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Geographical differences in maternal basking behaviour and offspring growth rate in a climatically widespread viviparous reptile

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ABSTRACT

In reptiles, the thermal environment during embryonic development affects offspring phenotypic traits and potentially offspring fitness. In viviparous species, mothers can potentially manipulate the embryonic thermal environment through their basking behaviour and, thus, may be able to manipulate offspring phenotype and increase offspring fitness. One way in which mothers can maximise offspring phenotype (and thus potentially affect offspring fitness) is by fine-tuning their basking behaviour to the environment in order to buffer the embryo from deleterious developmental temperatures. In widespread species, it is unclear whether populations that have evolved under different climatic conditions will exhibit different maternal behaviours and/or thermal effects on offspring phenotype. To test this, we provided extended or reduced basking opportunity to gravid spotted skinks (*Niveoscincus ocellatus*) and their offspring from two populations at the climatic extremes of the species' distribution. Gravid females fine-tuned their basking behaviour to the basking opportunity, which allowed them to buffer their embryos from potentially negative thermal effects. This fine-tuning of female basking behaviour appears to have led to the expression of geographical differences in basking behaviour, with females from the cold alpine regions being more opportunistic in their basking behaviour than females from the warmer regions. However, those differences in maternal behaviour did not preclude the evolution of geographic differences in thermal effects: offspring growth varied between populations, potentially suggesting local adaptation to basking conditions. Our results demonstrate that maternal effects and phenotypic plasticity can play a significant role in allowing species to cope in changing environmental conditions, which is particularly relevant in the context of climate change.

KEY WORDS: Maternal effect, Maternal buffering, Climate change, Phenotypic plasticity, Population, Spotted skink

INTRODUCTION

Maternal effects are the interactions between a mother and her offspring that affect offspring phenotype independently of the mother's genetic contribution. They have been described as being highly dynamic, and they vary in direction and strength depending on the environment or the context (Uller, 2008; Plaistow and Benton, 2009). Most studies to date describe maternal effects as varying between proximate contexts (i.e. the immediate maternal environment) (e.g. Benton et al., 2008; Hinde et al., 2009; Beldade

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et al., 2011). However, perhaps more overlooked is the fact that they can also vary between ultimate contexts (i.e. the environmental conditions under which they have evolved) and may in some cases become locally adapted (Ghalambor et al., 2007; Hof et al., 2011; Hoffmann and Sgrò, 2011). Typically, we would expect to see local adaptation in maternal effects in widespread species in which the immediate maternal environment differs consistently between populations (e.g. Räsänen et al., 2005; Doody et al., 2006; Doody, 2009).

In reptiles, the temperature experienced by embryos during development can affect numerous phenotypic traits such as date of birth, size at birth, sex, locomotor performance or behaviour (reviewed in Booth, 2006), all of which may have carry-on effects on fitness (e.g. Madsen and Shine, 2000; Chamaille-Jammes et al., 2006; While et al., 2009; Pen et al., 2010; Uller et al., 2011). Even though the thermal environment has an important role in determining the developmental temperatures experienced by reptilian embryos, mothers can manipulate those developmental temperatures through behaviour. For example, in oviparous species, females can choose nests that are more or less in the sun or can dig nests at different depths (e.g. Shine and Harlow, 1996; Shine et al., 2002; Doody et al., 2006; Telemeco et al., 2009). In viviparous species, gravid females can manipulate developmental temperatures through thermoregulation (i.e. basking behaviour) (Beuchat, 1986; Robert and Thompson, 2010; Schwarzkopf and Andrews, 2012a; Schwarzkopf and Andrews, 2012b; Shine, 2012). Maternal thermoregulation during gestation is thought to allow the maintenance of stable developmental temperatures (Shine, 1995) and/or to provide a buffer to embryos from unsuitable developmental temperatures (Kearney et al., 2009) as well as potentially provide fitness benefits to females through, for example, reduced basking length and the costs associated with reproduction (Schwarzkopf and Shine, 1991; Schwarzkopf and Andrews, 2012a; Schwarzkopf and Andrews, 2012b; Shine, 2012). Maternal manipulation of the offspring environment may also potentially allow females to 'pre-programme' offspring phenotype to better suit the environment the offspring will encounter (or be born into) (Marshall and Uller, 2007; Cadby et al., 2010a; Pen et al., 2010; Cadby et al., 2011; Uller et al., 2011). Maternal 'pre-programming' to future developmental temperatures could occur through maternal manipulation of offspring phenotype to fit the predicted environment and/or through embryonic acclimation to the thermal conditions experienced during development (Seebacher, 2005).

