1. Introduction

The geographical ranges of species vary enormously with many taxa being narrow-range endemics while relatively few are widespread. Several ecological and evolutionary processes may drive range size variation, including interspecific differences in evolutionary age, dispersal ability and fundamental niche breadth [1]. The niche breadth hypothesis predicts that species with broad fundamental niches have larger range sizes [2,3], with physiological traits which allow the exploitation of spatially and temporally variable environments facilitating their expansion [4].

Previous work on diving beetles found that thermal physiology is strongly related to latitudinal range size and position [5]. Since thermal tolerance relies on an organism’s ability to maintain cellular function under stress, more thermally tolerant species may also be expected to show higher metabolic plasticity [6]. For example, in Antarctic fish, it has been found that above their optimal temperature range, cellular processes switch from mainly carbohydrate (glucose and glycogen) to lipid and finally protein metabolism [6]. Other studies on marine gastropods into the effects of sub-lethal elevations in temperature reveal the accumulation of ‘end-product’ metabolites (lactate and succinate) while ATP concentrations remain stable, indicating an increased reliance on anaerobic metabolism with temperature, using carbohydrates as the energy source [7]. Plasticity of such metabolic processes may be vital in...
widespread, more northerly distributed species, as organisms encounter increasingly variable climates with latitude [8].

An organism’s ability to mount an immune response to parasites and pathogens can also be seen as a key component of its physiological niche. Evolutionary ecology predicts that such responses are costly, necessitating trade-offs with other nutrient-demanding metabolic processes [9]. In addition, the metabolic requirements of immunity and the indirect effects of mounting induced immune responses are likely to have life-history consequences [9]. In insects, front-line defences include antimicrobial peptides (AMPs), targeting mainly Gram-negative and Gram-positive bacteria but also fungi and viruses, and the phenoloxidase (PO) pathway, which produces melanin for cuticle pigmentation, sclerotization, wound healing and encapsulation, and is an important part of an arthropod’s armoury against parasite attack [9].

Despite the clear importance of metabolic plasticity in maintaining cellular processes under thermal stress and the potential trade-offs with immunity, we know very little about how animals respond to thermal stress and the species they are able to encounter across their latitudinal range central point to avoid possible confounding effects of local adaptation in range edge populations [11]. Specimens were transported to the laboratory and maintained in 5 l aquaria, containing aerated artificial pond water (pH 7.7, 15°C) and submerged vegetation for 7 days [5]. Animals were kept at 20 individuals per aquarium, with a 12 L : 12 D regime and fed chironomid larvae [5].

After acclimation, individuals used for metabolic assays were ramped to five environmentally relevant sub-lethal temperatures (15, 20, 25, 30 and 35°C, at a rate of 0.25°C min⁻¹) and held at temperature for 24 h, before being frozen in liquid nitrogen. ATP, t-lactate, succinate, protein, glucose, glycogen and lipids were measured in beetles held at each temperature (see the electronic supplementary material). Lower values were subtracted from highest values to calculate plasticities. Immunocompetence was assessed by measuring external parasite load, encapsulation ability, PO activity (rates of dopachrome production and consumption), and AMP defence against both Gram-positive and Gram-negative bacteria (see the electronic supplementary material). Acclimatory ability of upper and lower thermal limits (UTL and LTL), absolute thermal tolerance range (TR), relative dispersal ability (DA) and body mass (BM) were obtained from [5]. Phylogenetic relationships between taxa were obtained from [12].

To test for phylogenetic effects, the phylogram was compared against species traits using phylogenetically Generalized least-squares regression models (pgls, ‘caper’ package). Maximum-likelihood estimations of lambda, which measure the degree to which phylogeny predicts the pattern of covariance among species, were not zero for all parameters, indicating that phylogenetic correction was required [13]. Owing to low degrees of freedom limiting the number of variables that could be included in the regression models, the principal component (PC) scores from the first two PCs explaining most variation in mean immune (immPC1 and 2) and metabolic traits (metPC1 and 2) were used from PC analysis (prcomp; ‘stats’ package). TR, UTL, LTL, DA and BM were also included as independent parameters; AIC, Akaike’s Information Criterion set at 95% confidence; ΔAIC < 2 reported; AIC weight represents the likelihood of the model given the data; BIC = Bayesian Information Criterion, which unlike AIC takes into account n and K. Best-fitting models are highlighted in italic.

**Table 1.** Model selection to estimate factors influencing latitudinal range extent and central position in Deronectes, showing the best supported models reported for each dependent variable (ΔAIC < 1). In each case, absolute thermal tolerance range (TR), acclimatory ability of upper and lower thermal tolerance (ΔUTL and ΔLTL), body mass (BM), dispersal ability (DA), immPC1, immPC2, metPC1 and metPC2 were included as independent variables (for principal component loadings see the electronic supplementary material, table S2). Latitudinal range position is the latitude of the range centre. K = number of parameters; AIC, Akaike’s Information Criterion set at 95% confidence; ΔAIC < 2 reported; AIC weight represents the likelihood of the model given the data; BIC = Bayesian Information Criterion, which unlike AIC takes into account n and K. Best-fitting models are highlighted in italic.

