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A general model of the thermal constraints on the world's most destructive locust, *Schistocerca gregaria*

Running head: Thermoregulation in locusts

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Abstract

All terrestrial ectotherms are constrained to some degree by their thermal environment and the extent that they can behaviorally buffer variable thermal conditions. New biophysical modelling methods (NicheMapR) allow the calculation of the body temperature of thermoregulating animals anywhere in the world from first principles, but require detailed observational data for parameterization and testing. Here we describe the thermoregulatory biology of marching bands of the desert locust, *Schistocerca gregaria*, in the Sahara Desert of Mauritania where extreme heat and strong diurnal fluctuations are a major constraint on activity and physiological processes. Using a thermal infrared camera in the field, we showed that gregarious nymphs altered the microhabitats they used, as well as postural thermoregulatory behaviors, to maintain relatively high body temperature (nearly 40 °C). Field and laboratory experiments demonstrated that the preferred body temperature accelerated digestive rates. Migratory bands frequently left foraging sites with full guts before consuming all vegetation and moved to another habitat before emptying their foregut. Thus, the repertoire for behavioral thermoregulation in the desert locust strongly facilitates foraging and digestion rates which may accelerate developmental rates and increase survival. We used our data to successfully parameterize a general biophysical model of thermoregulatory behavior which could capture hourly body temperature and activity at our remote site using globally available environmental forcing data. This modelling approach provides a stronger basis for forecasting thermal constraints on locust outbreaks under current and future climates.

Keywords: body temperature, desert locust, general biophysical model, thermal infrared camera, NicheMapR, thermoregulatory behaviors

Introduction

In ecology there is an urgent need to develop better forecasting capacities so that we can anticipate how species of conservation or economic importance will respond to environmental change (Dietze 2017). Pest insects are one of the most economically important groups of species requiring forecasting capacity. Any efforts to predict environmental constraints on the behavior, distribution and abundance of terrestrial ectotherms such as insects must adequately capture how environment and behavior interact to determine body temperature, because virtually all biological processes are temperature dependent (Josephson 1981, Bennett 1985, Angilletta 2009). This is a significant challenge due the complex, nonlinear responses of heat exchange between organisms and their microclimates, but it is possible to compute such responses from first principles using the techniques of biophysical ecology (Porter et al. 1973, Gates 1980, Kearney and Porter 2004, 2009, Buckley 2008).

Crucial to the development of temperature-explicit predictive models of organisms is the inclusion of behavioral responses. The body temperature (T_b) of ectotherms is largely determined by environmental temperatures; however, behavioral thermoregulation, such as shuttling between sun and shade and altering posture (Chappell and Whitman 1990, Heinrich 1993), often allows ectotherms to maintain physiologically suitable T_b even when thermal conditions in their habitats are subject to variation (Heinrich 1999). Indeed, behavioral thermoregulation may buffer many of the negative effects of extreme thermal conditions (Kearney et al. 2009, Huey et al. 2012) in parallel to plastic and evolutionary adjustments in physiological heat tolerance (Cloudsley-Thompson 1975, Heinrich 1993, Araújo et al. 2013, Hoffmann et al. 2013).

Although the computational tools now exist for behaviorally explicit modelling of the field body temperatures of terrestrial ectotherms (e.g. Kearney and Porter, 2019), they require detailed field data for model parameterization and testing. In this study we report on an extensive field study of the field thermoregulatory behavior of one of the world's most destructive insects, *Schistocerca gregaria* (Forskål, 1775), living in the Sahara Desert - one of the world's most extreme thermal environments. We focus on how thermoregulatory behavior in this species is likely to affect its ability to feed and avoid predation and use our data to develop and test a general predictive model of its field body temperature.

The desert locust, *S. gregaria*, inhabits arid and semi-arid areas, where desert air temperatures cycle on a 24-hr period, potentially ranging from below freezing to over 40 °C in a single day (Symmons and Cressman 2001, Ward 2009, Maeno et al. 2016, 2019). The habitats of this species are patchily distributed and are frequented temporally depending on the amount and timing of erratic rain (Tucker et al. 1985, Sword et al. 2010, Showler 2019). Locusts exhibit density-dependent phase polyphenism. Specifically, solitarious individuals occur at low densities and are cryptic while gregarious ones occur at high densities, are attracted to each other, and move long distances in groups (Pener and Simpson 2009, Cullen et al. 2017, Ayali 2019). This collective movement is called “marching” in nymphs and “swarming” in flying adults (Ellis and Ashall 1957, Uvarov 1977).

To our knowledge, the gregarious nymphs of *S. gregaria* are the only ectotherms that diurnally march on the hot ground of the Sahara Desert, travelling up to 1.5 km per day (Ellis and Ashall 1957). Large marching bands deplete food resources quickly, necessitating frequent migration to new food resources. Diurnal migration in the Sahara Desert by walking or jumping is likely risky and energetically expensive for a variety of reasons. First, operative temperatures in open ground within their habitat may become lethal at midday, necessitating behavioral, physiological, and morphological responses to avoid overheating. Second, marching on hot ground increases metabolic and water loss rates, requiring the locusts to refuel efficiently or conserve energy and water resources during migration. Third, digestion and its nutritional outcome is extremely sensitive to body temperature (Miller et al. 2009b, Coggan et al. 2011, Clissold et al. 2013), enhancing the importance of thermoregulatory responses. Fourth, migratory bands are visually easy to detect by predators, which may lead to special anti-predatory strategies during migration. Predation risk also increases the importance of behavioral thermoregulation during cool mornings when anti-predatory behaviors, such as jumping, are constrained by low temperatures (Maeno et al. 2019).

