

# Individual behaviour mediates effects of warming on movement across a fragmented landscape

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## Summary

1. Global warming and habitat fragmentation impose dramatic and potentially interactive impacts on ecosystems. Warming induces shifts in species' distributions as they track temperature changes, but this can be hindered in fragmented landscapes. Corridors connecting habitat patches might ameliorate the combined effects of fragmentation and global warming.

2. Using novel automated tracking methods, the movement of woodlice (*Oniscus asellus*) ranging in body size from 15.3 to 108.6 mg was quantified across a temperature range from 15 to 25 °C as they moved around an experimental fragmented landscape. We used confirmatory path analysis to test causal effects of temperature and body size on individual movement and corridor crossing rates between two habitat patches.

3. Results showed that woodlice behaved differently in corridors than patches by moving, on average, faster and more often. This is congruent with natural systems where corridors generally provide lower quality habitat than patches. Although metabolic theory suggests positive scaling of movement with body temperature (up to a peak) and body size, we found that corridor crossing rate was (i) not directly affected by body size and (ii) negatively influenced by temperature, possibly due to its indirect effects via humidity.

4. Our path model revealed that metabolic scaling could only explain temperature effects on maximum body velocity, but decision-based behaviour explained most variation in corridor crossing rates. This led to direct and indirect effects of temperature and size on individual movement between habitat patches.

5. Our findings suggest that increasing mean global temperatures, coupled with increasing habitat fragmentation, could have synergistic negative impacts on populations through a combination of physiological and behavioural factors that mediate individual responses to temperature and fragmentation.

**Key-words:** automated tracking, fragmentation, global warming, habitat patch, metabolic theory, movement

## Introduction

Habitat fragmentation and global warming are two of the most important anthropogenic impacts affecting natural ecosystems and the services they provide (Thomas *et al.* 2004; Rosenzweig *et al.* 2008; Krauss *et al.* 2010). Although fragmentation and warming have individually gained much attention, information about how they interact to impact ecological systems remains limited (Brose *et al.* 2012). Global warming is altering the distribution and phenology of species as they attempt to track

changes in temperature to maintain their range within a climate envelope to which they have evolved (Parmesan & Yohe 2003; Root *et al.* 2003). On the other hand, fragmentation results in isolated habitat patches, reducing the ability of organisms to disperse across landscapes. Therefore, habitat fragmentation is likely to interact synergistically with climate change such that species' abilities to track the changing climate are hindered as landscape cohesion is reduced in a fragmented world (Opdam & Wascher 2004). Clearly, understanding the interplay between fragmentation and warming is necessary for predicting their combined effects on natural eco-

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systems and for deriving and assessing conservation strategies that can ameliorate these effects (Hof *et al.* 2011; Travis *et al.* 2013).

The facilitation of dispersal by constructing habitat corridors between isolated patches has been proposed as a solution for maintaining metapopulation persistence across fragmented landscapes (Gonzalez *et al.* 1998). This could reduce the synergistic effects of climate change and habitat fragmentation by allowing species to better track their preferred temperature (Opdam & Wascher 2004). The implementation of habitat corridors (i.e. relatively narrow tracts of suitable habitat that connect isolated habitat patches) has been broadly shown to enhance animal movement across fragmented landscapes (Gilbert-Norton *et al.* 2010). Habitat corridors can also have negative impacts on species persistence as they generally impose strong edge effects and can act as ecological traps or sinks, thus reducing metapopulation size (Simberloff *et al.* 1992). Nevertheless, corridors have been shown to reduce the extinction risk arising from small population sizes by increasing movement between patches (Lennartsson 2002; Corlatti, Hackländer & Frey-Roos 2009). In fact, Perdomo, Sunnucks & Thompson (2012) demonstrated that reducing patch isolation in an experimentally warmed moss-microarthropod system increased 'rescue effects' by enhancing dispersal of individuals into reassembling communities following heat shock. However, this study also found that community reassembly was dominated by larger species, resulting in a body size structure atypical of natural communities. Establishing a mechanistic understanding of how body size and temperature are likely to affect animal behaviour and movement among habitat fragments connected by corridors should aid with the development of a more predictive framework for assessing the efficacy of habitat corridors.

How often individuals use habitat corridors is the product of two factors: *corridor encounter rate* (the number of encounters with the corridor entrance per unit time), which depends on intra-patch movement and behaviour, and *corridor crossing probability* (the probability that the individual will then move across the corridor to the recipient patch), which should be less dependent on intra-patch movement and instead driven by exploratory behaviour outside of the patches (Chetkiewicz, St. Clair & Boyce 2006). The mechanisms that determine corridor encounter rate and corridor crossing rate are likely to be different (Chetkiewicz, St. Clair & Boyce 2006) and so deconstructing them in this way should allow greater insight into how and why animals use corridors.

According to metabolic theory, body size and environmental temperature (mostly pertaining to ectotherms) are likely to have strong impacts on movement (Peters 1983; Brown *et al.* 2004; Dial, Greene & Irschick 2008; Dell, Pawar & Savage 2011), and thus corridor encounter rate. All else being equal, larger-bodied individuals at higher temperatures tend to move faster than smaller-bodied individuals at colder temperatures; a pattern that appears quite

general across taxa and habitats, but is especially true for ectotherms because of the strong dependence of their body temperature on ambient temperature (Brown *et al.* 2004; Jetz *et al.* 2004; Dell, Pawar & Savage 2011; Ehnes, Rall & Brose 2011; Pawar, Dell & Savage 2012). While this suggests that movement across habitat corridors should increase with rising temperatures, certain taxa might exhibit opposite responses to temperature changes due to other effects, like decreasing humidity, that could override predicted metabolic responses from temperature alone (Dias, Hassall & Waite 2012). Once a corridor is encountered, a number of factors will determine whether the individual will enter the corridor, including how driven it is to leave its current patch and its perception of the corridor and recipient patch's quality (Bowler & Benton 2005). Whether the individual makes it to the recipient patch depends on its dispersal ability and the quality of the corridor (Ruefenacht & Knight 1995; King & With 2002). A low-quality corridor, for example with stronger edge effects or higher predation risk, decreases the chance of reaching the recipient patch alive (Simberloff & Cox 1987; Henein & Merriam 1990).

