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Consistent within-individual plasticity is sufficient to explain temperature responses in red deer reproductive traits

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Abstract

Warming global temperatures are affecting a range of aspects of wild populations, but the exact mechanisms driving associations between temperature and phenotypic traits may be difficult to identify. Here, we use a 36-year data set on a wild population of red deer to investigate the causes of associations between temperature and two important components of female reproduction: timing of breeding and offspring size. By separating within- versus between-individual associations with temperature for each trait, we show that within-individual phenotypic plasticity (changes within a female's lifetime) was entirely sufficient to generate the observed population-level association with temperature at key times of year. However, despite apparently adequate statistical power, we found no evidence of any variation between females in their responses (i.e. no "IxE" interactions). Our results suggest that female deer show plasticity in reproductive traits in response to temperatures in the year leading up to calving and that this response is consistent across individuals, implying no potential for either selection or heritability of plasticity. We estimate that the plastic response to rising temperatures explained 24% of the observed advance in mean calving date over the study period. We highlight the need for comparable analyses of other systems to determine the contribution of within-individual plasticity to population-level responses to climate change.

KEYWORDS
advancing phenology, climate change, IxE, phenotypic plasticity, within-subject centring

1 | INTRODUCTION

Although effects of weather on wild animal populations have long been recognized (Birch, 1957; Elton, 1924), understanding the links between climate and variation in phenotypic traits has become an increasingly prominent aspect of evolutionary ecology given rates of anthropogenically induced environmental change (Parmesan, 2006;

Walther et al., 2002). Variation in weather at critical timepoints can influence physiological, morphological, behavioural and life-history traits, many of which will, through their effects on fitness, have consequences for population and evolutionary dynamics (Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toigo, 2000; Ozgul et al., 2010; Sæther et al., 2000). Population-level changes in phenotypic traits have been increasingly widely documented in wild animal populations

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and have been interpreted as indicative of rapid responses to climate change (Thackeray et al., 2010). However, despite this growing interest, the mechanisms underpinning population-level relationships between trait expression and environmental variables such as temperature are not always well understood (Merilä & Hendry, 2014).

An important starting point in the analysis of population-level associations between trait and climate is the separation of *within*-individual phenotypic plasticity in response to current environmental conditions from the processes that can generate differences *between* individuals: between-individual (longer-term) plasticity, selective (dis)appearance and microevolutionary change (Boutin & Lane, 2014; Charmantier & Gienapp, 2014). For traits expressed multiple times throughout an individual's life, individual changes in trait expression in response to environmental variation may be of an equivalent magnitude to the observed population-level association (Figure 1a), indicating that the relationship between trait and environment can be driven entirely by within-individual plasticity (Nussey, Wilson, & Brommer, 2007; Pigliucci, 2001). Such plasticity may be adaptive, enabling individuals to respond to a variable environment, or it may simply reflect physiological constraints or resource limitation. However, population-level associations may also be driven by differences between individuals (Figure 1b; van de

Pol & Wright, 2009). For example, environmental conditions in an individual's year of birth may influence an individual's trait values throughout life (Monaghan, 2008), or selective mortality might remove individuals with different trait values under different climatic conditions. In the context of climate change, directional change in the environment may be associated with changes in the composition of the population over time. If these differences between individuals are genetically based, between-individual effects could be indicative of an adaptive evolutionary response to climate change (Gienapp, Teplitsky, Alho, Mills, & Merilä, 2008; Merilä & Hendry, 2014). The relative contributions of these different processes will ultimately determine a population's adaptation to environmental change.

Is within-individual plasticity sufficient to explain population-level patterns of response to climate change? The statistical approach of "within-subject centring" can be used to explicitly compare within-individual responses with the overall population-level response to environmental variation, to address this question (van de Pol & Wright, 2009). Thus, for example in a Canadian population of tree swallows (*Tachycineta bicolor*), within-individual plasticity in breeding time in response to spring temperatures is equivalent to the population-level change (Bourret, Bélisle, Pelletier, & Garant, 2015), and in barn swallows (*Hirundo rustica*) breeding in Denmark,
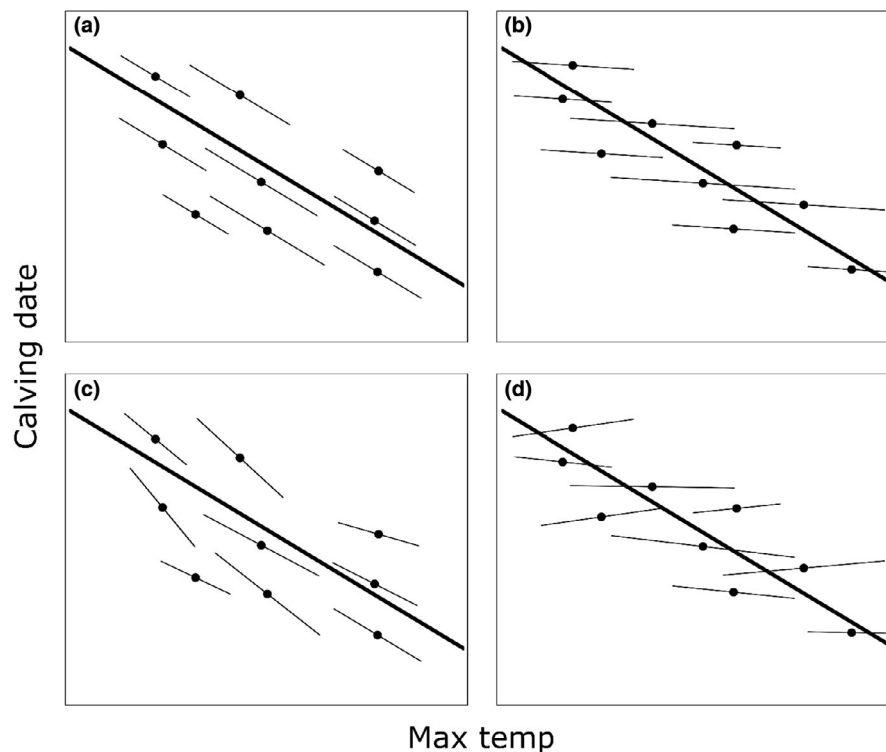