Much work has been done on the adaptations of gregarious desert locust nymphs to their physical and predatory environments, especially from laboratory studies (Maeno et al. 2013a). However, detailed field studies remain limited, especially where multiple limiting factors are jointly considered, and predictive models are lacking. Thus, in this study we aimed to collect detailed field observations of wild migratory bands of gregarious nymphs in their natural habitat in the Sahara Desert of Mauritania to jointly consider the hypotheses that: 1) the gregarious nymphs of *S. gregaria* have physiologically high heat tolerance and avoid overheating through certain behaviors associated with microhabitats, 2) they feed frequently, 3) they maintain relatively high *T*b to accelerate digestive performance when heat is available, 4) predation and parasitism are low due to high temperatures, and 5) gregariousness (i.e., aggregations) function to increase *T*b. We then used our data to develop a biophysical model of these responses to enable us to generalize the thermoregulatory response of *S. gregaria* through space and time and thereby enhance our predictive capacity of the thermal constraints on locust outbreaks.

Material and methods

Study area and climate

Mauritania, in West Africa, is an important area for desert locust outbreaks (Ould Babah

1997, Babah Ebbe 2010, Piou et al. 2017). The study site was 5 km × 5 km in size (19°23′N, 14°35′W) and was located near Akjoujt, northwestern Mauritania. The area is a vast plain with a variety of cover types, including dunes and playa. Sparse, low-growing desert annuals (grasses, herbs, vines, etc.) grew between the bushes and trees and plants were patchily distributed at the study site. *Calotropis procera* (Asclepiadaceae), *Acacia tortilis* (Fabaceae), *Maerua crassifolia* (Capparaceae), and *Boscia senegalensis* (Capparaceae) were frequently used as night-roosting plants (Maeno and Ould Babah Ebbe 2018). We conducted field surveys in November 2016. At this time, rain was scarce and the desert annuals were still mostly green, but began to dry out at the end of the study. Sunrise and sunset occurred at about 07:10 and 18:30 local time, respectively.

Study animals

We studied wild late instar (4th and 5th) nymphs of *S. gregaria*. The body length of the

5th instar nymphs was 43.04 mm ± 0.60 ($n = 50$) for females and 40.66 mm ± 0.60 ($n = 50$) for males. Near the survey site, group oviposition was observed approximately one month earlier (i.e., October), and most hatchlings had black bodies, which was typical coloration of the gregarious-phase state (Uvarov 1966, 1977). Almost all individuals had a yellow background with black patterns, and showed diurnal marching behavior, which was typical of the gregarious-phase state. Ground population densities ranged from 0 to more than 5,000 individuals/100 m^2. Hence, the locusts at our study were highly aggregated and patchily distributed, with dense locust aggregations forming in some areas. This type of distribution and behavior were indicative of the gregarious-phase (Uvarov 1977).

Thermoregulatory behavior

On November 10–19 and 24–27, 2016, at our study site, we surveyed T_b at various times of the day. In the field, we observed that most nymphs within a group behaved synchronously, but many individuals displayed different behaviors, including feeding, marching and resting, as reported by Ellis and Ashall (1957). Probably, these behaviors were caused by intraspecific differences in physiological states, especially hunger levels. We distinguished 12 behaviors, including thermoregulatory behaviors, within the daily behavior cycle classified according to Chappell and Whitman (1990), and measured the associated *T*b for each (Fig. 1). These behaviors were: 1), night-roosting, 2) basking on night-roosting plants, 3) descending from night-roosting plants, 4) first walking on the ground, 5) basking on the ground during the morning (locusts remained stationary on the ground and their longitudinal body axis was perpendicular to the sun’s rays, maximizing the total body surface area exposed to direct solar radiation) (07:00–12:00), 6) feeding, 7) marching, 8) stilting on the ground (extending its legs and lift their body from the ground and their body axis was parallel to the sun’s rays), 9) remaining under shade, 10) perching on plants, 11) basking on the ground during the afternoon (12:01–19:00), and 12) ascending into night-roosting plants. During the field survey, if any predation occurred, we recorded the predator and any potential predators.