Despite the importance of size and temperature for animal movement and behaviour, there are apparently no existing studies that experimentally disentangle their combined effects on movement across habitat corridors. Here, we use automated image-based tracking (Dell *et al.* 2014a) of woodlice (*Oniscus asellus*) moving around an experimental landscape to understand how temperature and body size affect their use of a habitat corridor. Woodlice are an ideal focal taxon for this experiment as (i) they are a globally cosmopolitan group and functionally important to many terrestrial ecosystems, (ii) they exhibit especially strong range shift responses to climate change (Hickling *et al.* 2006), (iii) habitat corridors are especially important for invertebrate movement throughout fragmented landscapes (Gilbert-Norton *et al.* 2010), and (iv) they are an ideal taxa to track with automated software because they do not have long appendages that can affect tracking success, and they move relatively slowly in two dimensions. We hypothesized that larger-bodied woodlice at higher temperatures would move more often and faster, leading to higher corridor encounter rates and ultimately higher crossing rates, unless the direct physiological effects of temperature were overridden by indirect behavioural responses, such as via decreasing humidity. Our use of automated image-based tracking enabled quantification of individual behaviour at spatiotemporal scales and resolutions not possible with manual approaches (Dell *et al.* 2014a). In conjunction with path modelling, we isolate the behavioural mechanisms underlying corridor crossing rate to a degree that would be difficult to obtain in the field, and impossible to obtain using only crossing data, such as from mark-recapture. As such, our results shed new light on the multifaceted influence of temperature and body size on animal behaviour and movement across fragmented landscapes.

## Materials and methods

### STUDY SPECIES AND COLLECTION

Woodlice occur in many terrestrial ecosystems world-wide. *Oniscus asellus* (Fig. 1a) is a widespread species generally found under stones, logs and leaf litter on the forest floor (Cloudsley-Thompson 1952). Although they can tolerate dry conditions, *O. asellus* generally prefer microhabitats that are moist, where they venture out at night from shelters to forage on decomposing vegetation (Cloudsley-Thompson 1952). *Oniscus asellus* generally avoids light (Abbott 1918), and their average body velocity and probability of moving increase with temperatures up to 35 °C, although thermal dependence of woodlice behaviour varies between species (Warburg 1964).

*Oniscus asellus* used in our experiments were collected in mid-November 2013, from an urbanized leaf litter layer in Göttingen, Germany (51°32'N, 9°54'E). Annual mean soil temperature here is 7.2 °C (measured from 1998 to 2002 at 5 cm soil depth), with minimum and maximum temperatures of -3.9 °C (January) and 21.6 °C (July) measured during this time, respectively (Panferov *et al.* 2009). Following collection of about 150 woodlice, each was weighed and allocated to one of three size classes: small (0–40 mg), medium (41–70 mg) and large (71–110 mg). Woodlice were kept in these size-based groups in plastic terraria with plaster floors and a thin soil and leaf litter layer collected from the same site. Terraria were positioned together in a climate chamber at 14–15 °C with constant light and sprayed with water every second day. Woodlice had constant access to leaf litter and non-bleached tissue paper for food, which were replenished every few weeks, and animals were kept a minimum of 10 weeks before experimental trials.

### EXPERIMENTAL SETUP

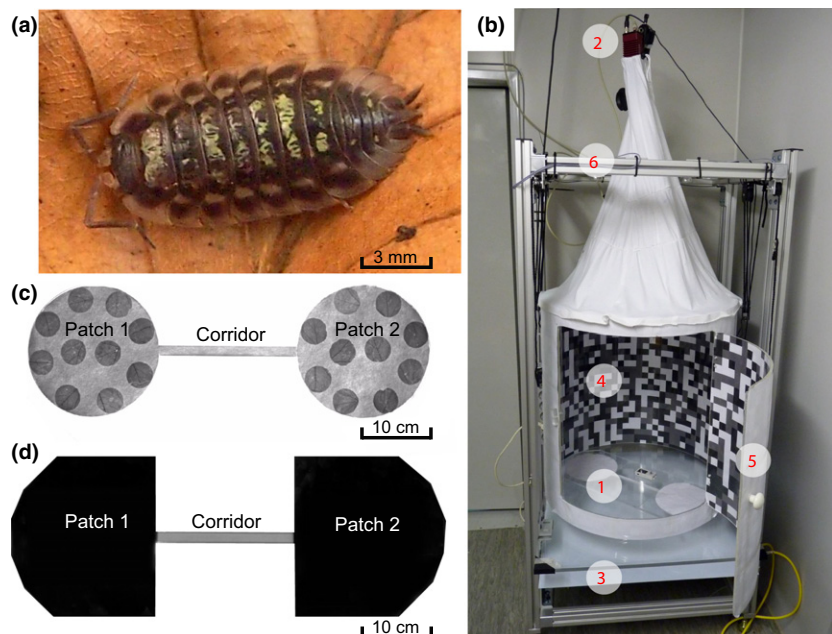
Experimental trials were undertaken in a controlled walk-in environmental chamber, using a custom-designed experimental set-up that allows video recording of movement and behaviour of a wide range of taxa. This set-up consisted of a high-resolution (1936 × 1454 pixel) CCD camera (Prosilica GX1920; Prosilica, Burnaby, BC, Canada) equipped with a 25-mm lens (Fujinon

