



Effects of temperature on the movement and feeding behaviour of the large lupine beetle, *Sitona gressorius*

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Abstract

Even though the effects of insect pests on global agricultural productivity are well recognised, little is known about movement and dispersal of many species, especially in the context of global warming. This work evaluates how temperature and light conditions affect different movement metrics and the feeding rate of the large lupine beetle, an agricultural pest responsible for widespread damage in leguminous crops. By using video recordings, the movement of 384 beetles was digitally analysed under six different temperatures and light conditions in the laboratory. Bayesian linear mixed-effect models were used to analyse the data. Furthermore, the effects of temperature on the daily diffusion coefficient of beetles were estimated by using hidden Markov models and random walk simulations. Results of this work show that temperature, light conditions, and beetles' weight were the main factors affecting the flight probability, displacement, time being active and the speed of beetles. Significant variations were also observed in all evaluated metrics. On average, beetles exposed to light conditions and higher temperatures had higher mean speed and flight probability. However, beetles tended to stay more active at higher temperatures and less active at intermediate temperatures, around 20 °C. Therefore, both the diffusion coefficient and displacement of beetles were lower at intermediate temperatures. These results show that the movement behaviour and feeding rates of beetles can present different relationships in the function of temperature. It also shows that using a single diffusion coefficient for insects in spatially explicit models may lead to over- or underestimation of pest spread.

Keywords Agricultural pests · Diffusion; Hidden Markov models · Movement ecology

Introduction

Insect pests pose a global threat to agricultural productivity (Oerke 2006; Dar and Laxmipathi Gowda 2013; Deutsch et al. 2018). Despite major advances in pest management approaches, the intensification of agriculture (Wilby and

Thomas 2002), climate change (Seidl et al. 2018; Koontz et al. 2021), reduction in landscape complexity (Larsen and Noack 2020) and an increase in human-mediated dispersal (Gippet et al. 2019) have resulted in an environment beneficial to the spread of existing and alien pests. However, predicting the dispersal capacity of biota in agricultural landscapes remains difficult (Irwin 1999; Jeger 1999; Azandémè-Hounmalon et al. 2014), especially in the context of global warming (Deutsch et al. 2018).

Many factors influence the rate and extent of pest spread, such as landscape complexity (Potgieter et al. 2015; Haan et al. 2020), crop management (Perrin and Phillips 1978; Rusch et al. 2013), abiotic factors (Martini and Stelinski 2017), population dynamics (Naranjo et al. 2009; Kausrud et al. 2011), and individual behaviour (Delgado and Penteriani 2008). Reliable information about these parameters can help predict pest spread in agricultural landscapes for developing effective mitigation strategies (Robinet et al. 2012; Jung et al. 2017; Xu et al. 2020). Therefore, an improved understanding of pest dispersal capabilities can lead to more

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sustainable pest management practices and improve pest and crop models (Mazzi and Dorn 2012).

Environmental temperature has a direct effect on insect physiological processes and metabolic demands because insects cannot directly regulate their body temperature (Bale et al. 2002; Zhang et al. 2020). Several studies have established that temperature has a wide range of short and long-term effects on insect behaviour such as foraging (Sentis et al. 2015), feeding rate (Rall et al. 2012; Lemoine et al. 2013; Zhang et al. 2020), reproduction (Seal et al. 2002) and movement (Lehmann 1999). An increase in temperature would likely increase feeding, reproduction and dispersal rates of agricultural pests (Taylor et al. 2018), which, in turn, would reduce crop yields and threaten global food supplies (Deutsch et al. 2018). However, previous studies also showed that an increase in temperatures can have non-linear responses on both feeding rates (Paudel et al. 2020) and locomotion of insects (Dell et al. 2014). While effects of temperature on many aspects of insect development are well established, little is known about how temperature affects pest movement and dispersal (Ratte 1984; Neven 2000; Dixon et al. 2009; Régnière et al. 2012; Andrew et al. 2013).

Movement dynamics are related to the majority of an organism's behavioural processes including foraging, dispersal, mating, host preference, evolutionary adaptation potential and response to resource limitation (Nguyen and Nansen 2018; Santana-Filho et al. 2020). Insects use flight to evade predators (Aukema et al. 2005), find mates (Kuriwada et al. 2014), oviposition sites (Schotzko and O'Keeffe 1986) and overwintering sites (Hamon et al. 1987). There is an increasing need to understand individual dispersal potential and movement behaviour to better inform population-level dispersal, allowing more accurate pest surveillance and models (Gui et al. 2012; Petrovskii et al. 2014; Bailey et al. 2020). Small-scale movement analysis of individuals can help understand how behavioural mechanisms influence insect movement patterns (Delgado and Penteriani 2008) and responses to environmental change (Kokko and López-Sepulcre 2006). Species may respond to changes in temperature by either dispersing (e.g. range shift), adapting (e.g. natural selection) or by altering their behaviour (Wong and Candolin 2015). Among these responses, behavioural change is normally the first defence mechanism because it is the quickest to implement (Allen et al. 2012; Beever et al. 2017).

In the twenty-first century, there has been major progress in the field of movement ecology due to technological developments in computing power, statistical methods (Gimenez et al. 2014) and tracking devices (Cooke et al. 2004; Tomkiewicz et al. 2010; Neumann et al. 2015; Börger, 2016; Remelgado et al. 2019). Technological advances have allowed for different species, such as insects, to be tracked using flight mills (Taylor et al. 2010; Ribak et al. 2017), video tracking systems (Spink et al. 2001), radio telemetry (Kissling et al.