Measurements of body temperature (T_b)

Obtaining T_b measurements of grasshoppers is technically difficult (Chappell and Whitman 1990). Direct measurements must be made quickly using fine-gauge thermocouples, because the small size and low heat capacity of grasshoppers lead to rapid changes in T_b when the animals are transferred to a different thermal environment for measurement. Free-living nymphs of *S. gregaria* are very sensitive to an approaching observer and can escape quickly (Maeno et al. 2013b). To overcome these problems, we adopted two techniques: First, preliminary trials showed that if the observer (always KOM) approached stationary resting locusts very slowly and silently, nymphs remained in position without fleeing. Second, instead of fine-gauge thermocouples, we used thermal infrared images, thus avoiding the need to capture or disturb the insects (Hunt et al. 2011). To take thermal images as close to free-living nymphs as possible, two additional methods were used, depending on whether locusts were stationary or moving. When locusts were stationary, the observer walked very slowly towards the locust until they were 2–3 m away. When migratory bands actively marched, the observer positioned himself in the predicted direction of the front of the head (more than 20 m), and waited for them to approach, to minimize disturbance. When they passed in front of the observer, thermal images were taken. Thermal images were taken by a handheld thermal imaging camera (FLIR E8, FLIR Systems, Inc.), with 320 × 240 pixels (9 Hz refresh-rate). This camera measured infrared wavelengths at a range of 7.5–13 μm. All images were taken from more than 50 cm away from the target insects and the emissivity of the camera was set to 0.95 to view locusts. To compensate for low resolution images, high resolution images were also taken using a digital camera (WG-5, Ricoh Imaging Company, Ltd) to confirm the location and posture of the locust. Each trial disturbed the locusts at the end of recording; thus, each group was recorded just once. Transects were not used in this study; instead, we randomly walked around the study area to find locusts, because gregarious nymphs actively march and frequently change direction and habitats. This procedure was repeated for 255 randomly chosen locusts over a period of 13 days. Locusts sometimes escaped before recordings were completed. In these instances, we only recorded the type of behavior and time, to examine the relationship between background temperature for substrate (T_s, see below) and occurrence of behaviors.

We used a thermo-hygro recorder (TR-72wf, ONDOTORI, Tokyo) to record air temperature and humidity in the shade at 50 cm above the ground. A thermo recorder probe (TR-71nw, ONDOTORI, Tokyo) was also placed above the sandy ground to record the surface temperature of the surface of sunlit soil every 10 min (Fig. 2a). To examine the interaction between behavioral repertoires for each recording and these environmental factors, the recordings of air temperature and humidity by loggers within 5 mins were used. Also, to assess the range of T_s available to *S. gregaria* throughout the day, we measured ground temperature in shade of spreading shrubs and medium-sized trees, *C. procera*, from 09:00 to 18:00 on November 12, 2016.

Thermal imaging

FLIR Tools software (FLIR Systems, Inc.) was used to extract surface temperature data from thermal images using methods modified from Vogel et al. (2016), specifically extracting the temperature value of the pixel at either the center of aggregating locusts (at least five locusts) or as the one closest to the thorax of an individual as possible. For measurements of individuals based on pictures where nymphs could be visible, the mean values of three insects were used (T_b). To compare these values against ground surface temperature, open ground within 2 m of the targeted locusts was also extracted. When locusts roosted on trees at night, the surface of the tree within 50 cm of the locust was extracted as the background temperature. Mean values of surface temperature within the selected area were used (T_s).

Feeding patterns

Gregarious nymphs mainly foraged during the daytime (Kennedy 1939). To examine the interaction between feeding patterns and thermoregulatory behavior, including night-roosting (06:00–09:00), stilting (11:00–15:00), marching (11:00–17:30), and group-basking (16:00–17:00), nymphs displaying one of these behaviors were dissected and the state of their foreguts was recorded. The foreguts were grouped into five size categories: 0), empty, 1) little, 2) full, 3) extended, and 4) fully extended, based on methods modified from Ellis (1951). The last three categories were considered to be actively digesting, while the first two were considered to be mostly digested. Size 0 and 1 were almost similar in appearance, but the contents of the foregut was recorded based on dissection.

Effects of preferred body temperature (T_b) on digestive rate under field conditions

The food processing rate (i.e., rate of passage) is used as an indirect indicator of the overall digestive rate (Dorcas and Peterson 1997). To examine whether preferred T_b during the daytime accelerated the digestive rate, marching last instar nymphs collected just after feeding in the field were housed in a nylon mesh cage (length × width × height: 100 cm × 50 cm × 50 cm). These nymphs were given no food and were exposed to either direct sunlight or shade. Their foregut size was recorded by dissecting 10 females and 10 males every 30 mins from 13:00 till 15:00 on November 24, 2016. Foregut size was categorized according to the criteria established here. At the same time, we documented the presence of any visible parasite inside the body.

Effects of preferred body temperature (T_b) on digestive rate under laboratory conditions