and infrared (IR) pass filter (850 nm; Midwest Optical Systems, Palatine IL, USA) to block out stray light (Fig. 1b). Preliminary trials indicated that successful automated tracking could be obtained at two frames per second. Below the experimental landscape was an infrared light-emitting diode (LED) light panel (850 nm; Smart Vision Lights, Muskegon, MI, USA) that provided an even and diffuse-illuminated area of 600 × 600 mm. Previous work has shown that *O. asellus* cannot see at wavelengths greater than about 800 nm (Lindström & Meyer-Rochow 1987). The experimental landscape was positioned between the camera and the IR light: 134 cm below the camera lens and 11.8 cm above the IR light panel (Fig. 1b). This backlighting technique provided crisp, high-contrast images necessary for automated tracking (Dell *et al.* 2014a). The filming chamber was lined with a random grey-scale checkerboard pattern to provide a non-uniform visual background with no directional bias (Branson *et al.* 2009). The chamber was covered by a white cloth, with a small hole through which the camera lens could pass, to diffuse light and remove any bias provided by the climate chamber ceiling (Fig. 1b). The floor of the filming chamber was a 10-mm thick sheet of clear Perspex through which the IR backlight could shine unimpeded. Light in the visual spectrum was provided by four LED's (LifeLite daylight mirror lamp, 5 W) positioned above the white cloth (Fig. 1b), which emitted  $126.10 \pm 0.04$  lux (mean  $\pm$  95% confidence intervals used hereafter) onto the arena floor.

We constructed an experimental fragmented landscape using 8 mm thick Perspex (Fig. 1c,d). Two 20 cm diameter circular holes represented two habitat patches that were connected by a single corridor measuring 20 cm in length and 1.5 cm in width. The surface of the patches and corridor was covered with 2 mm thick white acrylic felt to create a semi-natural substrate that remained moist, making the experimental landscape through which the woodlice could move 6 mm high (i.e. between the felt substrate and Perspex lid). This height was chosen because woodlice naturally move throughout narrow habitats, such as between leaves and under woody debris. Additionally, preliminary trials showed that heights much above 6 mm resulted in the constant movement of individuals throughout the trial, but when reduced to 6 mm, individuals started moving in a more natural, exploratory manner.

We modified habitat patches in three ways to make them more suitable habitat for woodlice than the corridor. First, 10 circular

**Fig. 1.** Study species and experimental set-up. (a) *Oniscus asellus*, the woodlice species used in this study. (b) Experimental set-up used to undertake trials. Our use of back-lighting meant the experimental landscape (1) was positioned between the camera (2) and the IR light panel (3). The filming chamber (4) was lined with a random checkerboard pattern, and the door (5) was closed during trials. Visual light was provided by four LED lights above the arena (6). (c-d) The experimental landscape (1 in b) consisted of two habitat patches connected by a single corridor. To increase the attractiveness of patches to woodlice, 10 circular leaf fragments were placed within each patch and IR sheets were placed over both patches to reduce visual light. (c) shows the image in IR, while (d) shows the same image as viewed by the naked eye, with habitats indicated.





pre-soaked leaf fragments (4 cm diameter) of *Acer platanoides*, a natural food and microhabitat for *O. asellus* (D. Ott, pers. comm.), were systematically placed throughout each patch (Fig. 1c). The protocol for collecting, preparing, and storing these leaves is described by Ott, Rall & Brose (2012). Secondly, patches were covered with a 2-mm thick IR sheet that blocked out ~95% of light below 800 nm (Luxacryl-IR; TTV GmbH, Geretsried, Germany), while the corridor was covered with a 2-mm thick clear sheet of Perspex that did not reduce visible light (Fig. 1d). Therefore, light in the visual spectrum was  $1.8 \pm 0$  lux in the patches, compared to  $126.10 \pm 0.04$  lux in the corridor. Thirdly, the felt substrate within patches was kept much wetter than the corridor. Combined, the higher habitat complexity provided by the leaf fragments, the reduced ambient light under the IR sheets, and the higher substrate moisture levels made the habitat patches preferable for *O. asellus* over the corridor (established in preliminary trials).

#### EXPERIMENTAL TRIALS

Trials were conducted across a temperature range from 15 to 25 °C and a body size range of 15.3–108.6 mg, comprising a total of 45 separate trials replicated evenly across the temperature and body size gradients (Fig. S1, Supporting information). The temperature gradient of 15–25 °C was chosen based on the experimental work of Warburg (1964), who established that *O. asellus* maintain movement at temperatures of 15–35 °C, but where most constant movement occurred up to 25 °C. Furthermore, the mean annual soil surface temperature at the site where woodlice were collected for our experiment is ~7 °C, but with maximum temperatures rising to at least ~21 °C. Therefore, in order to simulate a climate warming scenario where maximum temperatures could rise to the previously established upper ranges of active *O. asellus* movement, we matched our temperature range to that of Warburg's (1964) experiment.