FIGURE 1 Schematic depicting possible within- and between-subject relationships between a phenotypic trait and environmental variation (e.g. calving date and maximum temperature). The thin sold lines represent the within-subject slopes (β_W) of nine subjects (filled circles), and the thick solid lines represent the corresponding between-subject slopes (β_B) resulting from the relationship between average calving date and average maximum temperature. In scenarios a) and c), the within-subject response to temperature is equal to the between-subject response, indicating that the within-subject plasticity is sufficient to explain the population-level response to temperature. In scenarios b) and d), the between-subject differences are greater than the within-subject response, indicating that differences between individuals are responsible for the population-level response. In scenarios a) and b), there is no variation between individuals in their response to temperature, whereas in scenarios c) and d), there is evidence for IxE. Adapted from van de Pol and Wright (2009)

within-individual plasticity is sufficient to explain overall associations between body condition and vegetation measures (NDVI) in one part of the migration route (Balbontin et al., 2012). A recent study of big-horn sheep (*Ovis canadensis*) in Alberta, Canada, found that within-individual plasticity in response to autumn precipitation explained the population-level association with parturition date (Renaud, Pigeon, Festa-Bianchet, & Pelletier, 2019). Other studies have separated within- from between-individual level changes in response to climate, but without explicitly testing whether within-individual plasticity was sufficient to explain the population-level responses to changing climate (Dehnhard et al., 2015; Dobson, Becker, Arnaud, Bouwhuis, & Charmantier, 2017; Hinke, Polito, Reiss, Trivelpiece, & Trivelpiece, 2012; Lane, Kruuk, Charmantier, Murie, & Dobson, 2012; Lane et al., 2018). In general, empirical studies are therefore still too sparse to draw useful conclusions as to the prevalence of the alternative processes depicted in Figure 1 (or in Figure 1 of van de Pol & Wright, 2009 original paper).

Another potentially important component of the effects of climate is the extent to which individuals differ in their plastic responses (Figure 1c,d). These differences can be described formally as between-individual variation in the slope of the relationship between trait and climate or in individual "reaction norms" ("IxE", Nussey et al., 2007). A genetic basis to such variation implies genotype-by-environment interactions ("GxE"). Within-individual plasticity can be advantageous since it can allow individuals to respond immediately to ongoing environmental heterogeneity (Houston & McNamara, 1992), for example adapting condition-dependent decision-making to the current conditions. However plasticity is not always adaptive (Arnold, Nicotra, & Kruuk, 2019; Gotthard & Nylin, 1995): changes in phenotype may simply reflect physiological constraints or resource limitation, and flexibility may also come at a cost (DeWitt, Sih, & Wilson, 1998). Nevertheless, whether or not average plasticity is adaptive, variation in reaction norms would imply the potential for selection on plasticity. If variation for plasticity is also genetically based ("GxE"), there is in theory the potential for plasticity to evolve (Nussey, Postma, Gienapp, & Visser, 2005c; Pigliucci, 2005). Assessing this potential involves first establishing the extent of variation in plasticity between individuals.

Phenological traits such as calving date are frequently linked to environmental variables such as temperature, and advancing spring phenologies are among the most commonly documented responses to climate change (Parmesan, 2006; Thackeray et al., 2010). Among vertebrates, much work has centred on avian systems (particularly Northern Hemisphere passerines), with a particular focus on variation in egg-laying date because of its clear links with spring temperature, its significant fitness consequences and the apparent potential for adaptive plasticity (Charmantier & Gienapp, 2014; Visser, Both, & Lambrechts, 2004). The phenology of reproduction in long-lived mammals such as ungulates differs because long gestation periods often create a considerable time lag between conception and parturition (Boutin & Lane, 2014). Relationships between climate and traits such as calving date may therefore be more complex, acting over longer time frames (Renaud et al., 2019). Plasticity in these traits may

not necessarily be adaptive, but may be simply a consequence of changes in food availability and/or thermoregulatory requirements influencing individual condition at the time of conception (typically in the previous year); this contrasts with avian systems where plasticity in phenology can enable females to coincide offspring hatching with peak food abundance (e.g. Charmantier et al., 2008).

Morphological traits have also been linked to climate, and temperature in particular, in a range of systems. However, although body size is an important fitness-related trait, linked to survival and reproductive performance in many species (Kingsolver & Huey, 2008), its general response to climate change is not well understood and may be shaped by multiple potentially conflicting factors (Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011; Teplitsky & Millien, 2014; Villar & Naya, 2018). Bergmann's rule predicts an adaptive evolutionary decrease in body size in association with increased temperatures, owing to reduced thermoregulatory requirements (Bergmann, 1847). However, increased primary productivity associated with warming is expected to result in larger body sizes, which may arise from plastic responses to the environment, particularly on shorter timescales (e.g. Kruuk, Osmond, & Cockburn, 2015).