By manipulating the offspring environment, maternal effects can facilitate the potential for evolutionary adaptation and colonization of a new environment. For example, by reducing the costs of directional selection (e.g. maternal buffering of unsuitable conditions) they can provide time for a population to become established for standing genetic variation in combination with

mutation and/or recombination to provide a range of heritable phenotypes to respond to local selection pressures (Pigliucci, 2001; West-Eberhard, 2003; Ghalambor et al., 2007; Hoffmann and Sgrò, 2011; Hof et al., 2011). As a consequence, local adaptations in maternal effects should be common in widespread species (e.g. Gvozdik, 2002; Doody et al., 2006; Doody, 2009). In viviparous reptiles it remains unclear, however, whether populations that have evolved in different climatic conditions will exhibit locally adapted maternal basking behaviour or locally adapted gestational thermal effects on offspring development. Typically, you would expect the former to prevent the latter as the adjustment of female basking behaviour to the basking opportunity buffers and reduces the impact of environmental differences between populations and, thus, prevents the evolution of population-specific thermal effects (e.g. Hertz and Huey, 1981; Van Damme et al., 1990; Huey et al., 2003; Caley and Schwarzkopf, 2004) (but see Uller et al., 2011).

We used the viviparous spotted skink, *Niveoscincus ocellatus* (Gray 1845) as our model system. In this species, maternal basking opportunity affects offspring phenotypic traits such as date of birth and offspring size (Wapstra, 2000; Cadby et al., 2010b), with the potential for concomitant effects on offspring fitness (Atkins et al., 2007; Wapstra et al., 2010; Uller et al., 2011). Furthermore, this species is climatically widespread, with populations having evolved in distinct thermal environments (i.e. with different basking opportunities). At one extreme of the species range, mountain populations experience restricted basking opportunities and short summers, while at the other extreme, coastal populations experience warm conditions with extended basking opportunities and long summers (Atkins et al., 2007; Wapstra et al., 2009; Cadby et al., 2010b; Pen et al., 2010; Uller et al., 2011). This difference in climate has resulted in considerable variation in life-history and reproductive traits between populations, reflecting a combination of phenotypic and genotypic responses to environmental variation (Wapstra et al., 1999; Melville and Swain, 2000; Wapstra and Swain, 2001; Wapstra et al., 2009; Cadby et al., 2010b; Wapstra et al., 2010; Pen et al., 2010; Uller et al., 2011). For example, females from cold, mountain areas are typically larger, take longer to reach maturity, and give birth 2–4 weeks later than those from warm, coastal areas (Wapstra et al., 2001; Pen et al., 2010).

Using a reciprocal transplant experiment, we tested whether maternal basking behaviour can increase offspring fitness through maternal pre-programming or by buffering differences in basking opportunities. We further tested whether mothers from populations that have evolved in different thermal environments (i.e. with different basking opportunities) express differences in their basking behaviour and/or whether differences in maternal behaviour between populations preclude the evolution of population-specific maternal effects (Fig. 1).

RESULTS

Maternal body temperature was explained by maternal basking behaviour, with females that were observed to bask more frequently having higher body temperatures ($F_{1,124}$=109.39, r^2=0.47, $P<0.0001$). Maternal body temperature was significantly different between maternal basking regimes ($F_{1,124}$=229.27, $P<0.0001$) and between populations ($F_{1,124}$=20.68, $P=0.0001$) but there was no interaction between maternal basking regimes and populations on maternal body temperature ($F_{1,124}$=1.77, $P>0.1$). Females maintained higher body temperatures in the short basking regime than in the long basking regime, and females from the mountain population maintained higher body temperatures than females from the coastal population (Fig. 2A). Gestation length was not affected by an interaction between maternal
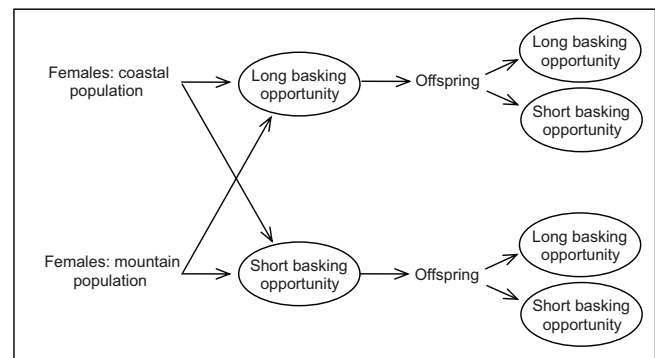