A single trial involved a single woodlouse navigating the experimental landscape for 60 min (Fig. 1c). Twenty minutes prior to the start of a trial, 20 leaf fragments of *A. platanoides* were placed in water in order to mimic typical conditions of leaf litter experienced by woodlice (Zimmer, Kautz & Topp 2003). The felt in each patch was then sprayed with water so that the substrate was saturated (30 sprays from a spray bottle per patch from a distance of *c.* 15 cm) and the 10 leaf fragments were then arranged symmetrically within each patch (Fig. 1c). Following this, a single woodlouse was randomly placed in one of the two patches and both patches were covered with the IR sheet and the corridor with clear Perspex (Fig. 1c,d). The woodlouse was allowed to move around the patch for 15 min while the corridor was blocked, to allow acclimation to the experimental conditions. The corridor was then opened, filming was started, and the 60-min trial commenced. Individuals were weighed immediately following each trial. Temperature and humidity in the filming chamber was measured immediately before and after each trial using an environmental logger (HOBO UX100-011; Onset Computer Corporation, Bourne, MA, USA).

#### AUTOMATED IMAGE-BASED TRACKING

Each 60-min video was tracked automatically using Ctrax (Branson *et al.* 2009), providing an estimate of the spatial position of the woodlouse throughout the landscape in all 7200 frames of each video. Tracking errors that arose after initial tracking were fixed using the FixErrors toolbox for MATLAB (The MathWorks Inc., Natick, MA, USA) that is packaged with Ctrax. Trajectory data, consisting of *x*-*y* coordinates for each frame, were exported for analysis in R (R Development Core Team 2013). Because even stationary animals can have nonzero body velocities when tracked

using automated methods, due to lighting fluctuations or movement of appendages while the animal is stationary, we defined individuals as stationary when its body velocity from the tracked data was  $<0.816 \text{ mm s}^{-1}$  (this was the maximum velocity measured during  $10 \times 30$  s sections of video where the animal appeared stationary to a human observer).

#### QUANTIFYING BEHAVIOUR AND CORRIDOR CROSSINGS

We first quantified the proportion of time an individual spent within each habitat (i.e. patch 1, corridor, patch 2). Then, assuming that how often an individual moves and its speed when moving affects both corridor encounter rate and crossing rate, we quantified three relevant behavioural traits of each individual: (i) *proportion time moving* was the proportion of the total trial time the individual was moving; (ii) *mean velocity* ( $\text{mm s}^{-1}$ ) was the mean body velocity of the individual when it was moving calculated over the entire trial; and (iii) *maximum velocity* ( $\text{mm s}^{-1}$ ) was the mean maximum body velocity of the individual, calculated as the mean of the highest 0.5% of all nonzero velocities for that individual over the entire trial (i.e. 36 of 7200 velocity measurements). *Corridor encounter rate* was calculated as the number of times the mid-point of the individual moved across the projected boundary separating the resident patch from the corridor per unit time, while *corridor crossing rate* was the number of times an individual moved across the entire corridor to the recipient patch per unit time.

#### STATISTICAL ANALYSIS

To determine whether woodlice behaved differently in patches compared to the corridor, we used ANOVA to test for differences in the proportion time moving, mean velocity, maximum velocity and proportion time spent in each habitat. To meet assumptions of normality, proportion time moving and proportion time in habitat were logit-transformed (Warton & Hui 2011). We used Tukey's HSD post hoc tests with Bonferroni corrections to detect significant differences between patch 1, patch 2 and the corridor. We determined the direct effects of temperature and body size on crossing rate using generalized linear models (GLM's) modelled on a negative binomial distribution to account for over-dispersed, Poisson-distributed count data (Ver Hoef & Boveng 2007).

We used a path modelling approach to disentangle the causal effects of temperature and body size on crossing rate, via behavioural traits and encounter rate. Path modelling allows for testing of causal hypotheses to distinguish the relative importance of mediating variables in complex experimental designs (Mitchell 1992). Specifically, we used a generalization of Shipley's (2009) d-separation method of generalized causal path analysis. Three major steps were taken to test the validity of the generalized causal path model representing a directed acyclic causal diagram (a unidirectional diagram without feedback loops). First, we established the basis set of independence claims that expresses the full set of dependence and independence claims within the causal diagram ( $\mathbf{B}_U$ ). Secondly, we obtained the probability  $P_i$  from each independence claim  $k$  included in  $\mathbf{B}_U$  using GLM's with Gaussian distributions for normally distributed endogenous variables and Poisson or negative binomial distributions for count data. Thirdly, we combined the  $P_i$  probabilities using  $C = -2 \sum_{i=1}^k \ln(P_i)$  and compared the  $C$  test statistic to a chi-squared ( $\chi^2$ ) distribution with  $2k$  degrees of freedom. This gave the probability  $P$  that the path model did not depart significantly from the expected structure (Shipley 2009). As such, we rejected the model if the  $P$ -value derived from the  $C$  statistic was smaller than the specified  $\alpha$  level ( $<0.05$ ). All predictors were centred on their means to aid with interpreting effects and to avoid issues with multicollinearity due to inclusion of interaction

terms in the structural equation model (Grace *et al.* 2007). Mean and maximum velocity were  $\log_{10}$ -transformed to linearize relationships, and the proportion time moving was logit-transformed to meet assumptions of normality (Warton & Hui 2011).

