

## Research



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# Experimental increases in temperature mean and variance alter reproductive behaviours in the dung beetle *Phanaeus vindex*

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Temperature profoundly impacts insect development, but plasticity of reproductive behaviours may mediate the impacts of temperature change on earlier life stages. Few studies have examined the potential for adult behavioural plasticity to buffer offspring from the warmer, more variable temperatures associated with climate change. We used a field manipulation to examine whether the dung beetle *Phanaeus vindex* alters breeding behaviours in response to temperature changes and whether behavioural shifts protect offspring from temperature changes. Dung beetles lay eggs inside brood balls made of dung that are buried underground. Brood ball depth impacts the temperatures offspring experience with consequences for development. We placed adult females in either control or greenhouse treatments that simultaneously increased temperature mean and variance. We found that females in greenhouse treatments produced more brood balls that were smaller and buried deeper than controls, suggesting brood ball number or burial depth may come at a cost to brood ball size, which can impact offspring nutrition. Despite being buried deeper, brood balls from the greenhouse treatment experienced warmer mean temperatures but similar amplitudes of temperature fluctuation relative to controls. Our findings suggest adult behaviours may partially buffer developing offspring from temperature changes.

## 1. Introduction

Increases in temperature mean and variance associated with climate change can greatly impact the physiology and ecology of ectotherms [1]. However behavioural plasticity could play a key role in helping organisms cope with stressful temperatures, potentially buffering organisms from temperature changes [2–8]. Importantly, behavioural plasticity of adults during reproduction may protect offspring from unfavourable conditions [9–11]. Understanding the capacity for reproductive plasticity is thus important for predicting how organisms may respond to climate change [12].

In ectotherms, reproductive behaviours of adults greatly influence the thermal environment of developing offspring with consequences for phenotype and fitness [11–14]. The temperatures experienced during development have profound effects on metabolism, growth rate, and adult body size [15–19]. In many ectotherms, early life stages (e.g. eggs) are sessile and offspring cannot move to more favourable microclimates [4]. Adjustments by adults in nesting location can alter the developmental environment of offspring with impacts on survival and fitness [10–12,14]. However, a critical question is whether plasticity of reproductive behaviours can modify the offspring environment enough to compensate for climate change [2,20].

We studied the breeding behaviour of the dung beetle *Phanaeus vindex* Macleay, 1819 to understand how simultaneous increases in temperature mean and variance affect breeding behaviours and whether adult behavioural plasticity buffers offspring from warmer, more variable temperatures. *Phanaeus vindex* (Coleoptera: Scarabaeinae) is a medium-sized, diurnal species that ranges in open habitats from the upper east coast to the southern USA and west to the Rocky Mountains [21]. To breed, the beetles find and mate at a dung source. Female *P. vindex* construct tunnels below the dung, transport dung in multiple trips from the surface to the bottom of the tunnel, model the buried dung into a pear-shaped brood ball, and lay a single fertilized egg [22,23]. Once hatched, the developing larva eats the dung, going through complete metamorphosis within the brood ball [22].

Maternal behaviour during reproduction, including brood ball number, size, and burial depth, shapes the environmental conditions of offspring with consequences for survival and fitness [10,11,14,24–27]. Because dung from the brood ball provides the only nourishment available to developing larvae, brood ball size can affect adult body size [28–31]. Importantly, smaller individuals have reduced fecundity and competitive ability relative to larger individuals [25]. Burial depth, which can be affected by maternal body size [14,28], soil type [32] and surface temperatures [11,14], impacts the temperatures experienced by offspring; offspring in brood balls near the soil surface experience warmer, more variable temperatures than those at greater soil depths [10]. Warmer temperatures are associated with faster development rates, smaller body sizes, and reduced survival [1,14,33–35]. However, few studies have examined whether adult behavioural plasticity can buffer offspring from both the warmer and more variable temperatures occurring with climate change.

