduction (the focal pathway), as well as the direct effects of temperature on reproductive success ($\frac{\partial \mathbf{Repro}}{\partial \mathbf{Temp}}$) and on population growth rate ($\frac{\partial \mathbf{Pop}}{\partial \mathbf{Temp}}$). The red arrows indicate the focal pathway that we are interested in, while the grey indicate direct effects of temperature that could occur via other unknown traits or demographic rates. The $R^2$ (between) values for each variable show the mean amount of variation explained by all pathways and among species, sites and over time. ICC gives the intra-class correlation coefficient, or the ratio of the among-species variance, for each pathway. Each box in the boxplots represents a species, the dotted vertical line shows a slope of zero, the solid black lines and grey areas shows the average slope and its 95% confidence intervals across all species and sites. The red dots show each species average slope and the boxplot displays the distribution of slopes across sites. Panel (ii) ‘Total Relationships’ shows the total effect of temperature on body condition, reproduction and population growth rate, based on the combined direct and indirect effects. Note: Here, we show the β estimates for the linear approximation of the logistic relationships. Species ordered from the top: chaffinch, bearded reedling, redstart, long-tailed tit, reed bunting, linnet, chiffchaff, Eurasian bullfinch, Eurasian reed warbler, house sparrow, Eurasian tree sparrow, blackbird, European robin, willow warbler, starling, dunnock, Eurasian wren, short-toed treecreeper, Eurasian blackcap.