Unravelling the mechanisms that drive trait–environment relationships in natural populations—and separating out potentially confounded effects of environment, time, age and lifespan—requires repeated measures of individuals throughout their lifetimes. Individual-based longitudinal data can be resource-intensive to collect, particularly in longer-lived species that are especially useful because they are more likely to experience a range of environments over multiple years (Clutton-Brock & Sheldon, 2010). In addition, identifying the relevant climatic drivers is not always straightforward, requiring a good understanding of the species' biology as well as appropriate weather measurements over time. Here, we present data from a long-running study of red deer (*Cervus elaphus*) on the Isle of Rum, Scotland (Clutton-Brock, Guinness, & Albon, 1982), for which a number of important trait–climate relationships have been identified. We focus on the maternal reproductive traits of calving (parturition) date and calf birth weight, which are recorded multiple times throughout an individual mother's life. We treat both traits as traits of the mother, rather than the offspring, because we are especially interested in maternal plasticity in response to climate change. Calving date is a trait of the mother because it depends on a female's condition around the time of the mating season (Albon, Mitchell, Huby, & Brown, 1986), and gestation itself shows little plasticity (Clements, Clutton-Brock, Albon, Pemberton, & Kruuk, 2011). Further, it is appropriate to consider calf birth weight as a trait of the mother because previous analyses of the population have shown that the proportion of variance in birth weight explained by maternal genetic effects is much larger than that explained by direct (offspring) genetic effects (~28% versus 4%; Kruuk & Hadfield, 2007). Both these traits have substantial fitness consequences in the population: earlier born and heavier calves are more likely to survive their first winter (Coulson, Kruuk, Tavecchia, Pemberton, & Clutton-Brock, 2003; Guinness, Clutton-Brock, & Albon, 1978), and males that are born heavier (Kruuk, Clutton-Brock, Rose, & Guinness, 1999) and

females who breed earlier or produce heavier calves tend to have higher lifetime breeding success (Bonnet, Morrissey, Clutton-Brock, Pemberton, & Kruuk, 2019).

Previous studies on the Rum red deer population have identified links between calving date and various weather variables in the year preceding birth, particularly surrounding the time of conception and early gestation (Coulson et al., 2003; Moyes et al., 2011; Stopher, Bento, Clutton-Brock, Pemberton, & Kruuk, 2014). They have also identified a substantial advance in calving date of 4.2 days per decade since 1980 (Moyes et al., 2011). Some part of this advance can be attributed to a genetic response to the selection of earlier birth dates (Bonnet et al., 2019), but our focus here is on the effect of warming temperatures on maternal traits. The average birth weight of calves on Rum has been consistently positively linked to temperatures experienced by mothers in spring, during late gestation (Albon, Clutton-Brock, & Guinness, 1987; Albon, Guinness, & Clutton-Brock, 1983; Coulson et al., 2003; Stopher et al., 2014). However, the contribution of within- versus between-individual differences to the population-level association between temperature and these reproductive traits has not been addressed. We focus on temperature for two reasons: first, we wanted to explore phenotypic plasticity in response to ongoing climate change, and raising temperatures are the clearest manifestation of this change. Second, a recent path analysis of reproductive traits in the study population including a range of climatic and non-climatic variables found temperature to be the most important (Stopher et al., 2014). We used a "sliding window" approach to identify the most relevant periods of temperatures in the 12 months preceding a calf's birth and then used a within-subject centring analysis (van de Pol & Wright, 2009) to decompose the responses of calving date and calf birth weight to the relevant temperature indices. Thus, we decomposed the population-level response into within- versus between-individual components, and then tested for variation between individual mothers in their response to changing temperature. We also quantified the extent to which the plasticity in response to temperature explained the observed temporal trend in calving date.

2 | MATERIALS AND METHODS

2.1 | Data collection

The population of red deer, *Cervus elaphus*, living in the North Block of the Isle of Rum, Scotland (57°01′N, 6°17′W), has been monitored since the early 1970s (Clutton-Brock et al., 1982). It has been unmanaged since the cessation of culling in 1972, following which the population density of deer living in the study area increased until around 1980, when population size stabilized around carrying capacity (Coulson, Guinness, Pemberton, & Clutton-Brock, 2004). Individuals born in the ~12 km^2 study site are marked so they can be recognized throughout their lives, and detailed individual life-history records are gathered through regular censusing throughout the year. Females come into oestrus and conceive during the annual rut in late September–October. Calves are gestated over winter, and females

give birth to a single calf in late May–June the following spring. During the calving season, females are assessed visually to determine whether they are pregnant, and daily observations ensure that the birth date of all calves is known with a high degree of accuracy. Newborn calves are captured shortly after birth and are weighed, blood sampled and marked (>75% of calves). Females that reach breeding age have an average longevity of around 11 years, meaning most females have multiple breeding records (median 4 calves per female; Walling et al., 2014). We defined a "deer year" such that deer year t runs from 1 May year t to 30 April year $t+1$. In this study, we used data from deer years 1980–2015, excluding the earliest years of the study to avoid confounding effects of rapidly changing population density in the 1970s (following Moyes et al., 2011). We used temperature data from the Met Office United Kingdom Climate Projections (UKCP09) gridded data sets. We used local daily minimum and maximum temperatures for the 5 × 5 km grid square covering the village of Kinloch on the Isle of Rum (142500E 797500N).

2.2 | Data analysis

Our analyses explored the relationship between weather and maternal reproductive traits relating to calf birth: the date a female gave birth to a calf in a given year and the birth weight of her calf. First, we identified associations between these birth traits and temperature using a "sliding window" approach. We then decomposed the population-level response to temperature into contributions of within-individual phenotypic plasticity and between-individual differences (details below). All analyses were conducted in a mixed model framework using the package *lme4* (Bates, Mächler, Bolker, & Walker, 2015) in the R statistical environment (R Core Team, 2018). When models with different fixed-effects structures were compared, for example when testing the significance of a fixed effect by comparing models with and without the term, maximum likelihood (ML) was used, otherwise restricted maximum likelihood (REML) was used. Response variables and continuous explanatory variables were standardized prior to inclusion in models (mean centred and divided by the standard deviation). Parameter estimates given in the text are followed by ("±") their standard errors (*SE*).