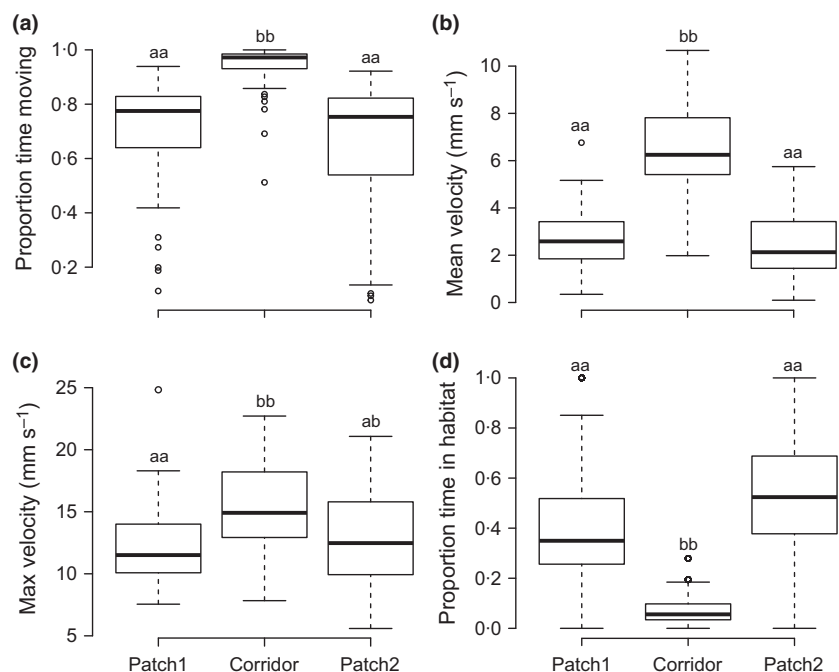
In order to visualize the relative effect sizes of exogenous and endogenous variables on response variables within the path diagram, we calculated standardized path coefficients (Gelman 2008). This was carried out by dividing the mean-centred predictor variables by twice their standard deviation, giving the unit change in the response variable with one standard deviation change ( $\pm$ ) in the predictor. This accounted for differences in measurement units among predictor variables assuming the variances of measured variables were equal. To obtain standardized path coefficients for nonlinear relationships, we calculated a composite variable from the polynomial terms by multiplying each polynomial of a predictor by its coefficient and then summing them together to create a new composite vector. This composite variable was then used in the structural equation, yielding a single standardized coefficient for quadratic polynomial predictors (Grace *et al.* 2007). All analyses were conducted in R (R Development Core Team 2013).

## Results

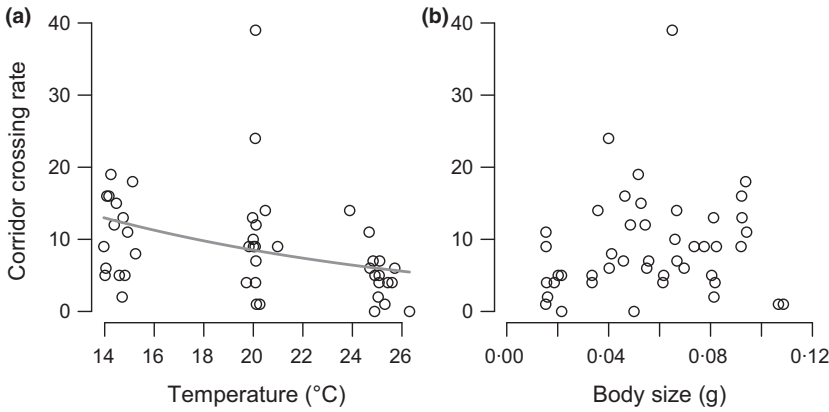
All but two of the 45 woodlice (id64 and id68; Fig. S1) used the corridor at least once over the 60-min trial, with a mean for all individuals of 8.911 ( $\pm$  SD of 7.144) crossings per hour. We found significant differences between both patches and the corridor for all behavioural traits, but no differences between patch 1 and patch 2 (Fig. 2). Proportion time spent in each habitat ( $F_{2, 129} = 48.632$ ,  $P < 0.001$ ), proportion time moving ( $F_{2, 129} = 32.245$ ,  $P < 0.001$ ) and mean velocity ( $F_{2, 129} = 54.830$ ,  $P < 0.001$ ) were significantly higher in the corridor than in patches (Fig. 2a,b and d), but maximum velocity in patch 2 was not significantly different from within the corridor (Fig. 2c;  $F_{2, 129} = 4.003$ ,  $P = 0.021$ ).

Generalized linear model analyses of the overall independent effects of temperature and body size on crossing rates revealed a significant negative effect of temperature (estimate =  $-0.070 \pm 0.024$ ,  $z = -2.811$ ,  $P = 0.005$ ; Fig. 3a), but no apparent effect of body size (estimate =  $5.485 \pm 4.258$ ,  $z = 1.288$ ,  $P = 0.198$ ; Fig. 3b). This is surprising given our expectations, based on metabolic theory (Brown *et al.* 2004), that larger-bodied animals at higher temperatures should encounter and cross-corridors more frequently. However, it is noteworthy that temperature also had indirect effects on woodlice movement via humidity, as temperature and humidity were strongly negatively correlated in our study ( $\rho = -0.898$ ).

The path model revealed that temperature played an important role in altering behavioural traits within patches but this was either dependent on, or acting in concert with, effects of body size (Fig. 4). The form and direction of relationships among temperature, body size, behavioural traits and corridor encounter and crossing rates were diverse (Fig. 5). There were significant negative effects of temperature and body size on both proportion time moving and mean velocity, although the strengths of the negative responses to body size were weaker than for temperature (Figs 4 and 5a,b). Temperature had a weak positive effect on maximum velocity that was negatively dependent on body size (Fig. 4), suggesting that the positive effects of temperature on maximum velocity are weaker for larger woodlice than for smaller ones. Although we found no apparent effects of maximum velocity on encounters or crossings, the path analysis did reveal a clear influence of the two other behavioural traits. After taking into account variance explained by all other predictors in our structural equation model, proportion time



**Fig. 2.** Differences in the movement behaviour of individuals between patches and the corridor for (a) proportion time moving, (b) mean velocity, (c) maximum velocity and (d) proportion of time spent in each habitat. Within each panel, different letters above boxes denote significant differences between habitats as determined by Tukey's HSD tests ( $P < 0.05$ ).