2014), harmonic radar (Maggiore et al. 2019) and robots (Pannequin et al. 2020). However, due to their size, tracking small insect pests remains challenging and consequently has been less pursued (Holyoak et al. 2009). Among these methods, video tracking is a prominent method that allows precise measurement of movement at small temporal scales, greater control of experimental conditions and increased statistical power, at low cost (Wiktorsson et al. 2004; Jopp 2006; Shcherbakov et al. 2010; Crispim Junior et al. 2011; Augustin et al. 2020).

The large lupine beetle (*Sitona gressorius*) is an agricultural pest which can be found across Europe (Andersen 1938). Little is known about this species even though it can cause widespread damage to leguminous crops (Williams et al. 1995; Ströcker et al. 2013). Due to their high protein content and suitability for sustainable production, white, yellow, and narrow-leaved lupines (*Lupinus albus*, *L. luteus* and *L. angustifolius*, respectively), could prove to be an alternative to soybean importation (Lucas et al. 2015; Gresta et al. 2017). *S. gressorius* larvae feed on root nodes, while adults feed on the leaves (Ströcker et al. 2013), causing severe crop losses. For organic farmers, there are currently no methods at hand to minimise *S. gressorius* damage and in conventional farming, only one insecticide treatment per year is permitted in Germany (Ströcker et al. 2013). The rise in temperature over the past few decades has led to a more favourable environment for the *S. gressorius* in Europe, among other agricultural pests, due to increases in feeding activity, fecundity, development rate, as well as earlier flight periods and enhanced winter survival (Robinet and Roques 2010).

The development of non-chemical pest control strategies requires a deeper understanding of the behavioural responses of *S. gressorius* to changes in environmental conditions. Therefore, the aim of this work is to evaluate the effects of temperature and light conditions on the movement and feeding rate of the *S. gressorius*. To achieve these goals, beetles were video-recorded under six different temperatures and two light conditions in the laboratory. Furthermore, the effects of temperature on the diffusion coefficient of pests were evaluated using hidden Markov models and random walks simulations. These findings should make an important contribution to development of precision-targeted monitoring and detection of pest outbreaks, spatially explicit pest models and in the implementation of mitigation strategies of the *S. gressorius*.

Materials and methods

Test beetles

Adult beetles were collected in an 8000 m² organic lupine crop field at the Leibniz-Centre for Agricultural Landscape

Research (ZALF) experimental field in Müncheberg, Brandenburg, Germany. In Brandenburg, *S. gressorius* is quite common due to sandy soils and weather conditions favourable to this species. Beetles were sampled by shaking lupine plants over a white sheet of paper (Augustin et al. 2012). Beetles were acclimatised to laboratory conditions two to three weeks prior to the experiment at a constant temperature of 25 °C. Beetles were sampled between July 15th and August 12th and experiments were conducted between August 5th and 26th in 2020. Sampled beetles ($n = 384$) had a similar length (0.849 ± 0.004 cm; mean and standard error) and weight (0.023 ± 0.000 g). Unfortunately, identifying sexual dimorphism, age and mating status of the large lupine beetle is not possible without dissecting the beetles. Therefore, these factors could not be identified before the experiments were conducted. Sampled beetles were randomly placed and kept in petri dishes with dampened tissues at a density of 10 *S. gressorius* per dish and were fed with fresh collected lupine leaves every 48 h.

Movement experiment design

Each experimental replicate consisted of eight randomly selected beetles from different petri dishes being released in a Plexiglass tray ($70 \times 70 \times 15$ cm) with a Plexiglass lid on top. White cardboard was glued to the exterior sides and floor of the tray to create a homogeneous white background. To prevent beetles from climbing the walls of the trays, Fluon (polytetrafluoroethylene) was applied to the each side edge of the tray to provide a non-toxic physical barrier for these beetles (Chadwick 1971; Dill 1975). Nine 10 cm long wooden sticks were glued upright and equally spaced, to the floor of the trays to allow beetles to vertically migrate. The wooden sticks were covered with white tape to maintain a homogeneous white background. The movement of beetles was recorded using a digital webcam (Logitech C925e) under six different temperatures (i.e. 10, 15, 20, 25, 30 and 35 °C) for three hours. Prior to the experiment, beetles were acclimatised to each temperature treatments in an environmental chamber and starved for 24 h to allow beetles to clear their guts. Temperature was gradually adjusted to each treatment by increasing or decreasing 5 °C every four hours to reduce thermal stress. Environmental chambers were kept on a 14:10 light/dark cycle. Two different light conditions were used to reflect day and night-time. During daytime, the lights in the environmental chambers remained on while during night-time, lights were turned off and UV LED strips were attached to the sides of the tray for the beetles to be recorded on camera. To ensure independence of treatments, different beetles were used in each light condition and temperature. Each temperature treatment had four tray replicates in both light and dark treatments, with a total of 384 beetles being recorded. The first 30 min of recording

were excluded from the analysis to allow beetles to acclimatise to the trays and reduce stress or escape responses. The position of each organism was digitalised to x/y coordinates using the software ImageJ/Fiji (Schneider et al. 2012) and the MtrackJ plugin (Meijering et al. 2012). Videos were broken into two-second frames and each video was analysed for 30 min of recording. The images were saved as 32-bit images, the background was subtracted, and the image was inverted. The brightness/contrast was adjusted to get the best-quality image of the beetles. An example of an analysed video recording is provided in Online Resource 1. Because matching each specific beetles ID to other factors after recordings are over (e.g. sex, age and mating status) is extremely hard, costly, time consuming and likely prone to errors, these factors were not included in the manuscript. Even though these are likely important factors affecting the movement of beetles, the logistics of this experiment, recording videos and specific species traits of *S. gressorius* prevented the inclusion of these factors in the analyses.