2.2.1 | Models of maternal reproductive traits

Our response variables were as follows: calving date (date on which a calf was born in days from 1 May, n = 3,000 observations of 717 females) and calf birth weight (mass of calf at capture in kg, adjusted for time since birth, n = 2,236 observations of 616 females; birth weight = capture weight – (0.01539 * age at capture in hours), following Clutton-Brock et al., 1982). See Table S1 for full details of sample sizes. Calves captured more than a week after birth were excluded from the analyses of birth weight (~3% of observations), and calves born before 1 May and after 31 July (~2.5% of observations) were excluded from the analyses of calving date to ensure normality of residuals (following Moyes et al., 2011; note that there were only 2 observations prior to 1 May). To ensure the exclusion of these outliers

did not influence our results, we re-ran our analyses using the full distribution of calving dates, log-transformed to improve the distribution of the residuals; these models produced exactly the same qualitative conclusions (see Table S2 for full model summaries). Both traits were modelled using a Gaussian error distribution and identity link function.

We included other factors known to influence these maternal reproductive traits in our models. The calving date model included female age in years (linear and quadratic terms); and female "reproductive status", describing a female's recent reproductive history (a 5-level factor: "naïve", first time breeder; "milk hind", gave birth last year and calf survived to 1 May; "true yeld", has bred before but no calf last year; "summer yeld", gave birth last year but calf died before 1 October; "winter yeld", gave birth last year but calf died between 1 October and 1 May). The calf birth weight model included the same terms and, additionally, calf sex (as a 2-level factor) and calf birth date (days from 1 May). Because our data included repeated measures of individuals and years, female identity and year (as a multilevel factor) were both included as random intercept terms to account for pseudoreplication and to estimate interindividual and interannual variance. We estimated 95% confidence intervals around the variance components using the bootstrapping method in the *confint.merMod* function in *lme4* (Bates et al., 2015).

2.2.2 | Identifying associations with temperature

A "sliding window" approach was used to identify critical periods of weather associated with average calving date and calf birth weight in the population (Husby et al., 2010; Kruuk et al., 2015; Phillimore, Leech, Pearce-Higgins, & Hadfield, 2016). We used daily minimum and maximum temperatures over the deer year preceding birth, that is 1 May–30 April year t−1 for females giving birth in May–June year t. We calculated the average minimum or maximum temperature over time periods (or windows) of varying start date and duration and tested the strength of associations with each of the birth traits. The start date and duration were varied by weekly intervals (windows ranged from 1 to 52 weeks prior to birth), and we used Akaike's information criterion (AIC) to identify the best model (that with the lowest AIC value) and therefore to determine the best window for each trait. All models included the fixed and random effects specified above (Section 2.2.1), and models with different windows were compared using maximum likelihood (ML). When considering the significance of temperature in the final models of calving date and calf weight, we added two additional degrees of freedom in our tests to account for the estimation of two parameters at this stage: the start date and duration of the window (following Phillimore et al., 2016).

2.2.3 | Decomposing the population-level response to temperature

Once we had identified the periods of weather most strongly associated with calving date and calf birth weight in the population, we decomposed this relationship to assess whether the relationship was driven by individual females responding plastically to year-to-year

changes in the environment (within-individual plasticity) or by consistent differences between individuals across their lifetimes, using van de Pol and Wright's (2009) within-subject centring approach. Our initial mixed model for each trait was of the form:

$$y_{ij} = \beta_0 + \beta_W(x_{ij} - \bar{x}_j) + \beta_B\bar{x}_j + \mu_{0j} + e_{0ij} \qquad (1)$$

where y_{ij} is the trait value (calving date or calf weight) of measurement i from subject j, and x_{ij} is the corresponding temperature value (note that the actual model fitted also contained other terms not related to the partitioning, as described in Section 2.2.1). The intercept of the regression equation is β_0, and the random intercept μ_{0j} and the residual error term e_{0ij} are drawn from normal distributions with mean zero and between-subject variance V_I and residual variance V_R, respectively. β_B is the between-subject component, which is the relationship between an individual's trait value (y_{ij}) and the average of the temperatures it experienced across all the years in which that individual bred ($\bar{x}_j$). β_W is the within-subject component, which is the relationship between the observed trait value (y_{ij}) and the deviation of the temperature in the given year (x_{ij}) from the average temperature an individual experienced ($x_{ij} - \bar{x}_j$). β_W therefore represents how females respond to variation in temperature over their own lifetimes and can be interpreted as within-subject phenotypic plasticity. If the within- and between-subject effects are in the same direction and the within-subject component is equal to or greater than the between-individual component ($\beta_W \geq \beta_B$), then the two components cannot be distinguished. In this case, a within-individual, plastic response to the environment is sufficient to explain the population response to temperature (van de Pol & Wright, 2009). To test this formally, we fitted a slightly different model to test explicitly whether the within- and between-subject components were significantly different:

$$y_{ij} = \beta_0 + \beta_W x_{ij} + (\beta_B - \beta_W)\bar{x}_j + \mu_{0j} + e_{0ij}. \qquad (2)$$

In this case, the parameter estimate for $\bar{x}_j$ gives the difference between the between- and within-subject effects ($\beta_B - \beta_W$). Where this term is close to zero and nonsignificant, the within- and between-subject effects are effectively the same (van de Pol & Wright, 2009). Our main results are based on data from all females. To check that our results were not unduly influenced by females with a limited number of observations in their lifetime, we repeated all analyses on the subsets of females for which we had two, three or four or more observations (≥2 observations: calving date n = 2,843 observations of 560 females; birth weight n = 2,047 observations of 446 females; representing 78% and 70% of individuals, respectively). The results remained unchanged (see Supplementary materials).

2.2.4 | Between-individual variation in phenotypic plasticity (IxE)

We went on to examine whether females differed in their individual responses to environmental variation using random regression models. By including a random slope term in Model 1, we tested whether

there was evidence for significant variation in slopes for the within-subject component of the model (van de Pol & Wright, 2009):

$$y_{ij} = \beta_0 + (\beta_W + \mu_{Wj})(x_{ij} - \bar{x}_j) + \beta_B \bar{x}_j + \mu_{0j} + e_{0ij} \qquad (3)$$

where μ_{0j} and μ_{Wj} are, respectively, the individual random intercept and random slope terms, drawn from a multivariate normal distribution with means of zero, intercept variance of V_I, slope variance V_S and intercept–slope correlation $r_{I,S}$. Variation in random slopes (i.e. V_S) would provide evidence for variation in phenotypic plasticity between different females, or IxE, indicating that some females respond more strongly to temperature variation than others. The significance of IxE was assessed using likelihood ratio tests (LRT) comparing models 3 and 1 with 2 degrees of freedom to account for the additional parameters of variance in slopes and covariance between intercepts and slopes.