The effects of preferred T_b on the digestive rate was also examined under laboratory conditions, based on methods modified from Baines et al. (1973). The *S. gregaria* nymphs used in this study were issued from a line maintained by the CBGP (Montpellier, France). Groups of approximately 100–200 individuals were placed in large cages (40 × 40 × 50 cm) at 32 ± 1°C, with a 12:12 h light:dark photoperiod and 20–50% relative humidity. They were fed wheat seedling and wheat bran *ad libitum*. Newly molted fifth-instar nymphs were removed from the stock cages each day and were kept in a small cage (20 × 20 × 35 cm) in groups not exceeding 40 insects per cage. Insects were maintained in the same rearing room. Only males that were 3 to 4 days old were used. The locusts were kept for 24 h without food, so that the whole gut was almost empty. Then, food (wheat seedling) was introduced and the locusts were watched until they stopped feeding. The remaining food was removed from the cages to prevent further feeding. Typically, the end of feeding was determined as the time when the locusts moved away from the food source and rested for a period by climbing the wall of the cages. After the test meal (within 25 min of introducing food), all insects were subjected to one of the three treatments. Specifically, they were placed in cages with (1) a heat lamp (100 W) at 32 °C, (2) no lamp at 32 °C, or (3) 20 °C with no lamp. In the first case, locusts were able to thermoregulate freely in the cage by moving closer to or further from the lamp. Locusts were killed at -20 °C after 1 h to examine their digestive rate. Locusts were dissected and only the foregut was weighed, because the midgut and hindgut does not significantly vary in migratory locusts, *Locusta migratoria* (Baines et al. 1973). As a control, the foregut of starved locusts (24 h) and just fed locusts were also examined. A total of 20 insects were examined for each treatment.

Statistical analysis

To evaluate the effects of 12 different behaviors on T_b and the effects of body temperature on the weight of the foregut, Tukey–Kramer HSD tests were conducted. To determine differences in temperature for T_s and T_b when they displayed either warming-up (group-basking), cool-down (stilting, remaining in shade, and perching on plants), marching, or feeding, we used the Wilcoxon rank-test. Statistical analyses were conducted using the software package R, version 3.5.0 (R Development Core T. 2018) and JMP (SAS Institute, Cary, NC, USA).

Modelling microclimates, body temperature and thermoregulatory behaviors

Biophysical modelling was done using the NicheMapR package (v. 2.0) which comprises a microclimate model (Kearney and Porter 2017) and an ectotherm model (Kearney and

Porter 2019). The microclimate model was forced with the global gridded weather data obtained from the National Centers for Environmental Prediction (NCEP) reanalysis dataset through the RNCEP package (Kemp et al. 2012). These data are at 2° resolution of and were downscaled using the microclima package via the NicheMapR function ‘micro_ncep’, as described in detail in Kearney et al. (2020). All default parameters of the ‘micro_ncep’ function were used except that an organic cap was not simulated at the surface (parameter ‘cap’ = 0, i.e. bare sand) and the longwave downwelling radiation was computed as a function of screen temperature, relative humidity, shade and cloud cover rather than directly using the NCEP longwave radiation. Microclimates were simulated for the year 2016 at the site (longitude/latitude 19.38023, -14.58222) and the local height simulated was 1 cm to approximate the midpoint of a standing locust.

The parameters of the ectotherm model were obtained from the present study and presented in table 2. By default the ectotherm model attempts to find a suitable environment for activity by first altering posture (adpressing to the substrate and orienting perpendicular to the sun’s rays when cool, orienting parallel to the sun’s rays when too hot), then raising core temperature above the preferred temperature to as high as the maximum foraging temperature, then seeking shade. To capture the fact that the locust retreats to trees at night, we overwrote the local 1 cm height values of air temperature, relative humidity and wind speed to that of the reference height (2 m) for nighttime hours, and altered the sky temperature to the shaded value, in the microclimate inputs prior to running the ectotherm model.

We compared the microclimatic information with the recorded temperature in the field as well as the prediction of the model of body temperature and behaviors with the field observations of November 2016. As the model predicted only basking and foraging activities we simplified the field data to 3 categories: inactive (night roosting, basking on plants on early morning and descending), basking (morning and afternoon group basking) and foraging (other behaviors).

Once the ectotherm model was verified against field observation from Akjoujt we explored the prediction of this model for the full 2016 year for the study site as well as for a site in Morocco in the Draa valley near Fam el Hisn (28°39’N, 8°52’W). The Draa valley is frequently hosting solitarious desert locust (some adults were observed at these coordinates in October 2016), and reproduction typically occurs in April to June (Piou et al. 2017); but no gregarious nymphs were observed since 2005 at this site.

Results

Daily thermal regime

Temperature and humidity varied greatly throughout each day in the Sahara Desert (Fig. 2). Following sunrise, air and ground temperature increased, while humidity decreased. Locusts experienced dynamic daily fluctuations in ambient temperature (mean, 26.7 °C; range, 14.3–38.7 °C) and ground temperature (mean, 28.7 °C; 11.5–56.4 °C). This wide range of thermal conditions exceeded the preferred temperature of species and low-temperature thresholds for certain behaviors (see Discussion). Relative humidity also varied greatly within a day (mean, 25.5 %; range, 6.6–60.3 %). Figure 3 shows an example of temperature variation over the course of a day in the field. When solar radiation was available, the range of available temperatures noticeably increased.