Feeding experiment design

Weighed beetles were individually placed in petri dishes with fresh, undamaged, lupine leaves of similar weight (0.095 ± 0.002 g; mean and standard error; $n = 120$) to assess the effects of temperature on the feeding rates of lupine beetles. Beetles were collected and acclimatised to each temperature treatment following the same procedures described above. The control treatment consisted of ten replicates per temperature of weighted lupine leaves without the beetle to account for autogenic change in leaf weight. After 24 h, leaves were re-weighed to estimate the feeding rate and autogenic weight loss. For each temperature treatment, ten beetles with similar length (0.850 ± 0.011 cm, $n = 60$) and weight (0.023 ± 0.000 g) were used.

Data analysis

All analyses, figures and simulations were performed in the R environment, version 3.6.2 (R core team 2019). Before statistical analyses were conducted, the beetles tracks were smoothed by applying a Savitzky–Golay filter with the trajr R package (McLean and Skowron Volponi 2018) to reduce errors associated with short temporal- and spatial-scale sampling (Edelhoff et al. 2016). Steps below or equal to 1 mm were classified as particle detection errors and considered as no movement. For each beetle, mean speed while moving (cm/2 s), total displacement (m), number of flights attempts, total time active (min) and time above ground (min) were calculated.

A Bayesian generalised linear mixed-effect model with the Logit link function was used to evaluate the effects of temperature and light conditions on the flight probability of

beetles. As recommended by Gelman et al. (2008), a Cauchy distribution was chosen as the prior for all parameters with centre and scale parameters set at 0 and 2.5, respectively. Bayesian general linear (i.e. assuming a normal distribution of the error terms) mixed-effects models were used to analyse the effects of temperature and light period on the mean speed, total distance travelled, activity time and time above ground. To account for the non-independence of beetles within each tray, the effect of each recording tray was included as a random factor in all analysis. Because the distribution of beetle's weight was slightly skewed to the right, the \log_e of beetles' weight was used as a covariate in all analyses. Because no information is available on the effects of temperature and light conditions on the movement of *Sitona* beetles, weakly informative *T*-student priors ($\mu = 0$, $\sigma = 2.5$ and $df = 3$) were set for all fixed parameters (e.g. light and temperature) (Bürkner 2017). Bayesian general linear models were also used to analyse the feeding rate of *S. gressorius*. Leaf weight losses were corrected for autogenic weight loss by using linear regressions with the initial leaf weight as a covariate. The \log_e of beetles' weight was also included as a covariate in the feeding rate analysis and temperature quadratic models of the first order were also considered.

Model selection was performed based on leave-one-out cross-validation (LOO) information criteria as described in Vehtari et al. (2017). Models were fit using Markov Chain Monte Carlo (MCMC) methods with a Hamiltonian sampler algorithm. Four independent chains were used in parallel with 2000 initial iterations for adaptation, followed by an additional 5000 iterations. Evidence ratios (ER) were used to test the one-sided hypothesis that parameters were higher or lower than the population mean. All models were fitted with the brms R package (Bürkner 2017).

Stochastic hidden Markov state-switching models (HMM) were used to analyse the movement states of the *S. gressorius*. A HMM is a state space model which assumes discrete hidden states in the data (Patterson et al. 2008). Because the number of flight attempts represented less than 0.2% of the dataset, detecting a "flight" state would be unfeasible. Therefore, only two state models were considered, where the first state represents a "resting" state, with no or reduced movement and less correlated steps, such in the case of when beetles have climbed the wood sticks, while the second state represents a "foraging" or active state, with more correlated and longer steps (Morales et al. 2004; Breed et al. 2009). A wrapped Cauchy distribution was fitted to the turning angles and an exponential, Weibull, or gamma distribution to the step length distribution. Temperature, light conditions, and *S. gressorius* weight were used as covariates. Because including explicit random tray effects is not possible in HMM (McClintock and Michelot 2018), models including the

fixed effect of trays were also considered. Quadratic models of the first order of temperature were also fitted to the data. Model selection was performed based on AIC weights. Pseudo-residuals and simulations of the total distance travelled were used to assess model fit. HMMs were fit with the momentuHMM R package (McClintock and Michelot 2018).

Based on the best fitted HMM, random walk simulations were conducted to calculate a daily diffusion coefficient of beetles. The daily movement of 400 beetles per temperature was simulated, considering a 14:10 light/dark cycle, for 10^5 days. First, the mean squared displacement (MSD) of beetles at a given time t in a two-dimension system is calculated as

$$\langle r^2(t) \rangle = \frac{1}{n} \sum_{i=1}^n \left[(x_i(t) - x_0(t_0))^2 + (y_i(t) - y_0(t_0))^2 \right] \quad (1)$$

where (i) n is the number of beetles; (ii) x_i and y_i are the Cartesian coordinates of beetle i at day t ; and (iii) x_0 and y_0 are the initial position of each beetle. The slope of the linear fit of the MSD in function of time equals to $4D$, where D is the diffusion coefficient (Qian et al. 1991). High-density confidence intervals were calculated by bootstrapping the daily movement of beetles 400 times and refitting the linear model. High-density confidence intervals were calculated with the bayestestR package (Makowski et al. 2019). A Bayesian general linear model was used to estimate the difference between diffusion coefficients following the same procedures described above. Evidence ratios were used to perform contrasts analyses to evaluate differences between parameter estimates.