2.2.5 | Power analyses for between-individual variation in phenotypic plasticity

Finally, we used a power analysis to estimate the minimum amount of variation in plasticity we could detect with our data set with a reasonable amount of statistical power. First, for both calving date and calf birth weight, we fitted a model including IxE (Model 3). Based on our data and these models (Table S3), we simulated data using the model parameters for the fixed effects, random intercept variances (female identity), intercept–slope correlations and residual variances, but we specified a value for the between-individual variance in slope (V_S) between 0.00001 and 0.1 (see Martin, Nussey, Wilson, & Réale, 2011). For each value of V_S, we simulated 1,000 response variables y_{ij}. We then tested the significance of between-individual variation in plasticity. We estimated the statistical power we had to detect IxE for a given level of V_S as the percentage of simulations that resulted in a significant variation in plasticity.

To put these different values of V_S into context, we estimated the proportion of the total phenotypic variance in the trait due to IxE, r_{IxE}, calculated as follows:

$$r_{IxE} = \frac{V_S V_x + E(x)^2 V_S + 2E(x)Cov(I,S)}{V_I + V_S V_x + E(x)^2 V_S + 2E(x)Cov(I,S) + V_R}$$

where $E(x)$ and V_x are the population mean and variance of $x_{ij} - \bar{x}_j$, and $Cov(I,S)$ is the intercept–slope covariance calculated as $r_{I,S} * \sqrt{V_I V_S}$. Since all variables were scaled to a mean of zero (i.e. $E(x) = 0$ in the previous equation) and a variance of 1 ($V_x = 1$) prior to the analysis, r_{IxE} could be simplified to

$$r_{IxE} = \frac{V_S}{V_I + V_S + V_R}$$

3 | RESULTS

3.1 | Climatic drivers of maternal reproductive traits

Variation in calving date was best explained by the average maximum temperature between 17 July and 20 November in the year preceding birth (Figure 2a; ΔAIC = −6.149 compared to null model), whereas variation in calf birth weight was best explained by the average maximum temperature between 5 February and 23 April, towards the end of gestation (Figure 2b; ΔAIC = −15.328 compared to null model). For both traits, the best windows identified for maximum temperature explained more variation than the best windows for minimum temperature (ΔAIC = −2.469 and −3.032 compared to models including the best windows for minimum temperature for calving date and calf weight, respectively). Calving date was negatively related to average maximum temperature during the critical window (Table 1a), meaning that average calving dates were earlier if temperatures were higher in the previous year (Figure 3a). Calf birth weights were positively related
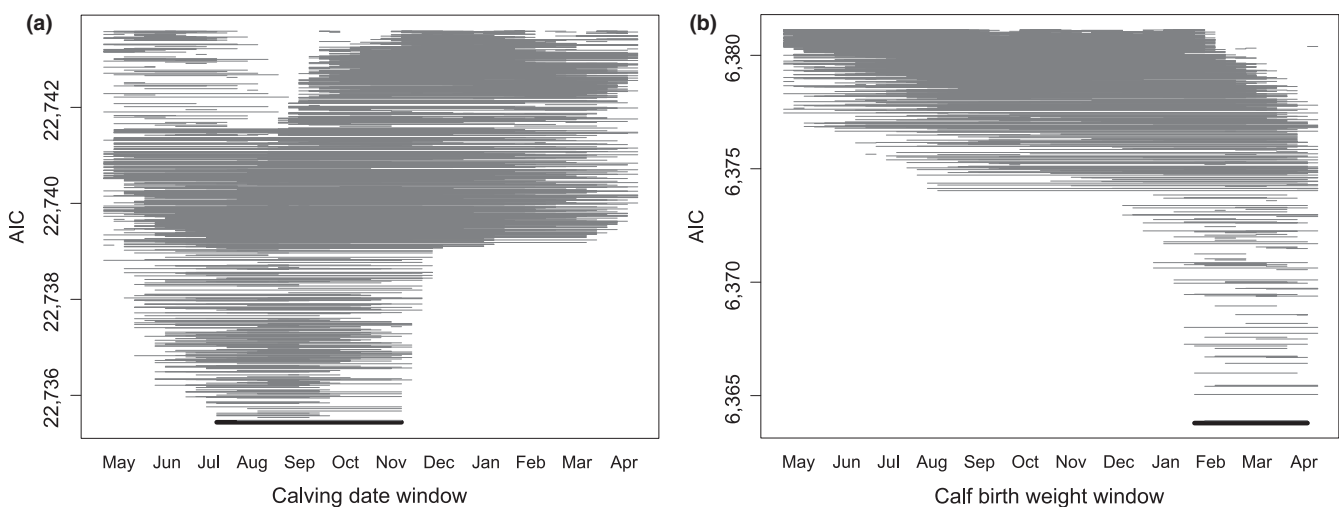

FIGURE 2 Comparison of AIC values for models including the average maximum temperature calculated over different windows for a) calving date and b) calf birth weight. Windows span the year preceding birth, and horizontal lines show the start date and duration of the window for each model. The model with the lowest AIC value was taken to be the critical window for each trait, highlighted in bold: ΔAIC from the null model was −6.149 and −15.328 for calving date and calf birth weight, respectively

to maximum temperatures during the critical window (Table 1b), meaning average birth weights were higher following warmer springs (Figure 3b).