We conducted a field experiment to examine plasticity of nesting behaviours of *P. vindex* in response to climate change by simultaneously increasing temperature mean and variance using mini-greenhouses. Our goals were to examine if females altered reproductive behaviours (i.e. brood ball number, size, and burial depth) in response to temperature changes and whether adult behavioural shifts protected offspring from temperature changes. We hypothesized that (i) females in greenhouse treatments would place brood balls deeper in the soil and (ii) greater burial depth would buffer offspring from warmer and more variable temperatures.

## 2. Methods

### (a) Beetle collection

We used pitfall traps baited with cow dung during two trapping sessions in May and June 2018 to collect adult *P. vindex* in Tennessee, USA (36°03'25.8" N, 84°04'19.8" W). We brought males ( $n = \sim 25$ ) and females ( $n = \sim 40$ ) to the laboratory and held them at 23°C in a plastic container (59 × 46 × 38 cm) covered with fibreglass screen and filled with a 4:1 topsoil:sand mixture. We placed the container near a window for natural light and fed beetles ad libitum autoclaved cow dung. We held beetles in this colony for 3–4 weeks to allow them to mature and mate [22,32,36]. We checked the colony weekly to see if females had produced brood balls. Once the colony began forming brood balls, the females were considered fertilized and ready for trials.

### (b) Experimental trials

We conducted experiments in an open field near our trapping location using four trials of 10 days each with start dates ranging from June to August 2018. We arranged 12, 7-gallon buckets (31 cm diameter (top) × 26 cm diameter (bottom) × 50 cm height) in two rows with 2 m between buckets. We drilled five holes into the bottom of buckets for water drainage. We buried buckets to the brim, backfilled them with soil from the field site, and compacted the soil. The soil in each bucket was 44 cm deep, leaving 6 cm of space between the top of the soil and top of the bucket to allow space for dung. We placed four HOBO data loggers (model: UA-001-64, Onset, Bourne, MA) in the buckets spaced 14 cm apart to cover the entire range of soil depths (i.e. 1, 15, 29, and 43 cm below the soil surface) and recorded temperatures every hour.