Relationship of daily cyclical behavior to T_b

Figure 4 and table 1 present an overview of the humidity, mean air and background temperature, and the surface body temperature of nymphs displaying various thermoregulatory behaviors. Locusts altered their behavior throughout the day, marching and feeding in a cyclical manner. At night and dawn, when the temperature was coolest, locusts roosted in trees and larger bushes. Locust T_b was very close to T_s before dawn, suggesting no scope for thermoregulation (Figs. 1a & 4; Tukey–Kramer HSD tests, $P >$ 0.05). Following sunrise, the locusts moved to the eastern side of the night-roosting plants (Fig. 1b), descended to the ground, and formed dense aggregations (Fig. 1c). Dense carpets of locusts on patches of bare ground (group-basking) were observed, with individuals warming their bodies via solar basking (Fig. 1b, c & d). Their T_b was higher than the T_s (Figs. 4 & 5a; Tukey–Kramer HSD tests, $P < 0.05$). They began to feed (Fig. 1e) and march, alternately, on relatively bare ground (Fig. 1f). Marching and feeding occurred at ground temperatures ranging between 21.2 °C and 54.1 °C throughout the day, while the T_b was slightly lower than the ground temperature (Fig. 4; Tukey–Kramer HSD tests, $P < 0.05$). At midday, when ground temperature exceeded 40 °C, the locusts often stopped marching and remained on the ground, exhibiting stilting behavior (Fig. 1g & h), and seeking shade in low bushes or on the ground in the shade of bushes (Fig. 1i). Some locusts perched on plants (Figs. 1j & 5c, d). Their T_b were maintained at almost 40 °C, within a set-point range that was cooler than the ground temperature (Figs. 4 & 5; Tukey–Kramer HSD tests, $P < 0.05$). In the afternoon, as air and ground temperature fell, locusts again began to march and forage cyclically. Near dusk, they basked in groups on the ground, with T_b being maintained higher than T_s, as observed in the morning (Fig. 1k). They also flew or climbed into trees and larger bushes for nocturnal roosting (Fig. 1l). Thus, group-basking appeared to have a warming effect, while stilting, remaining in the shade, and perching on plants served as a cooling mechanism.

To examine how the warm-up and cool-down behaviors influenced locust T_b, the T_b of either warming up or cooling down were plotted against T_s (Fig. 6a). When locusts displayed warm-up behavior, T_b exceeded T_s by 2.49 °C on average (Fig. 6b; Wilcoxon-test, $z = 4.29$, $n = 95$, $P < 0.001$). In comparison, locusts maintained lower T_b when they displayed cooling down behaviors, with T_b being 8.0 °C lower than T_s on average (Fig. 6b; Wilcoxon-test, $z = -8.55$, $n = 50$, $P < 0.001$). Before sunrise, T_b of night-roosting locusts was not regulated (Fig. 6b; Wilcoxon-test, $z = 0.825$, $n = 29$, $P = 0.41$).

No significant difference was found between T_b and T_s when locusts marched (Fig. 7; Wilcoxon-test, $z = -1.56$, $n = 53$, $P = 0.12$) and fed on grass (Fig. 7; Wilcoxon-test, $z = -0.81$, $n = 54$, $P = 0.42$), but their T_b remained below T_s when the background temperature exceeded 40 °C.

Environmental temperature and occurrence of thermoregulatory behavior

Within a day, warming behavior exhibited bimodal patterns, peaking in morning and around dusk (Fig. 8a). In comparison, cooling behavior peaked at midday (Fig. 8d). These patterns matched diel thermal patterns. For instance, warming behavior occurred at relatively low temperatures, while cooling behavior mainly occurred at hot temperatures (Figs. 8b, c, e & f). Marching and feeding occurred throughout the daytime, but the frequency was relatively low during the early morning (low temperature) and at midday (high temperature) (Fig. 9). Figure 10 shows the percentages of various thermoregulatory behaviors within a day. At night, almost all locusts roosted on large trees or large bushes, while various behaviors co-occurred during the daytime.

Feeding patterns and digestive rates

Some locusts fed on the leaves of trees in which they roosted at night, but most fed on grass during daytime. The foregut of locusts roosting on night plants was almost empty or small amounts of food were present in the morning (Fig. 11). In comparison, foregut size was large, and contained a large amount of food during the daytime, irrespective of their behaviors (Fig. 11).

When locusts were exposed to the sun or shade at midday, the digestive rate of locusts receiving solar radiation was faster than those in the shade (Fig. 12). Digestion was almost complete within 2 h in the sun. Digestion was also accelerated at preferred T_b under laboratory conditions, when measuring foregut weight instead of size (Fig. 13). When last instar male nymphs were allowed to thermoregulate in their preferred way, the weight of the foregut significantly reduced when compared to locusts kept at 20 °C (Fig. 13; Tukey–Kramer HSD tests, $P < 0.05$).

Modelling thermoregulatory behaviors

The microclimate model accurately predicted the observed temperatures (Fig. 14a, b) even though it was driven by down-scaled gridded data not directly measured on-site. Similarly, the ectotherm biophysical model predictions of body temperature corresponded closely to the measured ones (Fig. 14c). The relative mean squared deviation for surface temperature, air temperature at 2m and body temperature were, respectively, 5.1, 4.6 and 3.5 °C. These were relatively small errors given that the daily values of these metrics usually fluctuated more than 20 °C between days and nights. The temporal predictions of activity of the ectotherm model also corresponded to the field observations (Fig. 14d). The contingency matrix of the predicted vs. observed behaviors (Table 3) gave an accuracy of 66.6% with only 2 false predictions of inactivity during actual foraging and 8 false predictions of foraging during actual inactivity, but 90 predictions of foraging while actually basking (*n* =305). Hence, most of the inaccuracy of the model was not problematic as resided in the basking vs. foraging part of the confusion matrix.