3.2 | Within- and between-individual responses to temperature

Decomposing the relationships between maternal reproductive traits and temperature revealed significant within-individual variation in calving date (Table 2a, Model 1; Figure 3a) and calf birth weight (Table 2b, Model 1; Figure 3b) in response to temperature in these best windows, indicating that individual females showed plasticity in response to variation in temperature experienced at the time of breeding. For a one degree increase in the temperature index, individual females calved an average

of ~2.7 days earlier, and gave birth to calves that were on average ~200 g heavier (from a model with unstandardized covariates). There was also between-subject variation in both calving date (Table 2a, Model 1; Figure 3a) and calf birth weight (Table 2b, Model 1; Figure 3b). This indicates that females that experienced warmer temperatures on average across their lifetimes tended to give birth consistently earlier, and their calves tended to be consistently heavier (independent of the relationship between calf birth date and weight). There was no significant difference between the within- and between-subject effects for either calving date ($\beta_B - \beta_W$ = −0.027 ± 0.051; Table S3a, Model 2) or calf birth weight ($\beta_B - \beta_W$ = 0.051 ± 0.056; Table S3b, Model 2), implying that the within-individual, plastic response to temperature was sufficient to explain the overall population-level response to variation in temperature for both birth traits.

TABLE 1 Estimates from linear mixed-effects models for a) calving date and b) calf birth weight (kg), showing the relationship between each birth trait and temperature during the critical window identified in the sliding window analysis. Covariates were standardized prior to inclusion in the models, and parameters were estimated using REML. *p*-values come from models estimated with ML in the package *lmerTest* (based on Satterthwaite approximation for denominator degrees of freedom; Kuznetsova, Brockhoff, & Christensen, 2017). Values in bold illustrate the significance of the temperature term with an additional 2 degrees of freedom added to the model, to account for the estimation of an additional two parameters (for the start date and duration of the critical period) in the sliding window analysis

| a) Calving date	n = 3,000 (717 females)	Estimate	SE	p-value
Fixed effects	Age	−0.673	0.107	<.001
	Age^2	0.776	0.099	<.001
	Repro status: Naïve	−0.499	0.068	<.001
	Summer yeld	−0.818	0.054	<.001
	True yeld	−0.714	0.044	<.001
	Winter yeld	0.032	0.062	.598
	Max temp (17 Jul–20 Nov)	−0.164	0.056	.005
				.044
		Variance	95% CI	
Random effects	Female ID	0.172	0.134–0.215	
	Year	0.105	0.055–0.166	
	Residual	0.626		
b) Calf birth weight	**n = 2,236 (635 females)**	Estimate	SE	p-value
Fixed effects	Age	1.190	0.110	<.001
	Age^2	−1.216	0.101	<.001
	Repro status: Naïve	0.064	0.069	.426
	Summer yeld	0.491	0.057	<.001
	True yeld	0.424	0.045	<.001
	Winter yeld	−0.194	0.059	<.001
	Calf birth date	0.111	0.018	<.001
	Calf sex: Male	0.264	0.031	<.001
	Max temp (5 Feb–23 Apr)	0.129	0.028	<.001
				<.001
		Variance	95% CI	
Random effects	Female ID	0.412	0.352–0.477	
	Year	0.017	0.006–0.031	
	Residual	0.428		
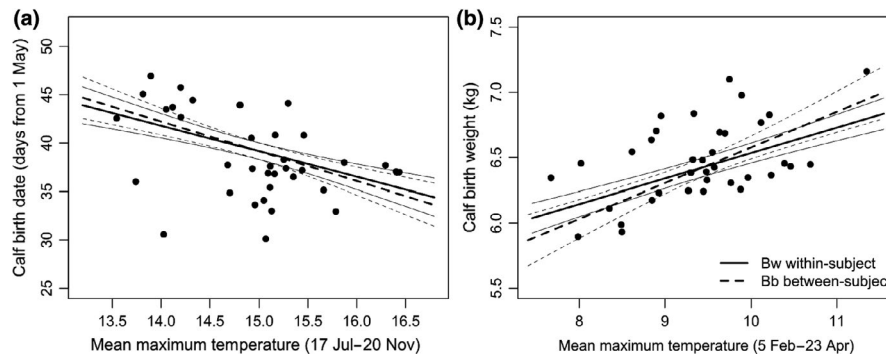
FIGURE 3 The relationship between average maximum temperature in the critical window and a) annual average calving date and b) annual average calf birth weight. Points show averages of raw data for each year (1980–2015). Black lines show predictions of linear mixed-effects models with unstandardized covariates, accounting for other fixed effects; the grey lines indicate standard errors around those predictions. Solid lines show the within-subject response to temperature (i.e. within-individual phenotypic plasticity, with slope β_W), and dashed lines show the between-subject response to temperature (with slope β_B)

3.3 | Tests for variation between individuals in plasticity

Models including a random slope term for the within-individual response to temperature did not explain more variation in the data than models with a random intercept only, indicating that the within-subject response to temperature did not vary significantly between females (Table 3; Table S4 for full model summaries). The same was also true if we instead included a random slope term for the population-level response to temperature, without first decomposing the effect into within- versus between-individual effects (Table S5). Therefore, there was no evidence of variation between individual females in their response to temperature for either calving date or calf birth weight.

3.4 | Power to detect between-individual variation in plasticity

The power analysis suggested that our data set provides reasonable power (over 80%) to detect significant between-individual variation in plasticity when the between-individual variance in the slope (V_S) was 0.007 or above for calving date, and 0.018 or above for calf birth weight (Figure 4). Expressing these values of V_S as a proportion of the phenotypic variance in the trait suggests that we have power to detect between-individual differences in plasticity that explain as little as 0.7% or 2.1% of the variance in calving date or calf birth weight, respectively. This means that if differences in plasticity between females were contributing to ~1%–2% or more of the variance in reproductive traits, our data set would provide sufficient power to detect IxE.