<table>
<thead>
<tr>
<th>model</th>
<th>K</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>AIC weight</th>
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<td>latitudinal range extent</td>
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</tr>
<tr>
<td>1. immPC2 + metPC2 + DA</td>
<td>5</td>
<td>21.18</td>
<td>0.00</td>
<td>0.48</td>
<td>-23.13</td>
</tr>
<tr>
<td>2. DA + ΔLT + TR</td>
<td>5</td>
<td>-21.09</td>
<td>0.08</td>
<td>0.46</td>
<td>-23.04</td>
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<tr>
<td>3. DA + BM</td>
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<td>-1.14</td>
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<td>0.87</td>
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<tr>
<td>4. ΔUTL</td>
<td>3</td>
<td>6.56</td>
<td>0.00</td>
<td>0.52</td>
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<tr>
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<td>0.99</td>
<td>-81.93</td>
</tr>
<tr>
<td>6. TR + BM</td>
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<td>0.00</td>
<td>0.98</td>
<td>-35.95</td>
</tr>
<tr>
<td>7. TR</td>
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<td>8. immPC1 + ΔUTL</td>
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<tr>
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<td>0.00</td>
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variables, and linear regressions run on untransformed and phylogenetic independent contrasts (‘ape’ package) to predict log10-transformed range extent and central position. In each analysis, models were constructed using all variable combinations and model selection was based on Akaike’s and Bayesian Information Criterion values (‘AICcmodavg’ package). Permutation testing was also performed on the best model fits (lmorigin; ‘ape’ package). All analyses were run in R v. 3.5.

3. Results and discussion

Previous studies of Deronectes [5,14] have pointed to the importance of physiology in shaping geographical range size and position. Studying a suite of metabolic and immunological parameters in both widespread and restricted species, we show that while variation in latitudinal range extent and position is related to thermal physiology, metabolic plasticity and immunocompetence also appear to play a role.

The best models for range extent and central position contained a measure of metabolic plasticity or immunocompetence without phylogenetic correction, as did that for range extent using contrasts (see the supplementary material, table S1), suggesting that a number of immunological and metabolic markers are related to a species’ biogeography (table 1). For uncorrected data, the best models for range extent and central position contained immPC1 and ΔUTL, and TR and BM, respectively (table 1; electronic supplementary material, figure S1). Significant loadings for immPC1 corresponded to the presence of AMPs against Arthrobacter globiformis (clear zone no.; electronic supplementary material, table S2).

Physiological trade-offs in thermal adaptation can restrict the biogeography of aquatic ectotherms, with lipid catabolism central to cold adaptation at high latitudes [6]. Our data suggest that more northerly distributed, wide-ranging species may use different energy reserves under thermal stress from their southerly endemic counterparts (figure 1). Maximum-likelihood estimates suggest that more northerly distributed, widespread species undergo more marked changes in lipid concentrations under thermal stress (table 2). Organisms are known to accumulate lipids during cold-acclimation as lipids are a more efficient energy store than others, such as glycogen [15]. However, the fat body in insects, which controls the synthesis and utilization of glycogen and lipids, is important not only in energy storage but also for metabolic activity, embryogenesis, flight and immune defence, producing AMPs [15].

In terms of immunity, maximum-likelihood estimates suggest that more southerly, range-restricted species have stronger antibacterial activity against Gram-positive and Gram-negative bacteria than their more wide-ranging counterparts (table 2 and figure 1; electronic supplementary material, figure S1). Lower latitude freshwaters may support a greater number of bacterial taxa [16], meaning that southerly, range-restricted species may require more, diverse AMPs. Alternately, it could be that high latitude species

Figure 1. Biplots for the most significant variables predicting latitudinal range extent and position. Codes: Deronectes bicostatus (bic), D. depressicollis (dep), D. hispanicus (his), D. moestus (moe) and D. latus (lat).
As species distributions respond to climate change, it is vital we understand the mechanisms shaping geographical ranges. It is suggested that further studies of the parameters measured here, on a range of arthropod groups, would improve understanding of the drivers of relative range size and position. In all cases, investigations should be conducted within a phylogenetically controlled framework and in a manner that controls for other possible drivers, such as relative DA. Future work should also incorporate these traits into predictive models, to aid the development of more accurate adaptation and mitigation strategies for conservation.

### Data accessibility

The datasets supporting this article have been uploaded in the electronic supplementary material.

### Authors’ contributions

D.T.B., A.J.M. and R.A.B. conceived the study; R.C., D.T.B., A.J.M. and R.A.B. designed it; R.C. conducted laboratory assays, analyses and drafted the manuscript; A.M. and D.T.B. coordinated fieldwork; all authors contributed and approved the final draft, and agree to be held accountable for the content therein.

### Competing interests

We have no competing interests.

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### References