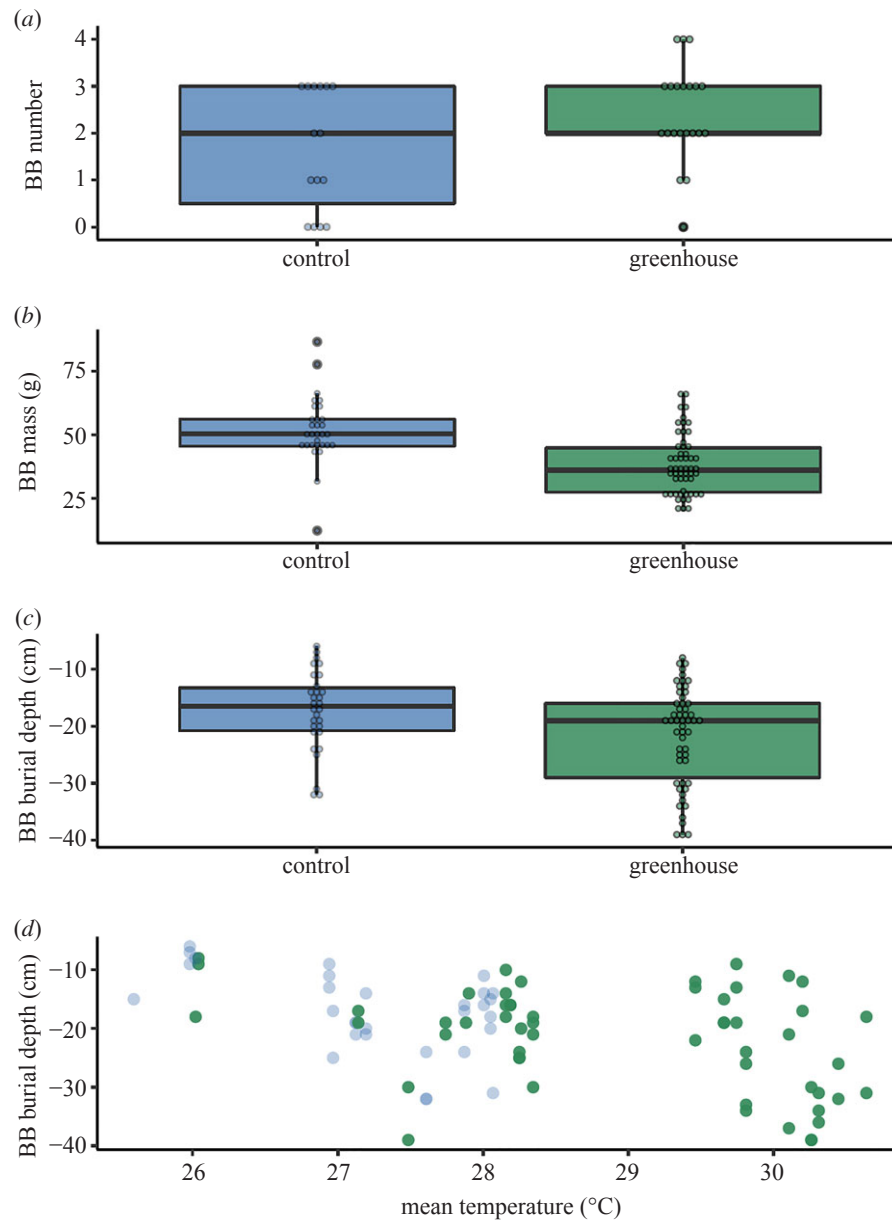
For trials, we removed females from the colony, recorded mass, and randomly assigned them to an experimental bucket. We added one female to each bucket, allowing us to eliminate the confounding effects of male behaviour. Fertilized females store seminal fluid and will independently construct tunnels and create brood balls [23]. Female *P. vindex* are known to produce as many as 34 brood balls across a season [37]. We put a flexible fibreglass screen over the bucket secured with bungee cords and followed by a large piece of 1.27 cm galvanized hardware cloth secured with stakes. The screen and hardware cloth prevented beetles from escaping and small animals from disturbing the trials, respectively, while also allowing for more natural conditions. We provided beetles with ~25 g of autoclaved cow dung at the start of the trial and every 2 days thereafter to ensure enough for consumption and continuous brood ball construction. During feedings, we removed dung left on the soil surface from the previous feeding before placing fresh dung.

For each trial, we randomly assigned six buckets to a heated (hereafter 'greenhouse') treatment and six to a control group. For the greenhouse treatment, we designed mini-greenhouses capable of passively and simultaneously increasing temperature mean and variance to simulate climate change. The greenhouses were made of 0.16 cm clear polycarbonate and shaped like a cone with a 61 cm bottom opening and a 7 cm top opening. The cone shape allowed for even heating around each bucket. Based on temperature data, the greenhouses simulated the changes expected under climate change, with an average increase of 2°C at the soil surface relative to control buckets (electronic supplementary material, figure S1). Temperatures in both bucket types showed natural, diurnal fluctuations and, with increasing soil depth, a decline in mean temperatures and a dampening of the amplitude of temperature fluctuation. However, temperatures at the soil depths where the loggers were placed were warmer and more variable in greenhouse compared to control buckets (electronic supplementary material, figure S1), thus effectively simulating conditions expected under climate change [38].

After 10 days, we carefully removed layers of soil to uncover brood balls, which in this species are distinct from food caches [22,23]. We recorded brood ball number, mass, and burial depth (measured from the bucket rim to the brood ball centre). We removed the temperature loggers and downloaded data. If a female produced brood balls in her first trial, we used her in subsequent trials. If a female did not produce brood balls, we did not use her again. Water in one bucket did not drain well during trials and we removed it from analyses.