Results

Flight probability

The best fitted model, based on LOO information criteria, was the additive model of temperature, light conditions, and beetles' weight. Results of model selection analyses are provided in Online Resource 2 (Table 1) and parameters estimates in Online Resource 3 (Table 1). Very strong evidence supports the hypothesis that the flight probability of beetles increases with temperature ($ER > 1,000$) and with beetles' weight ($ER = 109.1$) (Fig. 1). Very strong evidence also supports the hypothesis that the flight probability decreases under dark conditions ($ER > 1000$). Flight initiation was observed at a lower temperature in light conditions (i.e. 20 °C) in comparison to dark conditions (i.e. 25 °C). Random tray effects were also significant ($ER > 1,000$), suggesting strong tray and individual variation.

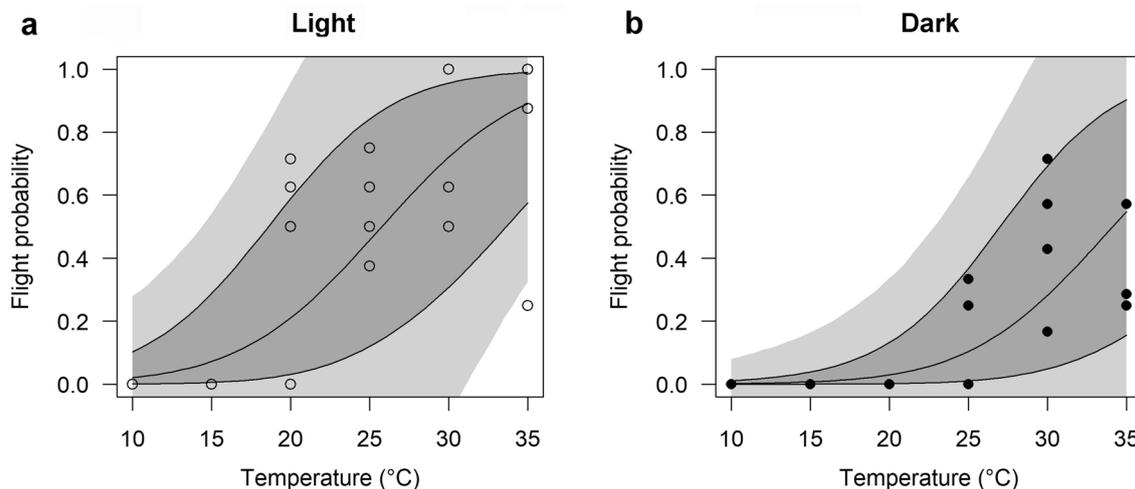


Fig. 1 Effects of temperature on the flight probability of beetles in both **a** light and **b** dark conditions. Each point in the plot represents a tray replicate. Dark and light grey shaded areas represent the 95% fitted and predicted credible intervals, respectively

Mean speed and total displacement

For both total displacement and mean speed while moving, the best model selected was the quadratic model that included the random effect of tray, weight of beetles, temperature, light condition and interaction terms (Online Resource 2, Tables 2 and 3; Online Resource 3, Tables 2 and 3). On average, beetles exposed to light conditions and higher temperatures travelled longer distances and had a higher mean speed while moving (Figs. 2 and 3). Strong evidence supports the hypothesis of a random tray effect for both mean speed and total distance travelled ($ER > 1000$),

suggesting strong tray and individual variation. For the total displacement of beetles, evidence ratios also indicated strong evidence to support the interaction effects between temperature and light conditions ($ER = 7.6$ for temperature and light conditions, and $ER = 31.6$ for temperature² and light conditions). These results indicate that an increase in displacement at higher temperatures under light conditions increases at a faster rate in comparison to dark conditions. Regarding the mean speed of beetles, strong evidence also supports the interaction effects between temperature and light conditions ($ER = 60$ and 116 for temperature and light conditions, and temperature² and light conditions, respectively).

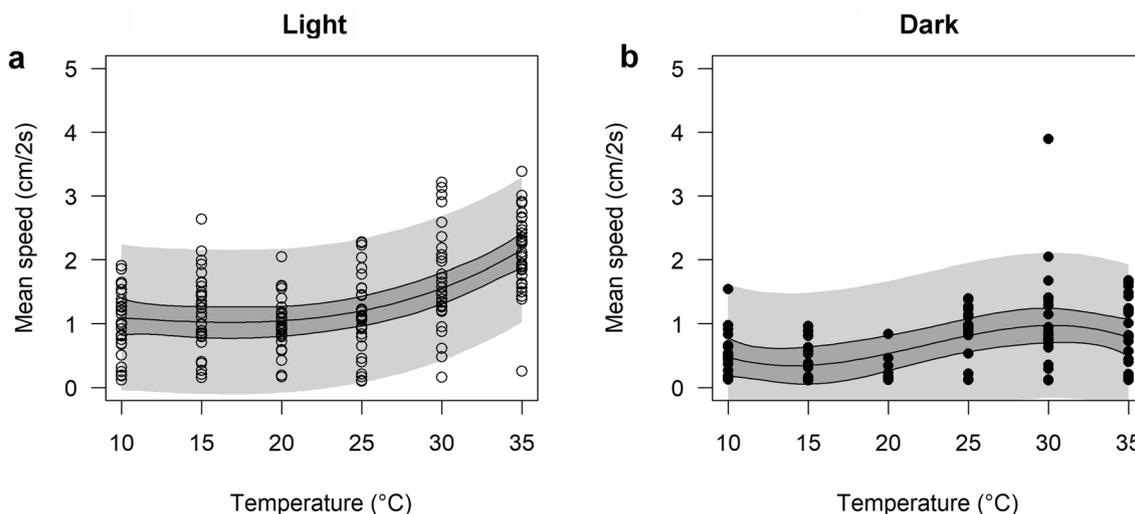


Fig. 2 Effects of temperature on the mean speed while moving (cm/2 s) of beetles in both **a** light and **b** dark conditions. Each point in the plot represents one organism. Solid dark line represents the

fitted model for the average organisms’ weight. Dark and light grey shaded areas represent the 95% fitted and predicted credible intervals, respectively