Fig. 1. Orthogonal experimental design. Gravid female spotted skinks (*Niveoscincus ocellatus*) were collected from two populations located at the climatic extremes of the species distribution and allocated randomly to a regime of either long or short basking opportunity. Newborn offspring were also allocated randomly to either a long or a short basking regime. Basking regimes reflected basking opportunity typically encountered at both population sites.

basking regime and population ($F_{1,87}$=1.32, $P>0.1$). Gestation length was similar between populations ($F_{1,87}$=0.19, $P>0.1$) but was significantly affected by maternal basking regime ($F_{1,87}$=208.01, $P<0.0001$). Gestation length was, on average, shorter (96±0.6 days) for females placed in the long basking regime than for females placed in the short basking regime (125±1.2 days). Maternal basking regime ($\chi^2_{1,124}$=14.23, $P=0.0002$) and population ($\chi^2_{1,124}$=7.63, $P=0.0057$) had a significant effect on the success of pregnancy. Females from the mountain population had more unsuccessful pregnancies than females from the coastal populations, and females placed in the short basking regime had more unsuccessful pregnancies than females placed in the long basking regime. Offspring snout–vent length (SVL) ($F_{1,79.7}$=7.52, $P=0.0075$) and mass at birth ($F_{1,84.1}$=6.11, $P=0.0155$) differed between populations; offspring from the coastal population were smaller and lighter (SVL 28.84±0.125 mm, mass 0.481±0.0066 g) than offspring from the mountain population (SVL 29.48±0.153 mm, mass 0.507±0.0508 g). However, these traits were similar between maternal basking regimes (SVL: $F_{1,79.7}$=1.32, $P>0.1$, mass: $F_{1,84.1}$=0.23, $P>0.1$) and there was no interaction between maternal basking regime and population on SVL ($F_{1,79.7}$=0.10, $P>0.1$) and mass at birth ($F_{1,84.1}$=6.11, $P>0.1$). Growth (in length) was not affected by a 3-way interaction between maternal basking regime, offspring basking regime and population ($F_{1,53.6}$=0.78, $P>0.1$). Furthermore, growth rate was not affected by an interaction between maternal and offspring basking regime ($F_{1,53.6}$=0.08, $P>0.1$), suggesting that offspring placed in the same basking environment as their mothers did not grow faster than offspring placed in a different basking environment from their mothers (i.e. there was no evidence of thermal acclimation during embryonic development). However, growth rate was affected by an interaction between maternal basking regime and population, with offspring growing faster when their mothers had access to basking opportunities similar to those they would typically encounter in their native environment ($F_{1,53.6}$=7.06, $P=0.0104$, Fig. 2B). Offspring growth rate was also affected by the independent effect of offspring basking regime ($F_{1,53.6}$=5.60, $P=0.0216$), with offspring placed in the long basking regime growing faster (0.07±0.002 mm day^{-1}) than offspring placed in the short basking regime (0.06±0.002 mm day^{-1}). Offspring growth rate was affected neither by the independent effect of population ($F_{1,53.6}$=0.97, $P>0.1$) nor by the independent effect of maternal basking regime ($F_{1,53.6}$=0.59, $P>0.1$).
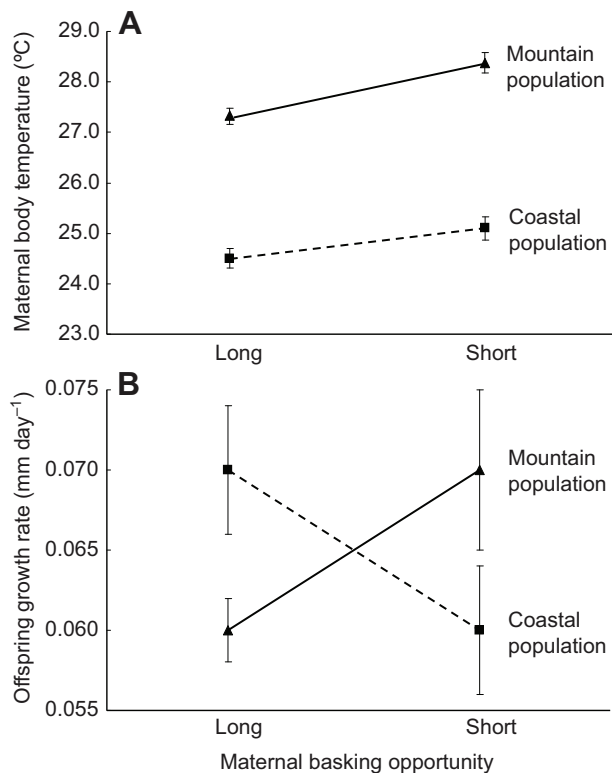
Fig. 2. Maternal body temperatures and offspring growth rates. The effects of population (mountain versus coastal) and maternal basking opportunity regime on the body temperature of gravid female spotted skinks (*N. ocellatus*) (A) and on the growth rate of their offspring (B).