### (c) Statistical analysis

To test for behavioural shifts, we fit linear mixed-effects (LME) models in R (package lme4, R v. 3.6.0) with the response variables of brood ball number, mass, or burial depth and the fixed effects of treatment type (greenhouse or control) and female mass since body size may affect responses [28]. We



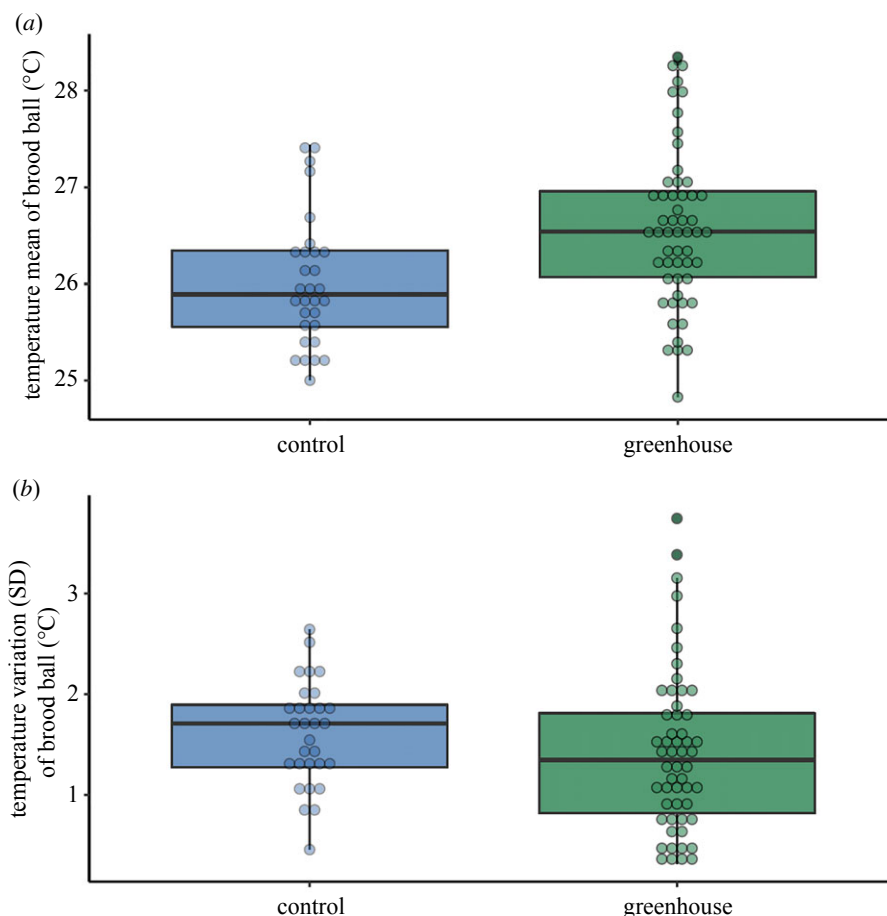
**Figure 1.** Plasticity of reproductive behaviours of female *Phanaeus vindex* in relation to brood ball (BB) number, size, and burial depth. Females in the greenhouse treatment produced a greater number (a) of smaller brood balls (b) buried deeper in the soil (c) compared with beetles in control buckets. (d) Burial depth was greater with increasing soil surface temperatures in both the greenhouse (green circles) and control (blue circles) buckets. Boxes (a–c) show median and first and third quartiles and whiskers show minimum and maximum values of brood ball number, size, or burial depth. Points on boxplots show values for individual brood balls.

included trial as a fixed effect because the number of trials was relatively small [39,40]. We included the random effect of beetle identification to account for the non-independence of brood balls from the same female [41], and used model selection to decide on the random effects structure [42]. In the models for brood ball number, we removed buckets where a female died during the trial. Null models included an intercept and the random effect of beetle identification. We selected the best-fit model considering  $AIC_c$  (Akaike information criterion for small sample sizes) values and the normality of residuals [42–44]. We calculated the Akaike weight of each model ( $wAIC_c$ ), which estimates the probability that the model is the best model among the candidate models considered [43]. Because our model for burial depth that included the fixed effect of treatment type and trial was only slightly better than the model with trial alone (electronic supplementary material, table S1), we also fit a model using the fixed effect of mean soil surface temperature recorded in each bucket rather than treatment type and all other variables

described above. This allowed us to account for differences in temperatures among buckets of the same treatment.