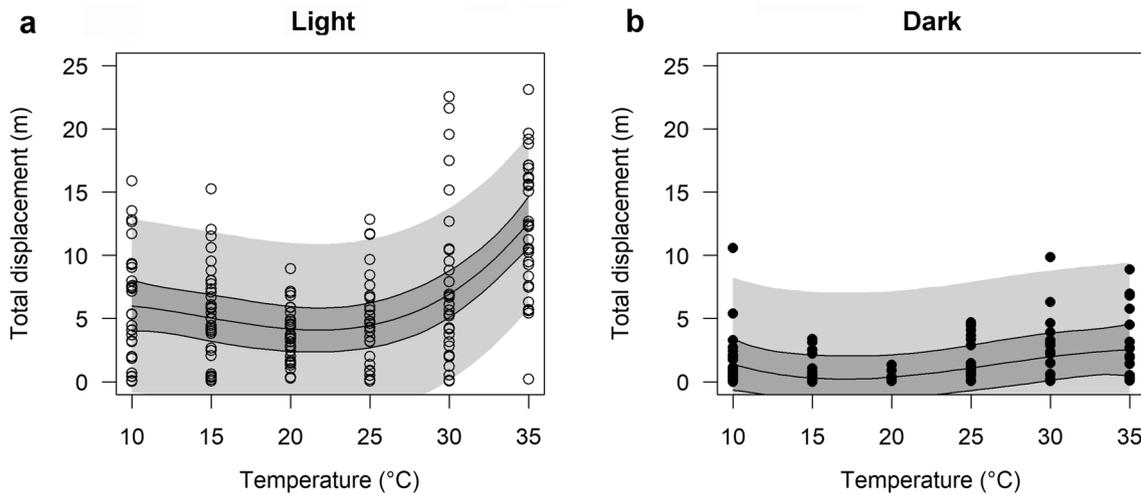


Fig. 3 Effects of temperature on the total displacement (m) of beetles in both **a** light and **b** dark conditions. Each point in the plot represents one organism. Solid dark line represents the fitted model for the average organisms' weight. Dark and light grey shaded areas represent the 95% fitted and predicted credible intervals, respectively

Activity time and vertical migration

The best fitted model evaluating the activity time of beetles was the quadratic model of temperature, light condition, and interaction terms (Online Resource 2, Table 4; and Online Resource 3, Table 4). Evidence ratios indicate strong random tray effects ($ER > 1000$), a positive effect of beetles' weight ($ER = 33.2$) and interaction terms of temperature and light conditions ($ER = 13.0$ for temperature and light conditions, and $ER = 18.6$ for temperature² and light conditions). On average, beetles exposed to light conditions spent 14.0 ± 7.1 min (standard deviation) being active, while in

dark conditions, beetles only spent 4.0 ± 5.4 min. Beetles tended to spend less time being active at intermediate temperatures (Fig. 4). However, beetles in the day condition tended to move less at slightly higher temperatures in comparison to beetles exposed to dark conditions. Regarding the vertical migration of beetles, the best model selected only included the random effect of tray (Online Resource 2, Table 5; and Online Resource 3, Table 5). This result suggests that both temperature and light conditions had no clear effect on the vertical migration of beetles (Online Resource 4). However, strong evidence supports the hypothesis of a random tray effect ($ER > 1000$), indicating strong tray and

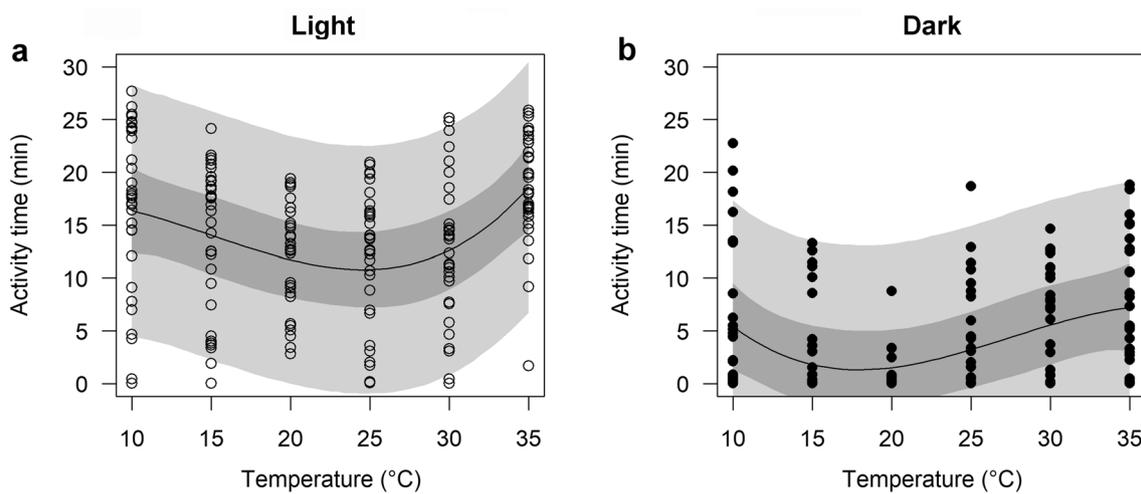


Fig. 4 Effects of temperature on the activity time (min) of beetles in both **a** light and **b** dark conditions. Each point in the plot represents one organism. Solid dark line represents the fitted model for the average organisms' weight. Dark and light grey shaded areas represent the 95% fitted and predicted credible intervals, respectively

individual variation. The estimated mean population time above ground was of 16.73 min.