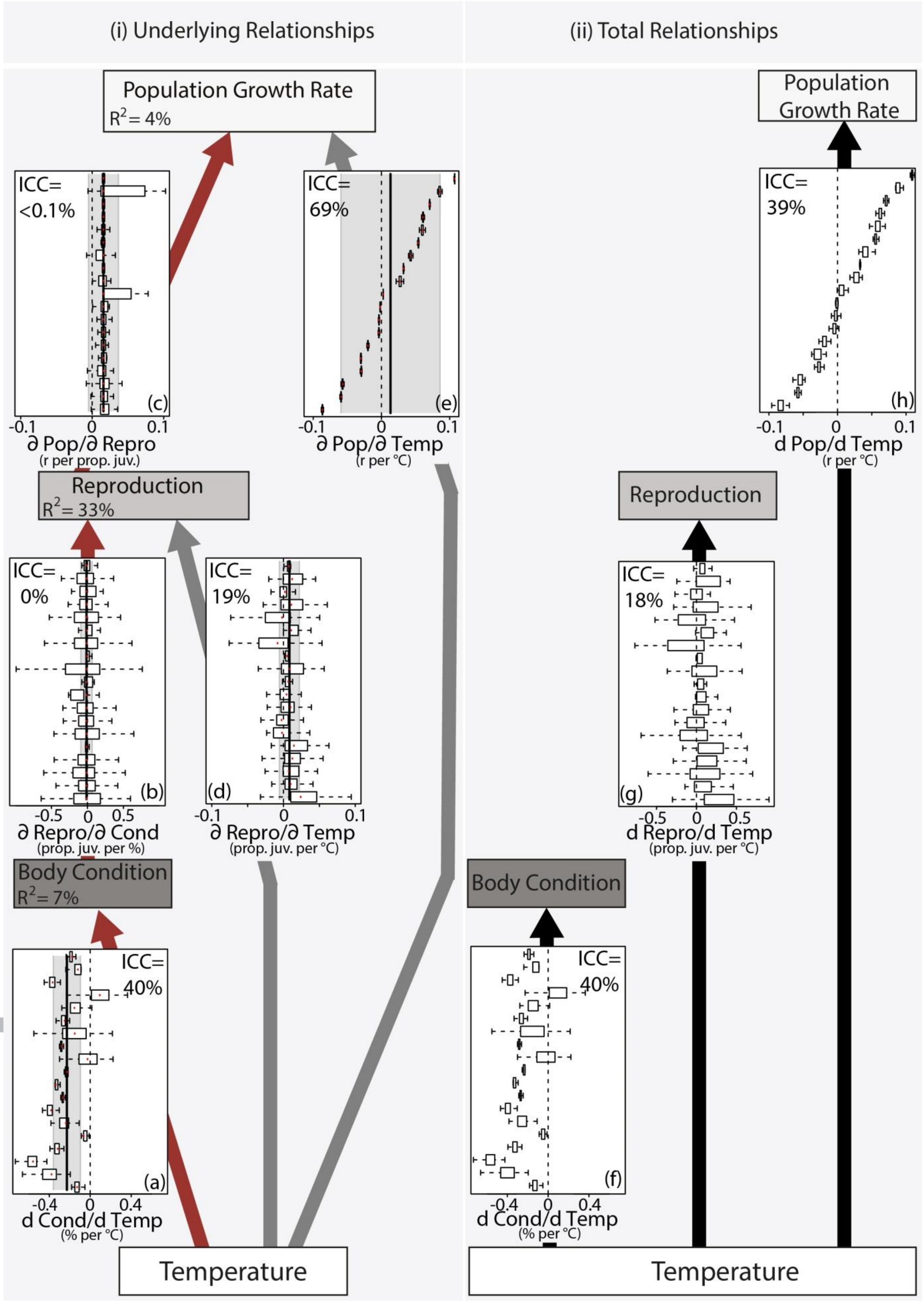

(i) Underlying Relationships
(ii) Total Relationships
Population Growth Rate
$R^2$= 4%
ICC=
<0.1%
(c)
-0.1
0
0.1
∂ Pop/∂ Repro
(r per prop. juv.)
ICC=
69%
(e)
-0.1
0
0.1
∂ Pop/∂ Temp
(r per °C)
Reproduction
$R^2$= 33%
ICC=
0%
(b)
-0.5
0
0.5
∂ Repro/∂ Cond
(prop. juv. per %)
ICC=
19%
(d)
-0.1
0
0.1
∂ Repro/∂ Temp
(prop. juv. per °C)
Body Condition
$R^2$= 7%
ICC=
40%
(a)
-0.4
0
0.4
d Cond/d Temp
(% per °C)
Temperature
Population
Growth Rate
ICC=
39%
(h)
-0.1
0
0.1
d Pop/d Temp
(r per °C)
Reproduction
ICC=
18%
(g)
-0.5
0
0.5
d Repro/d Temp
(prop. juv. per °C)
Body Condition
ICC=
40%
(f)
-0.4
0
0.4
d Cond/d Temp
(% per °C)
Temperature

**Figure 3** Relationships underlying the total effect of temperature on the population growth rate (a-c; d Pop/d Temp) and reproduction (d-e; d Repro/d Temp). The plots in the top row show the relationships between the total effects of temperature on the population growth rate with (a) the focal pathway (d Cond/d Temp * ∂ Repro/∂ Cond * ∂ Pop/∂Repro, or the indirect effect of temperature on population growth via body condition and reproduction), (b) the direct path between temperature and population growth (∂ Pop/∂Temp, or the direct effect of temperature on population growth unrelated to body condition and reproduction), and (c) the indirect path from temperature -> reproduction -> population growth (∂Repro/∂ Temp * ∂ Pop/∂Repro, or the indirect effect of temperature on population growth via reproduction only and unrelated to body condition). The plots on the bottom row show the relationships between the total effects of temperature on the proportion of juveniles (i.e. no population-level included) with (d) the focal pathway up to the level of reproduction (Cond/d Temp * ∂ Repro/∂ Cond, or the indirect effect of temperature on reproductive success due to body condition), and (e) the direct path between temperature and reproduction (∂Repro/∂ Temp, or the direct effect of temperature on reproductive success unrelated to body condition). The grey dots show all site estimates, and the black slopes show trends across sites for each species individually. The $R^2_{within}$ value indicates the mean $R^2$ estimated for each individual species, or how well an individual path explains variation in the total change on population or reproduction for an individual species. The $R^2_{between}$ value indicates how well the individual paths explain variation in the total change on population or reproduction across all species. Note that if the effects of temperature on reproductive success or the population growth rate worked solely via the focal/direct/non-focal pathway, we would expect all values to fall on the dotted line Y = X.