Model simulations over the full 2016 year for the Akjoujt field site (Fig. 15a) showed that foraging activity could occur throughout year, with activity possible immediately after sunrise from mid-May to end of September. In comparison, the predictions for the Draa valley site (Fig. 15b) inferred low-temperature constraints on morning foraging through most of the year, with numerous days of zero or limited activity due to cold weather in autumn, winter and spring despite sunny conditions.

Discussion

All organisms must maintain thermal homeostasis within their tolerance limits but how they achieve this, and the costs and benefits of thermoregulatory precision, will vary with the environment (Huey and Slatkin 1976). Avoidance of overheating through thermoregulatory behavior is essential for ectotherms living in hot environments with little shade, as in our study system. Our aim in this study was to obtain empirical data on the manner and extent to which *S. gregaria* thermoregulate in a desert environment, and then attempt to capture these responses with a mechanistic model integrating microclimatic calculations, heat budget calculations and behavioral algorithm.

Thermoregulatory behavior and tolerance of *S. gregaria*

We observed that gregarious nymphs of *S. gregaria* avoided overheating as reported previously in this species (Kennedy 1939; Ellis and Ashall 1957; Stower 1963; Culmsee 2002). We additionally found that they maintained relatively high T_b (nearly 40 °C) at midday by displaying a variety of behaviors in response to wide-ranging available T_e (from 28 °C to 56 °C). These field-estimated optimal body temperatures are consistent with the laboratory-determined preferred ranges of 38 °C to 41 °C (Chapman 1965). They also correspond to the preferred T_b of locusts and grasshoppers reported to range from 35 °C to 42 °C (Chappell and Whitman 1990, Miller et al. 2009, Coggan et al. 2011, Clissold et al. 2013).

We inferred that the upper lethal temperature causing 50% mortality was 50.9°C, which is similar to 50–51 °C tolerance documented for the desert-dwelling darkling beetle, *Onymacris plana* (Edney 1971), and 55.1 °C for the Sahara Silver ant, *Cataglyphis bicolor,* which is one of the most heat tolerant land animals alive (Wehner et al. 1992).

We frequently observed stilting as a cooling mechanism. This can be a potent regulatory mechanism because of the strong vertical temperature gradient above the ground surface during the day; temperatures can be up to 18 °C lower at just 1 cm above than on the ground (Whitman 1987). However, stilting was not always cooling enough and at these times locusts moved from open ground to cooler locations, such as vegetation and shade. Our data hence show that *S. gregaria* could successfully maintain high but tolerable temperatures in the hostile environment of the Sahara Desert.

Thermoregulation, feeding and assimilation

Enhanced thermoregulation is frequently associated with the processes of food uptake and assimilation (Angilletta 2009). In general, ectotherms tend to elevate T_b

following feeding (see review, Angilletta 2009) and the preferred T_b is expected to have evolved to match the temperature at which digestion is most efficient (Huey and Bennett 1987). Furthermore, the rate of energy gain at any temperature depends on the quantity and quality of food. Because T_b is closely associated with performance, thermoregulatory strategies have frequently coevolved with various life-history traits and spatiotemporal habitats (Angilletta 2009).

Why do gregarious nymphs of *S. gregaria* maintain relatively high T_b? To our knowledge, few studies have documented for locusts in the field the relationship between preferred T_b and spontaneous feeding, digestion, marching patterns, and anti-predatory strategies (Ellis and Ashall 1957). Laboratory experiments showed that the development and growth rates of grasshoppers are highly temperature dependent (Whitman 1988, Chappell and Whitman 1990)), including *S. gregaria* (Hamilton 1936, 1950, Symmons et al. 1974), driven by the effects of T_b on food intake, digestion and mobilization rates

(Baines et al. 1973, Whitman, 1987, Harrison and Fewell 1995, Miller et al. 2009, Coggan et al. 2011, Clissold et al. 2013). The present study showed that fed gregarious nymphs digested food at the preferred T_b (nearly 40 °C) through behavioral thermoregulation, even in the field. Locusts usually rest for 15 to 40 mins after feeding, to allow digestion (Ellis 1951, Dkhili et al. 2019). Maintaining a high T_b accompanied with stationary cooling down behaviors allows *S. gregaria* to digest food at the preferred T_b during post-prandial resting when high T_e (>40 °C) is available. When T_e was below 40 °C in the afternoon, locusts tended to bask in groups on the ground to raise T_b close to 40 °C. Although the ecological significance of aggregation has remained unclear (Uvarov 1977), this stationary group basking activity might facilitate heat gain by reducing surface-volume ratios and convective heat exchange, creating a thicker boundary layer of still air over the entire locust mass. This is important at our site because, under the cool nighttime conditions there was little scope for behavioral thermoregulation and the digestion rate was very slow.