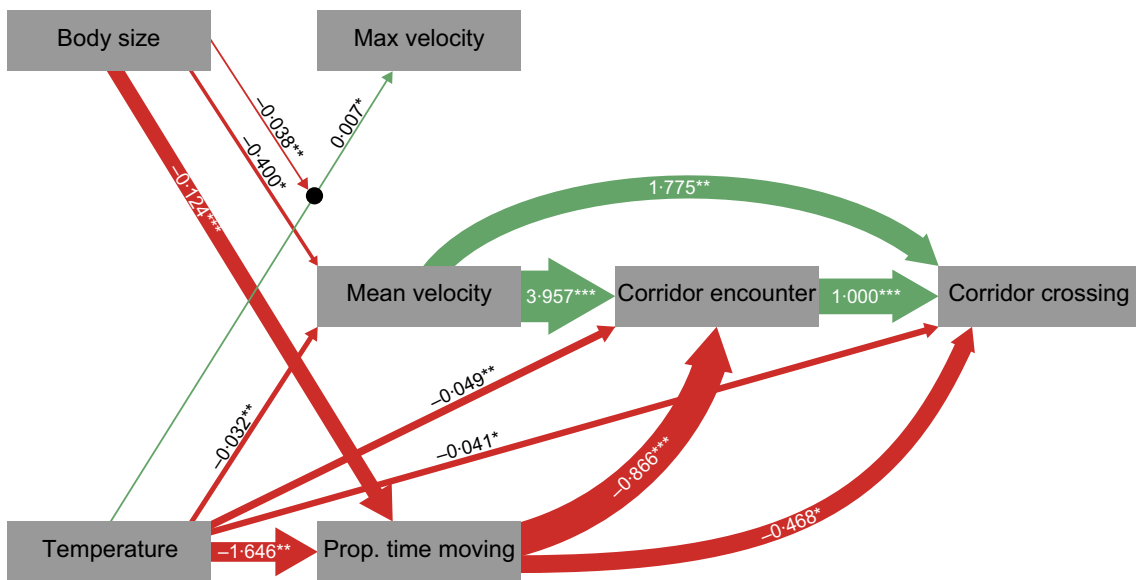
**Fig. 3.** Effects of (a) temperature and (b) body size on corridor crossing rate (crossings per hour) for all 45 woodlice moving for one hour. Grey line in (a) represents GLM modelled on a Poisson distribution ( $P = 0.005$ ). The GLM of body size was non-significant ( $P = 0.198$ ).

moving had a strong negative influence on both encounter and crossing rates (Figs 4 and 5c,d). These effects, however, were opposed by an even stronger positive effect of mean velocity on corridor encounter rate, and a relatively equal-strength effect on crossing rates (Figs 4 and 5c,d).

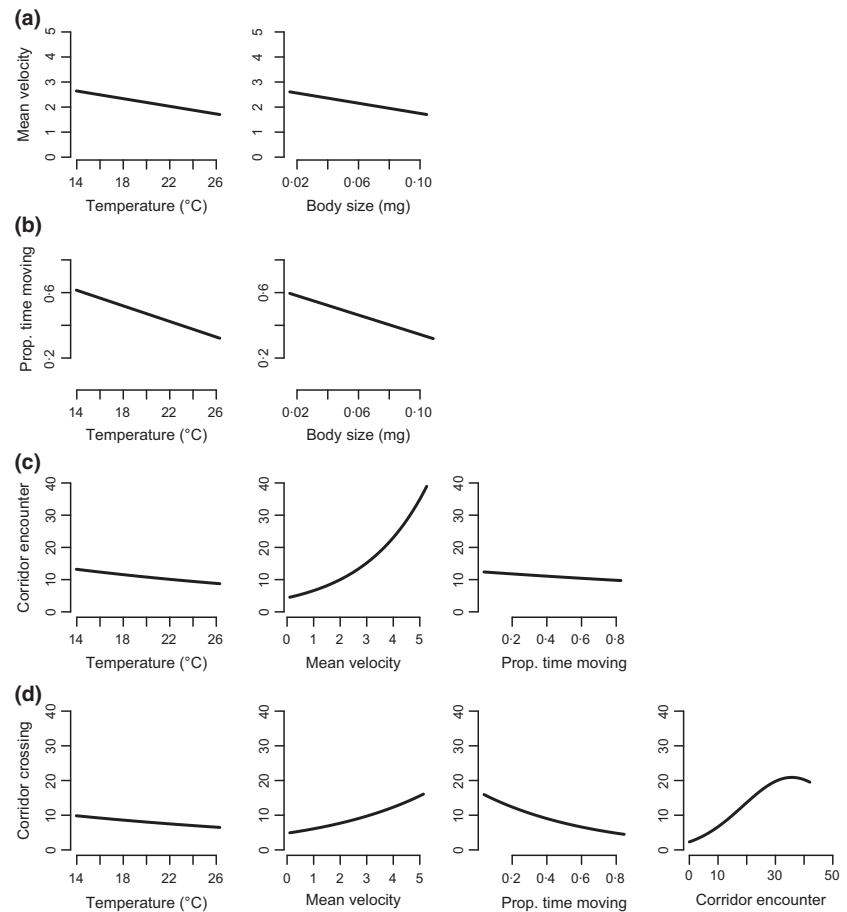
Taking into account the direct pairwise relationships discussed above, we were able to distinguish important causal pathways arising from the structure of the path analysis. For example, both temperature and body size impose indirect negative effects on crossing rate via their negative impact on mean velocity, which conversely had a positive effect on crossing rate. Furthermore, these negative effects also affected crossing rate via encounter rate, which had a strong positive nonlinear saturating effect on corridor crossings (Figs 4 and 5d). Interestingly, the opposite pattern was true for the pathway via proportion time moving. Here, the negative effects of temperature and body size on