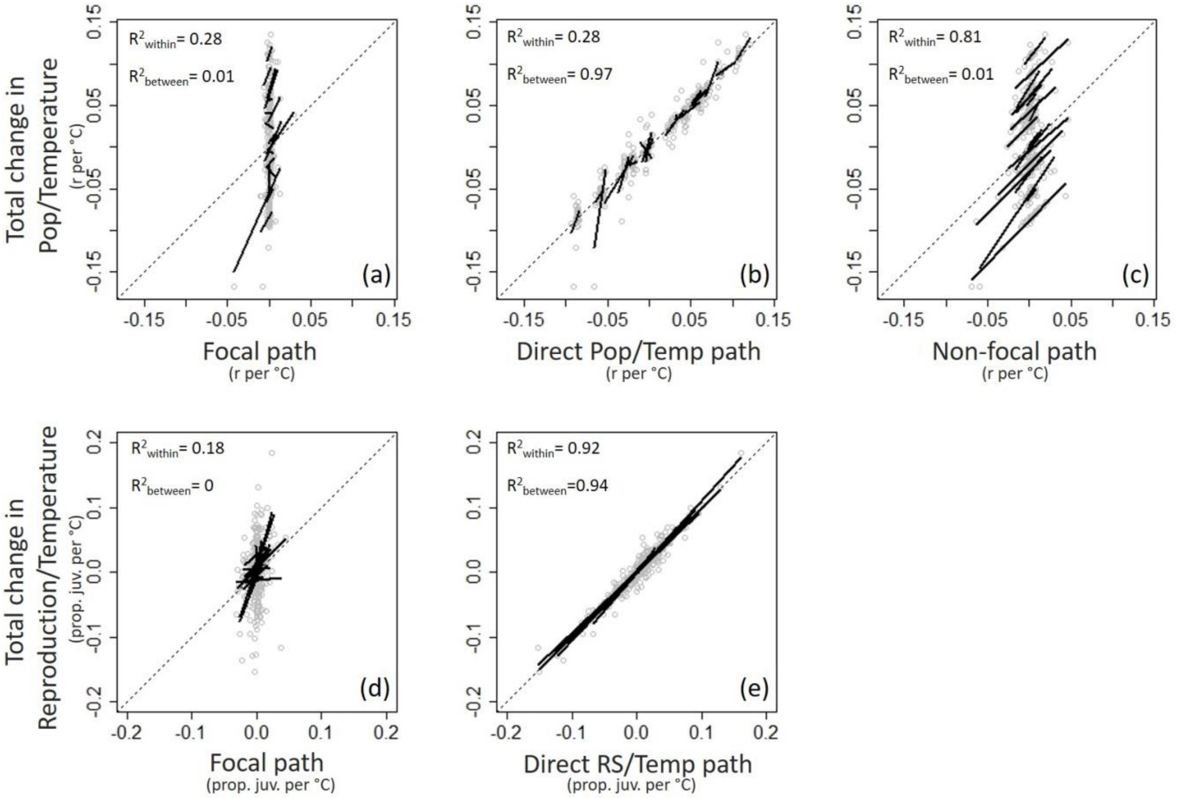
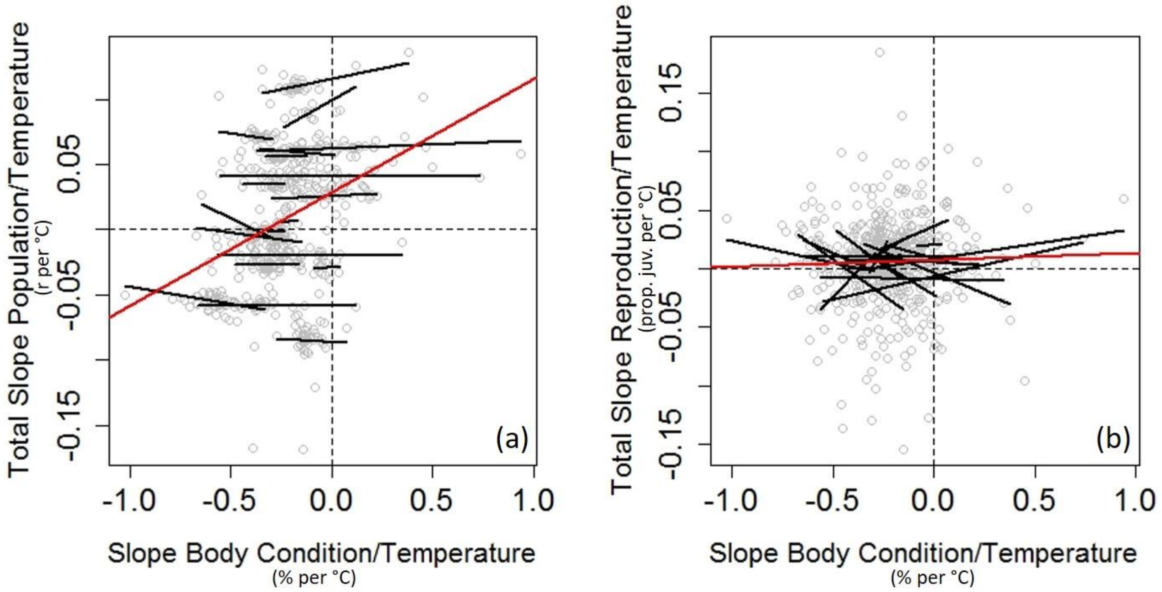