The feeding patterns of gregarious locusts in the field are poorly understood. Despite nymphs digesting most food in the foregut within 2 h during the daytime, we observed that large amounts of food were retained in their foregut throughout the daytime, supporting previous observations (Ellis and Ashall 1957), except when conditions were extremely hot at midday or cool during the early morning (Kennedy 1939). The present study did not monitor individual locusts to determine feeding patterns of meals' quantity and inter-meal intervals. However, our analyses of foregut contents and general observations show that gregarious nymphs frequently fed on small amounts of grass to continuously fill their foregut. Similar feeding patterns (i.e., small meals over short intervals) were observed for gregarious last instar nymphs of *L. migratoria* under laboratory conditions at a constant temperature with *ad libitum* feeding (Simpson 1982, Simpson and Raubenheimer 2000). And Dkhili et al. (2019) observed in the lab that previously fed *S. gregaria* hoppers stopped their organized marches to feed for a short time when encountering food.

Foraging and migration behaviors

Migration appears to be an adaptive strategy to access sufficient food resources (Dingle 2014). If emigration occurs from habitats that are still favorable for use, it is considered obligatory (Farrow 1990). This may be the case in our population of *S. gregaria* because we frequently observed that marching bands left foraging sites before all plants were consumed. This foraging strategy has a risk of failing to reach favorable habitats. We observed an isolated migratory band in the middle of dunes where food resource was scanty at another site in 2015 (data not shown) which had apparently migrated over a large distance but failed to reach a food resource. However, at our study site, we seldom observed gregarious nymphs with empty foreguts during the daytime, except for individuals just before molting. Thus, migration allows large numbers of gregarious *S. gregaria* nymphs to access sufficient quantities of food constantly, compensating for energy and water loss.

Thermoregulation and predation risk

In the wild, the thermoregulatory and foraging activity of prey ectotherms are frequently constrained by predation and the risk of being parasitized because feeding and basking in sunshine immediately exposes preys to predators (Huey and Slatkin 1976). Therefore, many prey ectotherms must trade-off the conflicting needs of thermoregulation and foraging with predation risk and thermal stress (Angilletta et al. 2002). Very high thermal tolerance functions as a defense mechanism if it allows an organism to live where predators cannot be active (Chappell 1983, Heinrich 1993). Although nymphs of *S. gregaria* may face much higher losses from bird predation, bird activity tends to be constrained during the hottest hours of the day (Mullié 2009). At our study site terrestrial mammalian and reptile predators were rarely detected. Such predators include jerboas (*Jaculus jaculus*), hedgehogs (*Atelerix albiyentris*), and terrestrial predatory insects. Also, parasitic insects were not detected inside last instar gregarious nymphs in the current study (n = 1150). Thus, high T_b might prevent locusts being parasitized or might kill the parasites (Thomas and Blanford 2003). At night, when the escaping performance of locusts was reduced, due to darkness and low temperature, they roosted on relatively high branches of trees and bushes, which might protect them from ground predators (Maeno and Ould Babah Ebbe 2018). This positioning is also favorable for basking in the early morning sun (Whitman, 1988). At low temperature, conspicuous body coloration may compensate low escaping performance as aposematic body coloration protects against predators when nymphs consumed toxic plants such as, *Hyoscyamus muticus* (Sword 1999, Sword et al. 2000). Aggregation might also function as “selfish herds” (Sword et al. 2005).

Predicting *S. gregaria* thermoregulatory behavior and activity constraints

We were able to use the biophysical modelling tools in NicheMapR to capture the thermal constraints on body temperature and foraging behavior in *S. gregaria* at our site. There are two major challenges to such an endeavor – capturing the available microclimates and properly incorporating behavioral thermoregulation.

To predict microclimates, we use a recently developed approach for downscaling the NCEP historical global weather data (Kalnay et al. 1996) from ~200 km grids to the microclimate scale, via the integration of the microclima and NicheMapR packages (Kearney et al. 2020). Our comparisons of locally measured air temperatures with locally measured surface and air temperatures indicate that this was successful (Fig. 14a, b). The ectotherm model of NicheMapR, which incorporated postural and shade-seeking thermoregulatory behavior, was then able to capture the observed body temperature and foraging patterns in *S. gregaria*.

The fact that we were able to accurately simulate the thermoregulatory behavior of *S. gregaria* has two implications. First, the simulation assumes that the organism behaves in a way to maximize its time foraging at its preferred temperature and only ceases foraging when it is not thermally suitable. The correspondence between the observations and predictions thus means that this species, at our site, is responding to its thermal environment in a manner to be expected if there were minimal costs to thermoregulation.

Second, because the model is a mechanistic one, we can use it to infer the thermoregulatory constraints and consequences at any other location or time. As an example, our simulation extended to the rest of the year at Akjoujt and for the whole year in Draa Waddy (Fig. 15) shows that the latter site would provide less foraging time, especially in the cooler months. More accurate estimates of body temperature and foraging constraints can be used as input into forecasting models of locust outbreak (Piou et al. 2019) and movement patterns. This should help improve forecasting capacity and preventive control, both short-term in response to weather events and long-term in response to climate change (Meynard et al. 2017).