DISCUSSION

Offspring length, mass, as well as date of birth, are temperature dependent and fitness related in reptiles (e.g. Chamaille-Jammes et al., 2006; Warner and Shine, 2007; Uller and Olsson, 2010) including in *N. ocellatus* (Wapstra et al., 2010; Uller et al., 2011), the focus of this study. Therefore, there may be selection on female basking behaviour to buffer against the potentially negative effects of reduced basking opportunity on offspring phenotype. Our study suggests exactly this – gravid female *N. ocellatus* maintained higher body temperatures when placed in the short basking opportunity regime than when placed in the long basking opportunity regime. This indicates that females compensated behaviourally for the short basking opportunity by basking more frequently (when basking was possible). This was confirmed at the birth of their offspring, as there was no effect of maternal basking opportunity on offspring length and mass. These results differ from previous findings in the same species (Wapstra, 2000; Wapstra et al., 2010) and in other viviparous species (e.g. Shine and Harlow, 1993), in which short basking opportunity resulted in smaller and lighter offspring. Reasons for this variation between similar experiments even within the same species are further explored in Uller et al. (Uller et al., 2011). Despite evidence for partial compensatory shifts in female thermoregulatory behaviour in the present experiment, females that had access to the short basking opportunity had longer gestation periods, suggesting that the physiological processes affecting gestation length are more thermally sensitive than those affecting offspring length and mass (Uller et al., 2011).

In addition to female thermoregulatory compensation to proximate basking restrictions, pre-programming of offspring to future basking conditions through maternal manipulation and/or embryonic thermal acclimation could further shape offspring phenotype. In this study, however, we found no evidence for female pre-programming and/or thermal acclimation of offspring. Growth rate was not affected by an interaction between maternal and offspring basking regime because offspring placed in the same basking environment their mothers experienced during gestation did not grow faster than offspring placed in a different basking environment from their mothers. Instead, the offspring placed in the long basking regime grew faster than offspring placed in the short basking regime, irrespective of maternal basking conditions. This suggests that all offspring benefited from the effects of warm temperature on feeding activity and metabolism (Angilletta et al., 2002).

If mothers are able to behaviourally compensate for variation in environmental conditions, then this adjustment to the environment may lead to the evolution of divergence in basking behaviour in populations that experience consistently different environments. Interestingly, we found that *N. ocellatus* gravid females from the cold alpine population maintained higher body temperatures (i.e. basked more frequently) than females from the coastal population. Although we would need to replicate populations from the mountain and the coastal environments to show evidence for local adaptation, it is possible that the observed differences in maternal behaviour result from differences in selection pressure between environments. The combination of limited basking opportunity and shortened activity season in the cold mountain areas places increased selection pressure on the basking behaviour of mountain females as they must optimise developmental temperatures so as to produce offspring early in the season to allow for offspring growth prior to hibernation (Olsson and Shine, 1998; Atkins et al., 2007; Wapstra et al., 2010; Uller et al., 2011). In contrast, selection pressure on basking behaviour is likely to be weaker in coastal populations of *N. ocellatus*, where basking opportunity is not as restricted and summers are longer. Similar responses are observed in other reptiles. For example, in the viviparous common lizards (*Zootica vivipara*), females from high altitude populations spend 50% more time basking than those from low altitudes (Gvozdik, 2002), while in the oviparous water dragons (*Physignatus lesueurii*), mothers dig nests more superficially at high altitude than at low altitude, thus compensating for the climatic differences between altitudes (Doody et al., 2006; Doody, 2009).