Total change in Pop/Temperature
(r per °C)
$R^2_{within}$= 0.28
$R^2_{between}$= 0.01
(a)
Focal path
(r per °C)
$R^2_{within}$= 0.28
$R^2_{between}$= 0.97
(b)
Direct Pop/Temp path
(r per °C)
$R^2_{within}$= 0.81
$R^2_{between}$= 0.01
(c)
Non-focal path
(r per °C)
-0.15
-0.05
0.05
0.15
Total change in Reproduction/Temperature
(prop. juv. per °C)
$R^2_{within}$= 0.18
$R^2_{between}$= 0
(d)
Focal path
(prop. juv. per °C)
$R^2_{within}$= 0.92
$R^2_{between}$=0.94
(e)
Direct RS/Temp path
(prop. juv. per °C)
-0.2
-0.1
0.0
0.1
0.2

Figure 4 The slope of body condition over temperature explains between-species variation in the total effect of temperature on the population growth rate (a), but not the total effect of temperature on reproduction (b). The red slopes show the overall (between-species) relationship between body condition sensitivity and population/reproduction sensitivity to temperature. The grey dots show all site estimates, and the black slopes show trends across sites for each species individually.



## Table Legend

**Table 1** List of species and site characteristics tested with linear models to explain variation in path slopes across species and sites. We also note our expected outcomes and the actual outcomes. Species/Site characteristics that are bold indicate that they are species characteristics, while un-bolded ones are site/local characteristics. Because some hypotheses specified specific sign outcomes (i.e. less fat insulation when warmer increases your reproductive success) while others only specified a stronger or weaker effect (i.e. temperature is likely to have a stronger impact on larger species) we have in some cases conducted these analyses on absolute values (noted with a * if this is the case). These hypotheses were identified partly from (McLean et al. 2016) and from expert opinion.

| **Pathway** | **Species/Site Characteristic** | **Hypothesis** | **Expected outcome** | **Actual outcome** |
|---|---|---|---|---|
| $\partial$Repro/ $\partial$ Cond | Predator density | If decreased body condition means you spend less time foraging and can fly better, then you might expect a decrease in body condition to be positive for reproduction in areas with higher predation as these birds avoid predators more effectively (Lima 1986). | Decreased condition = increased reproduction at sites with more predators | Decreased condition = lower reproduction at sites with more predators |
| | | | | |
| | Site mean body condition | If the population is on average heavier, then losing body condition may have less negative consequences, but if the population is on average already lighter it could have stronger negative consequences on reproduction because any mass lost will have a stronger biological impact. | Decreased condition = decreased reproduction at sites with more low mean body condition | No effect |
| | Population density | If low densities represent poor quality sites, you might expect decreases in body condition to have a negative association with reproduction. In good quality sites (with high population densities), decreased body condition may be less important if there is a more constant food supply or less stressors in | Decreased condition = decreased reproduction at sites with low population density | No effect |