Feeding rate

The quadratic model, with the additive effects of beetles' weight, was the best model selected based on LOO information criteria (Online Resource 2, Table 6). There is strong evidence that both temperature and organism weight had a positive effect on the feeding rate of beetles ($ER > 1000$ and 99, respectively), with the highest feeding rate occurring at 35 °C (Fig. 5; Online Resource 3, Table 6).

Hidden Markov models and diffusion estimates

Based on the AIC weights, a Weibull distribution provided the best fit to the step length distribution. The best fitted model was the quadratic model of temperature, with light condition and tray as covariates (Online Resource 2, Table 7). Beetles in the resting state had reduced mobility and less correlated steps in comparison to the active state (Fig. 6a, b). Beetles tended to stay in the more active state at higher temperatures and less active at intermediate temperatures, around 20 °C (Fig. 6c). Beetles also were more likely to remain in a more active state under light conditions (Fig. 6d). The stationary probability of remaining in each state was also highly variable depending on the tray (Fig. 6e), indicating high individual and tray variation. Evidence ratios showed strong evidence in favour of the hypothesis that the mean diffusion coefficient between all temperature treatments is different from each other

($ER > 1,000$ for all contrasts). The lowest diffusion coefficient was observed in the 20 °C treatment ($5.76 \pm 0.42 \text{ m}^2 \text{ day}^{-1}$, 95% credible interval), while the highest diffusion rate was observed in the highest temperature treatment ($7.8 \pm 0.48 \text{ m}^2 \text{ day}^{-1}$) (Fig. 6f).

Discussion

Understanding how insect pests move and disperse is essential for developing effective pest control strategies (Mazzi and Dorn 2012). Temperature and light are two key abiotic factors which usually co-affect herbivorous insect movement (Niesenbaum and Kluger 2006; Bale et al. 2002; Lemoine et al. 2013; Niziolek et al. 2013). With the aid of video recording techniques, this work shows that—with exception of the vertical movement—both temperature and light conditions affected all movement metrics of *S. gressorius* evaluated in this work and, consequently, the daily diffusion coefficient. Overall, beetles tended to be more active and move at higher speed in higher temperatures and in light conditions. However, beetles were generally less active at intermediate temperatures in both light conditions (Figs. 3, 4 and 6c). Furthermore, beetles also had a higher flight probability at higher temperatures.

Environmental conditions and metabolic requirements necessary for flight initiation vary among Coleoptera species (Taylor 1963; Jones et al. 2019). However, the results of this work are consistent with studies of five other *Sitona* species, where few flight attempts were made below 20 °C (Stein and Rezvani 1973). Also, flight of the *S. lineatus* was found to be triggered at 12.5 °C in individuals and in most of the population at 16° C in the field (Hamon et al. 1987). However, the highest flight probability of the *S. gressorius* occurred at a higher temperature than other *Sitona* species (Stein 1972). Nevertheless, a general decrease in flight activity at a higher temperature was not clearly observed in this work. Therefore, a higher experimental temperature is needed to determine the upper temperature flight threshold for *S. gressorius*, which is expected in ectotherms (Sunday et al. 2014; Jones et al. 2019). For instance, the proportion of *S. lineatus* flying in the field decreased above 35 °C (Hans 1959). Under dark conditions, beetles also had lower flight probabilities (Fig. 1). As the flight probability of *S. lineatus* also increases with light intensity (Hans 1959), this suggests that most flights of *Sitona* species occur during the day.

Even though no flight attempts were observed at lower temperatures, *S. gressorius* was still able to walk at the lowest temperature treatments. Similarly, Anderson (1938) found that *S. gressorius* could walk at temperatures as low as 2 °C. Also, movement of the Warren root collar weevil was observed at temperatures as low as 6 °C in the field (Machial et al. 2012). This is likely because flight