Geographic differences in maternal basking behaviour can prevent population-specific maternal thermal effects by buffering the differences in climate between populations and, thus, inhibiting evolutionary changes in thermal physiology. Interestingly, however, we observed geographical differences in offspring growth. Offspring grew faster when their mothers had access to similar basking opportunities to those they would typically encounter in their native environment (irrespective of offspring basking conditions). Offspring growth typically relies on the concerted performance of foraging, consumption, digestion, absorption and anabolism, all dependent on body temperature in ectotherms (reviewed in Angilletta et al., 2002), and it is often related to fitness in reptiles (e.g. Madsen and Shine, 2000; Shine et al., 2002). Our results may indicate that selection on the thermal optima of growth can still vary in direction and strength between populations and can be mediated, in part, by maternal influences (see also Wapstra, 2000; Caley and Schwarzkopf, 2004; Wapstra et al., 2010; Uller et al., 2011). Our observations are similar to those made in another climatically widespread viviparous reptile (*Eulamprus quoyii*) (Caley and Schwarzkopf, 2004) but seem to diverge from those obtained in

climatically widespread oviparous species, where the post-hatching environment is predominant in shaping offspring growth (e.g. Qualls and Shine, 2000).

In conclusion, our results are further evidence of the benefits of viviparity as mothers were able to buffer their embryos from environmental heterogeneity, especially by increasing their basking in less suitable environmental conditions (i.e. short basking opportunity). Furthermore, this benefit is context specific because there was an evolutionary component (i.e. population effect) to maternal basking behaviour as well as to offspring growth rate. This population effect on maternal basking behaviour presumably results from past selection: females from the cold mountain population have to be more opportunistic in their basking in order to produce embryos early in the summer (Atkins et al., 2007; Uller et al., 2011). Similarly, offspring growth rate was optimised in the thermal environment in which they evolved. More broadly, our results highlight the need to take ultimate contexts (divergent evolutionary differences between populations) into account when studying maternal effects in species with broad geographic or climatic distributions. Finally, our results are relevent in the context of climate change as maternal basking behaviour may play a significant role in allowing ectothermic species to cope with changing environmental conditions by buffering changes in the environment (Ghalambor et al., 2007; Charmantier et al., 2008; Hof et al., 2011) and/or by facilitating evolutionary adaptation (Beldade et al., 2011; Hoffmann and Sgrò, 2011).

MATERIALS AND METHODS
Field and laboratory protocol
This study was approved by the Animal Ethics Committee at the University of Tasmania. *Niveoscincus ocellatus* is a small skink (3–10 g, 60–80 mm SVL), widespread in Tasmania, Australia. We collected 60 gravid females from a coastal site (42°34′S, 147°52′E; elevation 30 m) and 65 gravid females from a mountain site (41°59′S, 146°44′E; elevation 1200 m) by noosing or mealworm 'fishing' in October [i.e. early in gestation, timing determined as described elsewhere (Wapstra et al., 1999)]. Our two sites are at the climatic extremes of the species' distribution and were adjacent to those used in previous studies that have documented climate-driven phenotypic and genotypic differences between populations (e.g. Melville and Swain, 2000; Wapstra et al., 2001; Wapstra et al., 2009; Cadby et al., 2010b; Pen et al., 2010). Females were brought to the laboratory where they were measured (SVL ±1 mm) and weighed (±1 mg). Females were housed in plastic terraria (200×300×100 mm) that contained a rock for basking and a terracotta pot for shelter. They were fed three times a week with mealworms (*Tenebrio* larvae) and fruit purée. Water was available *ad libitum*. The laboratory was air-conditioned and maintained at 15°C. Bright fluorescent tube lighting (20,000 lx) and UV lighting reproduced daylight conditions (14 h light: 10 h dark).