| | | | | |
|---|---|---|---|---|
| | | general. | | |
| ∂Repro/ ∂ Temp | Wet/dry habitats | Temperature might have a stronger negative effect on populations in dry habitats because wet habitats might lessen the direct effects of hot weather through easy re-hydration or the opportunity for bathing (and therefore cooling) in available standing water (Oswald et al. 2008, McLean et al. 2018). | Increased temperature = decreased reproduction in dry habitats | No effect |
| | Population Density | If low densities represent poor quality sites, then changes in temperature may have a stronger effect on reproduction. In good quality sites (with high population densities), decreased body condition may be less important if there is a more constant food supply or less stressors in general. | More dense = weaker relationship between temperature and reproduction | More dense = stronger relationship between temperature and reproduction;<br>No direction |
| | | . | | |
| | **Life expectancy*** | Short-lived species (i.e. fast-species) are more sensitive to changes in reproductive success, and therefore they are typically better adapted to keep reproductive success as stable as possible (Sæther and Bakke 2000, Gaillard et al. 2000). Consequently, temperature may have a weaker effect on reproduction in short-lived species. | Short-lived = weaker relationship between temperature and reproduction | Short-lived = stronger relationship between temperature and reproduction No direction |
| | **Migration*** | Reproductive success of long-distant migrants may be more sensitive to changes in food conditions, or physiological heat stress after only just returning from their migrations (Both et al. 2006). | Migrants = stronger relationship between temperature and reproduction | No effect |
| ∂ Pop/ | | | | |
| | | | | |

| | | | | |
|---|---|---|---|---|
| ∂Repro | Density dependence* | Species that experience strong density-dependent regulation might have weaker, more negative relationships between reproduction and population growth if, for instance, increases in reproduction at one life-stage are counteracted by decreases in another life-stage. For example, reduced annual fledgling production due to changes in phenology can be counteracted by increased post-independence survival of offspring (Reed et al. 2013b). | Strong density dependence = weaker relationship between reproduction and population growth | Strong density dependence = stronger, positive relationship between reproduction and population growth |
| | **Life expectancy***| Expect a stronger relationship between reproduction and population growth in species that are short-lived as the population growth rate is more sensitive to changes in reproduction in such species (Morris et al. 2008). | Long life expectancy = stronger relationship between reproduction and population growth | No effect |
| | **Structural Size*** | Expect a stronger relationship between reproduction and population growth in species that are smaller as these species are likely to be ‘r’ species and thus the population growth rate is more sensitive to changes in reproduction (Sæther and Bakke 2000). | Smaller structural size = stronger relationship between reproduction and population growth | No effect |
| ∂ Pop/ ∂Temp | Density dependence* | Changes in temperature might have a weaker effect on population growth for species that experience strong density dependence because changes to reproduction or survival are likely to be ‘counteracted’ or buffered by reduced/increased competition (Reed et al. 2013b). | Strong density dependence = weaker relationship between temperature and population growth | No effect |
| | **Life expectancy*** | If temperature effects work via survival, then more long-lived species would be more likely to have stronger changes in population growth rates (Sæther and Bakke 2000). | Long life expectancy = stronger relationship between temperature and population growth | No effect |
| | **Migration*** | Changes in conditions at the breeding areas might have stronger effects on | Migrants = stronger relationship between | No effect |

| | | | | |
|---|---|---|---|---|
| | | migrant species, if they are more sensitive to poorer conditions or if a ‘mismatch’ with important resources occurs (Both et al. 2006). | temperature and population growth | |
| | Wet/dry habitats* | Temperature might have a stronger effect on populations in dry habitats as heat effects may be stronger (Oswald et al. 2008, McLean et al. 2018). | Dry habitats = stronger relationship between temperature and population growth | No effect |
| | Population Density* | If low densities represent poor quality sites, then changes in temperature may have a stronger effect on reproduction. | Low density = stronger relationship between temperature and population growth | No effect |