4 | DISCUSSION

Our analyses showed that calving dates in our red deer study population were earlier following warmer summers and autumns, the period leading up to and surrounding conception and early gestation (Figures 2a and 3a; Table 1a), and calf birth weights were higher following warmer temperatures in late spring, the period corresponding to the final stage of gestation (Figures 2b and 3b; Table 1b). We compare these results with previous analyses of the Rum red deer study population (which essentially found similar relationships) and discuss the possible reasons why warmer temperatures should advance calving dates and cause in utero calves to grow larger, in more detail in the Supplementary material. Here, we focus on the inferences we can draw from the mean-centring decomposition into within- versus between-individual responses. This decomposition showed that individual females responded plastically to variation in the temperature they experienced at different points during their lifetimes (Figure 3; Table 2). However, there was no evidence for variation between females in these responses.

Within-individual phenotypic plasticity was sufficient to explain overall population-level responses to temperature: the slopes of the average within-individual responses were equal to or greater than the between-individual responses in both traits (Table 2). Previous work in this study population documented a substantial temporal trend in average calving date (Moyes et al., 2011). Our data here show that mean calving dates advanced by ~11.5 days between 1980 and 2015 (Figure S1c). However, despite there being a significant increase in the average maximum temperature during the critical window for calving date over the same period (of ~1°C; Figure S1b), the association between calving date and temperature identified in this study is not sufficient to fully explain the temporal trend. Based on the association between calving date and temperature identified here (Figure S1a), and the temporal trend in critical temperatures, we would predict an advance in calving date. However, the product of the regression slopes for these relationships predicts an advance of ~2.8 days between 1980 and 2015 (Figure S1c), which represents only ~24% of the observed change in calving date over this period.

These calculations suggest that although within-individual phenotypic plasticity in calving date is sufficient to explain the

TABLE 2 Estimates for the within- (β_W) and between-subject effects (β_B) of temperature on birth traits, from linear mixed effects models of a) calving date and b) calf birth weight, using the average maximum temperature in the best window for each trait. Model structures used to separate within- and between-subject effects are described in the Section 2 (Model 1). Covariates were standardized prior to inclusion in the models, and parameters were estimated using REML. *p*-values come from models estimated with ML in the package *lmerTest* (based on Satterthwaite approximation for denominator degrees of freedom; Kuznetsova et al., 2017)

a) Calving date	n = 3,000 (717 females)	Estimate	SE	p-value
Fixed effects	Age	−0.676	0.106	<.001
	Age^2	0.778	0.098	<.001
	Repro status: Naïve	−0.499	0.068	<.001
	Summer yeld	−0.818	0.054	<.001
	True yeld	−0.714	0.044	<.001
	Winter yeld	0.033	0.062	.593
	β_W Max temp	−0.157	0.057	.008
	β_B Max temp	−0.183	0.067	.006
		Variance	95% CI	
Random effects	Female ID	0.173	0.139–0.213	
	Year	0.102	0.059–0.160	
	Residual	0.625		

| b) Calf birth weight	n = 2,236 (635 females)	Estimate	SE	p-value
Fixed effects	Age	1.168	0.110	<.001
	Age^2	−1.194	0.101	<.001
	Repro status: Naïve	0.056	0.069	.426
	Summer yeld	0.489	0.057	<.001
	True yeld	0.423	0.045	<.001
	Winter yeld	−0.195	0.059	<.001
	Calf birth date	0.112	0.018	<.001
	Calf sex: Male	0.264	0.031	<.001
	β_W Max temp	0.124	0.028	<.001
	β_B Max temp	0.173	0.057	.002
		Variance	95% CI	
Random effects	Female ID	0.412	0.345–0.484	
	Year	0.017	0.007–0.030	
	Residual	0.429		

Response	Female ID	df	logLik	χ^2	p value
Calving date	Random intercept	12	−3866.32	0.322	.852
	Random intercept + slope	14	−3866.16		
Calf birth weight	Random intercept	14	−2686.88	0.361	.835
	Random intercept + slope	16	−2686.70		

TABLE 3 Likelihood ratio tests comparing mixed-effects models of calving date and calf birth weight including and excluding a random slope term for the within-subject response to temperature (as described in the Section 2, Model 3). Models also included other fixed effects shown in Table 1. (Please note that the addition of a random slope term requires 2 extra degrees of freedom, to account for variance in slopes and their covariance with intercepts)

population-level response to temperature, the temperature effects observed here cannot fully explain the overall temporal shift in calving date observed across the study period. It may be that the critical temperature period we have identified does not adequately capture all of the relevant impacts of climate on calving date or that there

are other unmeasured changes such as the composition of available food resources. Further, there could potentially be differences between the individuals alive early in the study and contemporary females, for example due to microevolutionary change. In a recent quantitative genetic analysis (Bonnet et al., 2019), we have found