To examine whether adult behavioural shifts altered offspring development temperatures, we used data from temperature loggers in each bucket to calculate temperatures experienced by brood balls. Specifically, we fit a linear model to temperatures between neighbouring pairs of loggers to predict the mean and standard deviation of temperature for each brood ball based on its burial depth. To test whether offspring in different treatments experienced different temperatures, we fit LME models with the response variables of either temperature mean or standard deviation at the location where the brood ball was placed and the fixed and random effects described above. For all final models we computed the proportion of variance explained by fixed effects (marginal  $R^2$ , or  $R^2_{mv}$ ; [45]).

Because females in greenhouses nested deeper, we calculated the temperatures offspring would have experienced had females in greenhouses nested at control depths. For each control brood



**Figure 2.** Temperatures experienced by brood balls of *Phanaeus vindex*. Brood balls in the greenhouse treatment experienced warmer mean temperatures (a) but the same temperature variation (b) compared with brood balls in the control buckets. Boxes show median and first and third quartiles and whiskers show minimum and maximum values of temperature mean or variation (measured as standard deviation) experienced by brood balls. Points on the boxplots show values for individual brood balls.

ball, we calculated what temperatures would have been for that brood ball in each of the six greenhouse buckets from that trial, thus translating shifts in nesting depth into a value of temperature compensation.

### 3. Results

Our goals were to examine if females altered reproductive behaviours in warmer, more variable temperatures and whether behavioural shifts buffered offspring from temperature changes. During the four trials, 21 females produced 84 brood balls. Females produced more brood balls in greenhouse (mean of 2.4) than control (1.7) buckets (figure 1a), and the best-fit model for brood ball number included treatment type and trial ( $\beta_{\text{greenhouse}} = 0.76$ ,  $\beta_{\text{trial}} = -0.39$ ,  $w\text{AIC}_c = 0.45$ ,  $R_m^2 = 0.21$ ; electronic supplementary material, table S2). Beetles produced smaller brood balls in greenhouse (mean 38.5 g) than control (52.0 g) buckets (figure 1b); the best-fit model for brood ball mass included treatment type and trial ( $\beta_{\text{greenhouse}} = -13.37$ ,  $\beta_{\text{trial}} = 3.19$ ,  $w\text{AIC}_c = 0.52$ ,  $R_m^2 = 0.27$ ; electronic supplementary material, table S3). Beetles also buried brood balls deeper in the greenhouse (mean 21.6 cm) than control (17.3 cm) buckets (figure 1c), although the model with treatment type and trial ( $\beta_{\text{greenhouse}} = 4.18$ ,  $\beta_{\text{trial}} = -2.11$ ,  $\text{AIC}_c = 578.01$ ,  $w\text{AIC}_c = 0.39$ ,  $R_m^2 = 0.13$ ) was only marginally better than the model with trial ( $\text{AIC}_c = 578.95$ ,  $w\text{AIC}_c = 0.25$ ; electronic supplementary material, table S1). When we examined burial depth in response

to the surface temperature of buckets (figure 1d), the best-fit model included mean soil surface temperature ( $\beta_{\text{surface temperature}} = 2.49$ ,  $w\text{AIC}_c = 0.36$ ,  $R_m^2 = 0.17$ ; electronic supplementary material, table S4).