Basking opportunity and maternal basking behaviour
Basking conditions were supplied by a 25 W spotlight positioned 120 mm above the basking rock. When the basking light was on, the temperature reached 35°C on the basking rock and diminished on a gradient with distance from the basking rock to a minimum of 15°C. For each population, we assigned females randomly to a basking regime consisting of either long or short basking opportunity. In the long basking opportunity regime, females had access to a warm rock 10 h day^{-1}, while in the short basking regime, females had access to a warm rock for 4 h day^{-1}. Females could thermoregulate freely when the basking light was on. These experimental basking regimes were chosen to replicate the natural basking opportunities (i.e. hours of sunshine) typically experienced by individuals during gestation at the coastal (extended basking opportunity) and the mountain (reduced basking opportunity) areas (Wapstra, 2000; Uller et al., 2011).

To evaluate differences in maternal basking behaviour between basking regimes and populations, we measured maternal body temperature (±0.1°C)

every second day by manually placing an infrared thermometer (Testo 805 Infrarot-Thermometer, Testo India Pvt Ltd, Pune, India) 10 mm above the female's back and taking a temperature recording of her dorsal surface. To confirm that maternal body temperature reflected maternal basking behaviour, we made behavioural observations during the experimental period. We scored females as 'basking' if they were under the basking lamp or 'not basking' if they were feeding or under their shelter. Observations were spread over gestation at irregular times of the day but always when the basking lights had been on for at least 60 min. We then calculated the proportion of time a female was observed basking as the number of times the female was observed basking divided by the total number of observations for that female.

Offspring phenotypic traits and basking opportunity regimes
From the beginning of December, terraria were checked three times a day for neonates. Females that had given birth were weighed (±1 mg) and offspring were measured using digital callipers (SVL ±0.01 mm), weighed (±1 mg) and given a unique toe clip for permanent identification. Gestation length was calculated from the date of ovulation (1 October for coastal females and 15 October for mountain females) until the date of parturition (Wapstra et al., 2009). Unsuccessful pregnancies (those for which at least one dead neonate was found or where females did not give birth) were recorded. Females were released at their site of capture within 7 days of giving birth.

In order to test for maternal pre-programming and/or embryonic thermal acclimation (Marshall and Uller, 2007), each litter was randomly assigned to either a long (10 h day^{-1}) or a short (4 h day^{-1}) basking opportunity regime (Fig. 1). Laboratory conditions were identical to those described for females. Offspring were fed every second day with white worms (*Enchytraeus albidus*) and fruit purée enriched with soy protein (Nature's Way Instant Natural Protein Powder). To determine growth rate, each offspring was measured (SVL ±0.01 mm) every 10 days for 6 weeks. Early growth is linear in this species (Wapstra, 2000) and so growth was calculated using the slope of the least squares regression line of length (SVL) and days since birth. We also calculated mass-specific growth rate of offspring but our results were similar to SVL specific growth rate and, thus, we do not report the results further. At the completion of this 6 week period, offspring were released at their mother's site of capture.

Statistical analyses
Analyses were conducted using SAS 9.1 (SAS Institute, Cary, NC, USA). In all cases, variables were either normally distributed, or were so following log transformation. Linear regression (proc reg) was used to determine whether the body temperature of females was dependent on the proportion of time a female was observed basking. We used 2-way ANOVA [proc glm (general linear model)] to compare female body temperature between populations and maternal basking regimes. We used a 2-way ANOVA (proc glm) to assess the effects of maternal basking regime, population and their interaction on gestation length. The effects of maternal basking regime and population on the success of pregnancy were evaluated using a logistic regression with 'successful' and 'not successful' as dependent variables. We used a mixed model (proc mixed) to assess the effects of maternal basking regime, population and their interaction on offspring SVL and mass at birth. We used a mixed model (proc mixed) to assess the effects of maternal basking regime, offspring basking regime and population on offspring growth rate. When analysing offspring traits, the 'litter effect' was taken into account by considering maternal identity as a random factor. We adjusted for multiple comparisons within each set of analyses (female and offspring data) using the false discovery rate procedure (Benjamini and Hochberg, 1995). A P-value of ≤0.05 after the false discovery procedure was statistically significant. For all mixed models, the degrees of freedom were calculated using the Satterthwaite approximation (Littell et al., 1996). All values are reported as means ± s.e.m.

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