FIGURE 4 Power to detect between-individual differences in plasticity, IxE (solid lines) and proportion of variance explained by IxE, r_{IxE} (dashed lines) for different values of slope variance (V_S) for a) calving date and b) calf birth weight. The vertical grey lines indicate the value of V_S for which power is 80%
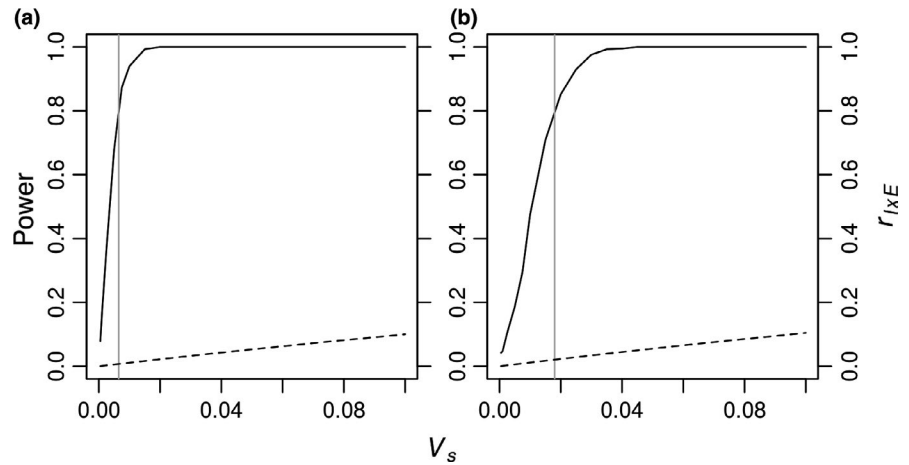
evidence of a genetic component to the phenotypic trend in calving date, indicating a contribution of microevolution. Female calving date is both heritable and under selection in favour of earlier dates, and estimates of the trend in average "breeding values" (individual genetic merit) fit unusually well with theoretical predictions for an adaptive evolutionary response to the observed selection—although they also cannot be distinguished from genetic drift. The estimated contribution of this genetic component is 15%–23% of the observed phenotypic change (15% from the most conservative model, 23% from a less conservative analysis), which is somewhat smaller than the change estimated here due to plasticity to autumn temperatures. Overall, we can therefore explain at most about half of the observed phenotypic trend. This is a sizeable portion, but means there are clearly other processes at work yet to be identified.

We found no evidence for significant variation between females in individual plasticity in reproductive traits in response to temperature (Table 3). These results contrast with earlier work in this population, which suggested differences between females in their plasticity for calving date and calf birth weight (Nussey, Clutton-Brock, Albon, Pemberton, & Kruuk, 2005a; Nussey, Clutton-Brock, Elston, Albon, & Kruuk, 2005b). However, our analyses involved a different data set to that analysed previously: we included 14 years of more recent data, but (following Moyes et al., 2011) excluded the earliest period of the study (1971–1979) which was characterized by rapid changes in population density in response to cessation of culling in the population (Clutton-Brock et al., 1982). Re-running the models including these early years (from 1971) did not, however, change our conclusions: there was still no evidence for IxE for either calving date (LRT: $\chi^2_{(2)} = 1.52$, $p = .470$) or calf birth weight (LRT: $\chi^2_{(2)} = 0.575$, $p = .750$). Restricting analyses to females with at least two or four observations, following these earlier studies, also did not change conclusions (Tables S6 and S7). The previous study of plasticity in calving date used a different climatic variable, examining variation in response to autumn rainfall (Nussey et al., 2005b), which could explain the different results. For birth weight, we believe the most likely cause of the difference is use of a different statistical method, with the earlier paper having extracted and then analysed best linear unbiased predictors (BLUPs) for estimates of individual plasticity. This

approach has since been shown to be anticonservative, since it does not account for the uncertainty associated with the estimation of BLUPs (Hadfield, Wilson, Garant, Sheldon, & Kruuk, 2010).

Although the lack of evidence for variation in plasticity is clearly a null result, our power analysis suggested that our data sets provided enough statistical power to detect even a small amount of between-individual variance in plasticity. We note also that our sample sizes easily meet the criteria recommended by Martin et al. (2011) and van de Pol (2012) for such analyses: the size and duration of this study make it, to our knowledge, one of the more powerful tests of IxE in a wild vertebrate population. Given the estimates of between-individual variance in plasticity obtained for models of both calving date and calf weight, we consider the nonsignificant results to be due to a lack of biologically important effect rather than a lack of statistical power. Our failure to detect IxE could also be because the temperature variables that we included in our analyses are necessarily proxies of the true environmental variables that causally influence calving date and calf birth weight. If these proxies are only weakly correlated with the true environmental variables, this may result in an underestimate of IxE. We therefore also conducted a Finlay–Wilkinson regression analysis (Finlay & Wilkinson, 1963), using the mean annual trait values as the environmental variables against which the trait was regressed instead of temperature. The annual trait means are expected to capture all environmental influences on the trait (though they will also be influenced by the structure of the population). Using this approach, we still found no support for random slope variance among individuals (calving date: $\chi^2_{(2)} = 4.806$, $p = .090$; calf birth weight: $\chi^2_{(2)} = 1.269$, $p = .530$). This suggests that the lack of IxE is not simply because we are unable to identify the true causal driver of variation in our reproductive traits. A lack of substantial difference between females in their response to temperature is interesting, particularly given the range of environmental conditions experienced by individuals in this population over multiple decades. Similarly, a recent study of common terns (*Sterna hirundo*) found little support for individual variation in plasticity of lay date in response to temperatures experienced during the nonbreeding period, despite large sample sizes (Dobson et al., 2017), and

a study of big horn sheep found no variation in plasticity of parturition date in response to autumn temperature or precipitation (Renaud et al., 2019). These results imply no potential either for genotype–environment interactions (GxE), nor for selection on individual plasticity—both of which would be required for plasticity itself to evolve (Gienapp & Brommer, 2014).

In conclusion, we have identified associations between the maternal reproductive traits of calving date and calf birth weight and temperatures in the year leading up to birth. Decomposition of the population-level associations with temperature revealed that individual females responded plastically to variation in temperature they experienced during their own lifetimes, and give a clear indication that within-individual phenotypic plasticity was sufficient to explain population-level responses to temperature in this population. The analysis also indicated consistency between females in their response to climate change. Determining which of the scenarios depicted in Figure 1 underlie a population's response to warming temperature is an important component of understanding the effects of climate change on natural populations: here, our long-term records on red deer indicate strong support for the scenario depicted in Figure 1a, that consistent within-individual plasticity may be sufficient to explain the overall population-level response. Our analysis also indicates that this plasticity in response to warming temperatures contributes a sizable proportion of the observed temporal phenotypic trend in calving dates.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA ACCESSIBLITY

Data supporting this publication can be found in the Dryad Digital Repository: http://doi.org/10.5061/dryad.dd97q1p.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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