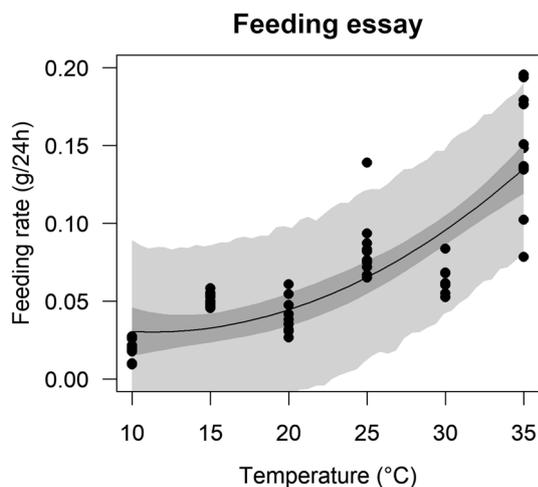
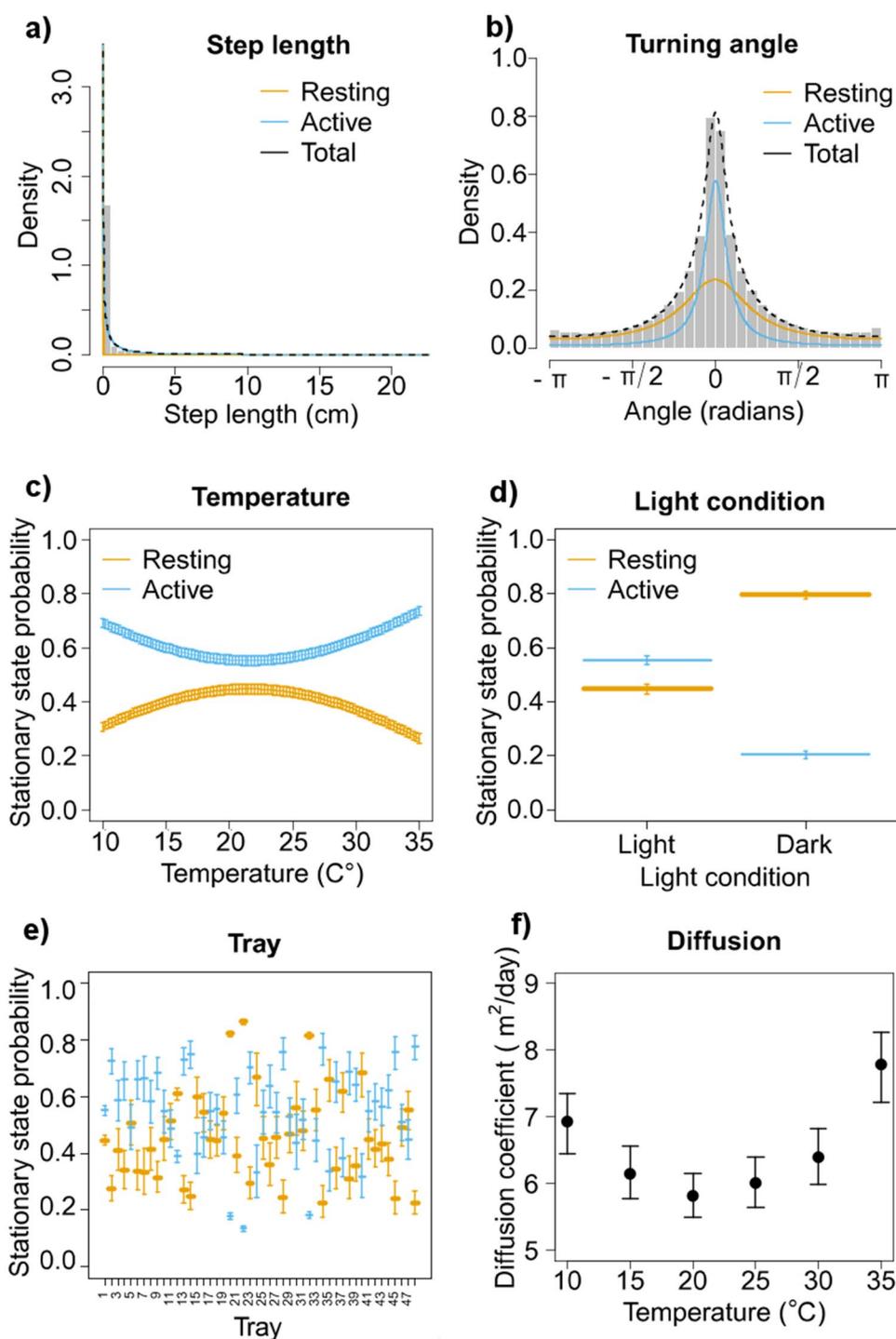


Fig. 5 Effects of temperature on the feeding rate (g/24 h) of beetles. Each point in the plot represents one beetle. Solid dark line represents the fitted model for the average beetle' weight. Dark and light grey shaded areas represent the 95% fitted and predicted credible intervals, respectively

Fig. 6 Results of the best fitted 2-state hidden Markov model: **a** histogram of the step length distribution and fitted Weibull distributions for the resting (orange) and active (blue) state; **b** histogram of the turning angle distribution and fitted wrapped Cauchy distribution for each state; **c** estimated stationary state probabilities and 95% confidence interval as a function of temperature under light conditions; **d** estimated stationary state probabilities and 95% confidence interval for light conditions under the mean temperature; **e** estimated stationary state probabilities and 95% confidence intervals for the effects of tray under light conditions and mean temperature; and **f** estimated diffusion coefficients (m^2/day) and 95% high-density confidence intervals



requires higher body temperatures compared to walking (Hans and Thoesteinson 1961; Nielsen and Jensen 1993). As expected, increases in temperature lead increased beetle movement speeds, but at different rates in light and dark conditions (Fig. 2). Previous work on *S. gressorius* also reports an increase in beetles' speed as a function of increasing temperature within the same range reported in this work (Andersen 1938).

Even though beetles moved slower in the lower temperature treatments, total displacement was lowest at intermediate temperatures of around 20 $^{\circ}\text{C}$ (Fig. 3). Similar results were also reported by Augustin et al. (2020) who found that the total displacement of the *Anaphes listronoti*, a parasitoid wasp, was lower at intermediate temperatures. Under low and high temperatures, biochemical adaptations can compensate for thermodynamic effects on performance (Angilletta

et al. 2010). Therefore, this could be interpreted as behavioural mechanisms to escape unfavourable conditions and consequently increase in activity despite a thermodynamic constraint imposed upon them (Benard and McCauley 2008; Abram et al. 2017). However, these plastic responses may be limited at extreme low and high temperatures as movement may be physiologically inhibited (Drury et al. 2016). Because movement was measured at a small temporal and spatial scale, it is likely that the observed increase in movement under low temperatures may be unsustainable for longer periods of times (i.e. weeks and months). Species always optimise the cost–benefit ratio for movement (Goossens et al. 2020), which can lead to an increase in movement in the short term but an overall reduction in movement in the long term. Therefore, even though video recording experiments allow precise movement measurements, they could also lead to bias estimates of the daily diffusion coefficients at extreme temperatures.