Compared with controls, brood balls in greenhouse buckets were located in areas with higher mean temperatures (26.6°C versus 26.0°C), but similar temperature variation (1.4°C versus 1.6°C) (figure 2) and maximum temperatures (29.7°C versus 29.5°C) (electronic supplementary material, figure S2). If females had nested at the same depth in greenhouse buckets as they did in control buckets, greenhouse brood balls would have experienced mean temperatures nearly a degree warmer— $26.9 \pm 1.7^\circ\text{C}$ —than those in control buckets. The best-fit model for mean temperature where brood balls were placed included treatment type, female mass, and trial ( $\beta_{\text{greenhouse}} = 0.63$ ,  $\beta_{\text{female mass}} = -1.53$ ,  $\beta_{\text{trial}} = -0.25$ ,  $w\text{AIC}_c = 0.60$ ,  $R_m^2 = 0.32$ ; electronic supplementary material, table S5). We found no effect of treatment on the temperature variation where brood balls were placed; the best-fit model for temperature variation including trial ( $\beta_{\text{trial}} = -0.13$ ,  $w\text{AIC}_c = 0.31$ ,  $R_m^2 = 0.05$ ; electronic supplementary material, table S6).

### 4. Discussion

We demonstrate that female *P. vindex* altered their breeding behaviours in response to simulated climate change by

producing a greater number of smaller brood balls that were buried deeper in the soil. This plasticity in burial depth did not fully compensate for temperature changes. Despite being buried deeper, brood balls from the greenhouse treatment were placed in warmer mean temperatures. Warmer temperatures during development can result in faster development rates, smaller adult body sizes, and depending on the temperature, lower survival [11,14,19]. However, the mean temperatures experienced by *P. vindex* brood balls in the greenhouse and control buckets are well below the temperatures that lead to high mortality rates in adult *P. vindex* [46] and offspring of other dung beetle species [11,14].

By contrast to mean temperatures, brood balls experienced similar temperature fluctuations in the greenhouse and control buckets. Increased temperature variation associated with climate change may be more stressful than shifts in mean temperature alone [47] and can lead to smaller body sizes in dung beetles [35,48]. Plasticity of nest depth may thus buffer offspring from increased temperature variation that could otherwise negatively impact fitness.

Increased nest depth may protect offspring from stressful temperatures, but time and energy spent constructing tunnels could impact other fitness traits [11]. *Phanaeus vindex* produced smaller brood balls in greenhouse than control buckets. Increased nesting depth may thus come at a cost to brood ball size, a fitness-linked trait [28–31]. Negative relationships between reproductive behaviours in response to temperature changes have been observed in other dung beetle species. *Onthophagus taurus* beetles exposed to warmer temperatures [14] and increased temperature variation [49] produced fewer brood balls. Interestingly, a congener, *O. hecate*, showed no trade-off in reproductive behaviours; individuals produced more brood balls of the same size and buried them deeper in warmer temperatures [14]. Even when trade-offs are not observed, fitness could be impacted in other ways, including reduced egg production and quality. In the ball-rolling dung beetle *Sisyphus rubrus*, warmer treatments did not affect the size or number of brood balls, but beetles buried fewer brood balls, which are more likely to contain eggs than unburied brood balls [13].

Thus, shifts in one behaviour in response to temperature changes may come at a cost to other fitness-linked traits.

Although we did not examine fitness, we found potential trade-offs that suggest the behavioural plasticity we observed is adaptive. Brood balls were smaller in the greenhouse treatment, which can reduce fitness via impacts on adult body size [28–31]. However, beetles produced more brood balls in the greenhouse treatments. Warmer temperatures—up to an optimum—increase ectotherm locomotor performance [1], which may have helped females dig and transport dung faster to create more brood balls. In addition, by digging deeper, females buffered offspring from potentially stressful temperatures. Thus, behavioural plasticity to temperature change may be adaptive in *P. vindex* by producing more offspring with greater potential for survival even if the smaller brood balls result in smaller individuals. Understanding the behavioural adjustments made by ectotherms to temperature change is a key step in predicting the potential impacts of climate change [50].

**Ethics.** All experiments complied with the laws of the United States and international ethical standards. Field trials were performed with landowner permission.

**Data accessibility.** Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.cfxpvnv7m>.

**Conflict of interest declaration.** We declare we have no competing interests.

**Authors' contributions.** W.H.K.: data curation, funding acquisition, investigation, writing—original draft, writing—review and editing; K.S.S.: conceptualization, data curation, formal analysis, funding acquisition, methodology, project administration, resources, supervision, validation, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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