proportion time moving resulted in a net positive influence on between-patch movement, due to their reduction of the negative influence of proportion time moving on encounter and crossing rates (Fig. 4).

Even after including the three behavioural traits as mediating endogenous variables, all variation in encounter and crossing rates in response to temperature was not captured by these behavioural variables. This was evident in the path model because, while holding the behavioural trait variables constant at their means, temperature was found to impose direct negative effects on both encounter and crossing rates (Figs 4 and 5c,d). These residual effects of temperature are shown in the path model by direct arrows to corridor encounter and crossing that bypass the three behavioural traits (Fig. 4), and likely represent temperature effects on more complicated decision-based locomotory behaviour.



**Fig. 4.** Directed acyclic diagram of confirmatory path analysis testing the causal effects of body size and temperature on the use of a habitat corridor via mediating behaviour using the structure determined by the  $B_U$  set of independence claims ( $\chi^2 = 36.520$ , d.f. = 28,  $P = 0.130$ ). Boxes depict predictor and response variables and arrows indicate significant positive (green) and negative (red) effects. The black circular node intersected by arrows leading to max velocity from body size and temperature represents a significant interaction between these predictors. Values within and adjacent to arrows are unstandardized path coefficients with significance level ( $*P < 0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$ ). Line weightings indicate relative strength of effects derived from the standardized path coefficients.



**Fig. 5.** Regression fits of all significant pairwise relationships between predictors and response variables (a) mean velocity, (b) proportion time moving, (c) corridor encounter rate and (d) corridor crossing rate, within the confirmatory path analysis. Regression lines are fitted for the relationships between each predictor and response variable while holding all other covariables in the model constant at their means. Full details of regression parameters are given in Table S1.

## Discussion

Using automated image-based tracking (Dell *et al.* 2014a) and path modelling (Shiple 2009), we show that temperature and body size have important, albeit somewhat unintuitive, effects on the rate at which individuals encounter and cross-habitat corridors in a fragmented experimental landscape. Automated tracking, combined with path modelling, allowed us to isolate the behavioural effects of temperature and size in order to mechanistically understand the more emergent patterns of corridor encounter and use. In our experiment, woodlice spent less time but moved faster and more often in corridors, suggesting that corridors were used to move between patches and not as suitable habitat. The propensity of animals to disperse into adjacent habitat patches depends on factors such as patch size in relation to the size of the animal (individuals should be more likely to leave patches that are small relative to their body size; Jetz *et al.* 2004), patch quality, matrix-patch contrast, and the perceived distance and quality of the recipient patch (Ruefenacht & Knight 1995; King & With 2002; Kupfer, Malanson & Franklin 2006). Therefore, it is essential that our results are considered in the context of the experimental landscape we used. For example, the length (20 cm) and width (1.5 cm) of the corridor used in our

experiment was relatively small compared to the body size of the woodlice, which certainly played an important role in the way the corridor was used (Gilbert-Norton *et al.* 2010). Nonetheless, experimental approaches like ours allow greater control of environmental conditions, better allowing the isolation of mechanisms that link individual behaviour to population-level processes, such as movement between habitat patches.

Contrary to our expectations (Peters 1983; Brown *et al.* 2004; Dell, Pawar & Savage 2011), higher temperatures reduced crossing rates by about half between 15 and 25 °C. While it is possible that this decline in movement was due to the higher temperatures falling beyond the thermal optimum for movement in *O. asellus*, this was not supported by the continuous linear decline found in corridor crossings with increasing temperature. It is more likely that, because temperature and atmospheric humidity were negatively correlated in our study ( $\rho = -0.898$ ), woodlice reduced their movement throughout the experimental landscape at higher temperatures in order to avoid potentially lethal desiccation (Dias, Hassall & Waite 2012). By experimentally disentangling temperature and humidity effects, combined with additional parameters like predation, competition and resource availability, a deeper and more general understanding of animal movement under varying climate change scenarios should be obtained.



Similarly, although we expected body size to positively impact crossing rate, simple pairwise tests showed no significant relationship (Fig. 3b). One explanation for this is that the range of body sizes in our experiments (15.30–108.60 mg) was not sufficient to detect allometric effects, which are often only apparent over ranges of several orders of magnitude in size (Peters 1983; Brown *et al.* 2004). Therefore, it is possible that behavioural effects such as decision-making, which may be unrelated to size (but see Dial *et al.* 2008), were more dominant. Furthermore, movement and behaviour are likely to vary with ontogeny due to variation in body geometry (Hirst, Glazier & Atkinson 2014) and other correlated traits that likely influence dispersal patterns and distributions of terrestrial ectotherms (Kearney 2012). While this was beyond the scope of our study, our approach provides a powerful framework under which these mechanisms can be directly tested.