In many cases, the climbing behaviour of beetles presents a diel periodicity (Cram and Pearson, 1965; Wen et al. 2005), with temperature being a key factor in initiating climbing behaviour (Blau and Stinner 1983). In the case of *Sitona* species, both *S. cylindricollis* and *S. lineatus* exhibit negative geotaxis (Hans 1959; Hans and Thoesteinsson 1961). Also, the proportion of *S. lineatus* found on host plants in the field decreased as temperature increases (Hans 1959). However, temperature and light conditions had no clear effect on the vertical migration of the *S. gressorius* in this study. Nevertheless, this may be due to use of wooden sticks in laboratory conditions, which do not provide any thermal or light regulation control (e.g. shadow from leaves) or food resources, which would be expected in field conditions. However, the use of host plants in video recording experiments is challenging as it hinders the visual detection of beetles in the tray.

There was also a significant individual variation in all other movement metrics evaluated in this work, which is regarded a normal occurrence in Coleoptera species (Taylor 1963; Shaw, 2020). In the literature, there is considerable intraspecific variation in flight and movement of *Sitona* species, which is consistent with the results from this study (Stein and Rezwani 1973; Landon et al. 1995). For instance, there is great intra- and interspecific variation in the flight distance capabilities of Curculionoidea where most beetles usually fly short distances and very few fly long distances (Ávalos et al. 2016). Many factors could explain intraspecific variation in the movement of individuals, such as sex, age, internal state and boldness (Palmer et al. 2014; Shaw 2020). For instance, heavier beetles were more prone to flight, being more active and moving at a higher speed. This is also consistent with what Hirt et al (2017) found for other invertebrate herbivores. In this experiment, beetles' weight encompasses many different individual traits such as

sex, with females being heavier than males, age and internal status. As previously stated, sex and age could not be included in this study due to the logistics of camera recording experiments (i.e. matching the specific beetle ID to other factors after the recordings are over) and specific traits of *S. gressorius*. Because organisms were randomly sampled and assigned to each treatment, however, any confounding effects from these factors would have been distributed as random errors and not affect our conclusion. Disentangling the effects of such individual traits in future experiments might also help our understandings of mechanisms behind individual variation in *Sitona* beetles.

As predicted, a positive relationship was observed between temperature and feeding rates. As temperature increases, metabolic demands of beetles also increases (Brown et al. 2004; Lemoine et al. 2014). However, there is substantial intra- and interspecific variation in the effect of temperature on herbivore consumption with increasing temperatures. Some species increase the consumption with increasing temperature while other species reduce their consumption rates beyond a certain optimum temperature (Lemoine et al. 2014). Landon et al. (1995) found that the temperature threshold of 12 °C led to a triggering of feeding throughout a *S. lineatus* population, with the maximum feeding taking place at 19 °C, although there was significant individual variation in the temperature required to initiate feeding. Calkins (1969) also reported that *S. cylindricollis* adults had the highest feeding rates at 24 °C (Calkins, 1969). In the case of the large lupine beetle, a higher temperature treatment would be necessary to identify an upper temperature threshold for feeding inhibition. One should also note that an increase in temperature does not necessarily mean a reduction in crop yield from increased feeding rates, as increasing temperatures may also have an influence on legume crop yield and growth (DeLucia et al. 2012; Jamieson et al. 2012). Therefore, future research which includes plant–insect interactions with temperature increase on crop yield may better elucidate the co-effects of temperature.

Because this work was conducted under controlled laboratory conditions, it is important to note that other important environmental factors, such as biotic cues (Kiedrowicz et al. 2017), wind speed, solar radiation (Stein and Rezwani 1972; McKibben et al. 1991), population size (Shaw 2020), and predation pressure (Poethke et al. 2010) may also affect the movement and dispersal of organisms. Furthermore, the *S. gressorius*'s movement space in this experiment was restricted to a tray, and consequently the limited movement and flying space are not reflective of field conditions. Even though video recording experiments provide a precise method for measuring movement of beetles in the short temporal and spatial scale, they can also lead to both under- or overestimates of the daily diffusion coefficient of beetles at extreme low and high temperatures. Therefore, long-term

field experiments on the movement of insect pests are necessary to test this hypothesis. Despite the limitations, this laboratory experiment offers an increased control of selected environmental conditions and enhanced statistical power that cannot be replicated in the field.

Conclusion

This study set out to determine how temperature affects the movement, diffusion and feeding rates of the *S. gressorius*, an agricultural pest. Results demonstrate that the *S. gressorius* exhibit nonlinear responses in function of temperature when it comes to movement and diffusion. It also shows that the movement and feeding rates of beetles can present different relationships in function of temperature. The temperature-dependence of movement observed, has several important implications. As temperatures increase, there will be an increased probability of movement and diffusion of beetles and, consequently spread of pests in agricultural landscapes. From a potential crop damage perspective, this is even more worrisome considering that increase in temperature also increases the feeding rate of beetles. Secondly, the results show that assuming a single diffusion coefficient in spatially explicit models may both under or overestimate the spread of pests. This paper provides a low-cost method to estimating insects' pest movement and diffusion and contributes to the understanding of pests' dispersal in a warming climate planet.

Author contribution

All authors conceived and designed the research. MK and SH: conducted the experiments. MK: analysed the data. SH, MK and CN: wrote the manuscript. All authors read and approved the manuscript.

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Data availability The datasets generated in this study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethical approval The experiment was evaluated as essential and ethically and scientifically justified, and is thus in line with the EU regulations on animal experimentation (Directive 2010/63/EU).

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