The path model revealed that effects of temperature and size on corridor use are predominantly indirect, whereby effects on the behaviour of individuals were more important than direct effects on crossing rates. Aside from the positive effect of temperature on maximum velocity, temperature negatively influenced all other movement variables in the path model, which contradicted our hypothesis based on metabolic theory (Brown *et al.* 2004; Dell, Pawar & Savage 2011). We suspect this is due to behavioural effects, whereby woodlice reduce their mean velocity and frequency of movement at higher temperatures to prevent desiccation with decreasing humidity (Warburg 1964; Refinetti 1984). Furthermore, although corridor encounter must be a prerequisite of crossing, the saturation of their nonlinear relationship indicates that above a particular rate of encounter the probability that individuals will cross does not further increase. The mechanisms yielding saturation are unknown, but probably reflect behavioural decisions by individuals.

The path model also revealed that the negative effects of temperature on proportion time moving translated into indirect positive effects on corridor crossing, but negative effects via encounter rates due to the negative effects of proportion time moving on corridor encounter and crossing rates. Although only speculative, this could be explained by the seemingly erratic behaviour observed in particular individuals that spent a higher proportion of time moving (Fig. S1). In contrast, individuals that moved less often at higher temperatures may have been moving more directionally with the intent to cross-corridors and find a new habitat patch, but this requires further investigation. Our results suggest that individual variation in general behavioural responses could be a result of individual behaviour syndromes (Sih, Bell & Johnson 2004), which may predispose individuals to respond to temperature differently.

Body size had similar indirect positive effects on encounter and crossing rates that accumulated via proportion time moving; although larger individuals moved less often,

they apparently discovered and crossed the corridor at higher rates. One potential explanation is that because larger-bodied individuals can better maintain thermal equilibrium under varying temperatures (Stevenson 1985), large individuals moved less often in response to suboptimal temperatures. This hypothesis was supported by the negative interaction of body size and temperature on maximum velocity, suggesting that the influence of ambient temperature on individual maximum velocity decreases with body size. While temperature and body size had similarly negative (although weaker) effects on mean velocity of individuals, their effect pathways via mean velocity resulted in a strong negative effect on crossing rates (Fig. 4). Furthermore, mean velocity had the strongest influence on corridor encounter rate, which was then amplified through to crossing rate. Combined, these results suggest that individuals moving less often but faster, on average, have a higher propensity to encounter and cross-habitat corridors. Because metabolic rates scale positively with temperature and body size (Gillooly *et al.* 2001; Brown *et al.* 2004; Ehnes, Rall & Brose 2011), our expectations were that mean and maximum velocity should also increase (Peters 1983; Brown *et al.* 2004; Dell, Pawar & Savage 2011, 2014b). However, our results reveal that (i) temperature (and its interaction with body size) appears to have indirect effects on woodlice movement via correlated variables, such as humidity (Warburg 1964; Refinetti 1984; Stevenson 1985; Dias, Hassall & Waite 2012), rather than direct positive effects due to metabolic scaling relationships (Brown *et al.* 2004); and that (ii) these physiological constraints may vary considerably due to individual variation in behavioural complexes (Sih, Bell & Johnson 2004).

As global mean temperatures rise (IPCC 2014) animal populations will be forced to either locally adapt, or to move to more climatically suitable habitat patches (Visser 2008). Such effects are already occurring in a vast diversity of taxa and environments (Loarie *et al.* 2009; Burrows *et al.* 2011; Chen *et al.* 2011). With the continuing increase in habitat fragmentation across the globe (Ewers & Didham 2006), species face increasing challenges to track Earth's shifting thermal landscape (Hof *et al.* 2011). Habitat corridors are touted as a potential solution to this problem (Haddad 2008), but their effectiveness remains questioned (Gilbert-Norton *et al.* 2010). In our study, we show that in fragmented landscapes, warming may have a twofold negative impact on species persistence. On the one hand, species will need to disperse to new patches as temperature extremes increase; otherwise, they will likely face local extinction if conditions move outside their thermal windows. On the other hand, species that exhibit behaviourally mediated negative responses to temperature (such as the woodlice in our study) are likely to reduce their use of habitat corridors in fragmented landscapes. This would suggest a potentially worse-than-expected scenario whereby temperature imposes not only direct negative effects on populations, but also indirect effects via their movement and behaviour that could hinder the ability of



individuals, and thus their populations, to cope with worsening climate scenarios.

Recent attention has been directed towards developing mechanistic dispersal models that depend on knowledge of species-specific movement patterns under varying temperatures (Travis *et al.* 2013). By applying a novel experimental approach, we present a method of disentangling the mechanistic drivers of animal movement in response to climate warming. As such, our approach can be used to better understand the general mechanisms underlying animal movement and, thus, should provide information that could lead to predictive dispersal models in fragmented landscapes. As global climatic conditions are not only expected to become warmer on average but also to increase in extremes (Thompson *et al.* 2013; Vasseur *et al.* 2014), the next step for these types of experiments would be to incorporate realistic climatic variation. Our study focused on a single species moving around a simplified experimental landscape within patches that were clearly smaller than the size of their natural home ranges. Future work should examine how our results scale as the relative size of patches increases and the frequency of movement between patches potentially decreases. Clearly, a fuller understanding of the combined effects of fragmentation, global warming and body size will emerge from research that incorporates experimental, theoretical and field-based research.

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## Data accessibility

The data used in this paper are deposited in the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.1m54f> (Barnes *et al.* 2015).

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## Supporting Information

Additional Supporting information may be found in the online version of this article:

**Fig. S1.** Trajectories of individual *O. asellus* within the experimental landscape.

**Table S1.** GLM summary outputs for endogenous variables in the path analysis.