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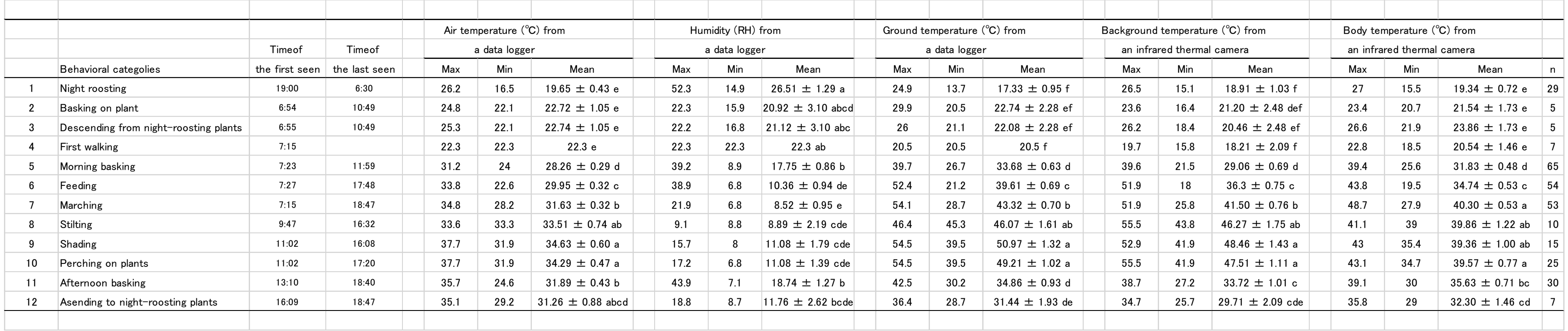
Table 1. Maximum, minimum, and mean air temperature, humidity, ground temperature, background (ground or plants) temperature, and locust body temperature, as well as time when locusts were first and last seen over13 days when locusts displayed 12 different behaviors within a day.



				Air temperature (℃) from			Humidity (RH) from			Ground temperature (℃) from			Background temperature (℃) from			Body temperature (℃) from			
		Timeof	Timeof	a data logger			a data logger			a data logger			an infrared thermal camera			an infrared thermal camera			
	Behavioral categolies	the first seen	the last seen	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	n
1	Night roosting	19:00	6:30	26.2	16.5	19.65 ± 0.43 e	52.3	14.9	26.51 ± 1.29 a	24.9	13.7	17.33 ± 0.95 f	26.5	15.1	18.91 ± 1.03 f	27	15.5	19.34 ± 0.72 e	29
2	Basking on plant	6:54	10:49	24.8	22.1	22.72 ± 1.05 e	22.3	15.9	20.92 ± 3.10 abcd	29.9	20.5	22.74 ± 2.28 ef	23.6	16.4	21.20 ± 2.48 def	23.4	20.7	21.54 ± 1.73 e	5
3	Descending from night-roosting plants	6:55	10:49	25.3	22.1	22.74 ± 1.05 e	22.2	16.8	21.12 ± 3.10 abc	26	21.1	22.08 ± 2.28 ef	26.2	18.4	20.46 ± 2.48 ef	26.6	21.9	23.86 ± 1.73 e	5
4	First walking	7:15		22.3	22.3	22.3 e	22.3	22.3	22.3 ab	20.5	20.5	20.5 f	19.7	15.8	18.21 ± 2.09 f	22.8	18.5	20.54 ± 1.46 e	7
5	Morning basking	7:23	11:59	31.2	24	28.26 ± 0.29 d	39.2	8.9	17.75 ± 0.86 b	39.7	26.7	33.68 ± 0.63 d	39.6	21.5	29.06 ± 0.69 d	39.4	25.6	31.83 ± 0.48 d	65
6	Feeding	7:27	17:48	33.8	22.6	29.95 ± 0.32 c	38.9	6.8	10.36 ± 0.94 de	52.4	21.2	39.61 ± 0.69 c	51.9	18	36.3 ± 0.75 c	43.8	19.5	34.74 ± 0.53 c	54
7	Marching	7:15	18:47	34.8	28.2	31.63 ± 0.32 b	21.9	6.8	8.52 ± 0.95 e	54.1	28.7	43.32 ± 0.70 b	51.9	25.8	41.50 ± 0.76 b	48.7	27.9	40.30 ± 0.53 a	53
8	Stilting	9:47	16:32	33.6	33.3	33.51 ± 0.74 ab	9.1	8.8	8.89 ± 2.19 cde	46.4	45.3	46.07 ± 1.61 ab	55.5	43.8	46.27 ± 1.75 ab	41.1	39	39.86 ± 1.22 ab	10
9	Shading	11:02	16:08	37.7	31.9	34.63 ± 0.60 a	15.7	8	11.08 ± 1.79 cde	54.5	39.5	50.97 ± 1.32 a	52.9	41.9	48.46 ± 1.43 a	43	35.4	39.36 ± 1.00 ab	15
10	Perching on plants	11:02	17:20	37.7	31.9	34.29 ± 0.47 a	17.2	6.8	11.08 ± 1.39 cde	54.5	39.5	49.21 ± 1.02 a	55.5	41.9	47.51 ± 1.11 a	43.1	34.7	39.57 ± 0.77 a	25
11	Afternoon basking	13:10	18:40	35.7	24.6	31.89 ± 0.43 b	43.9	7.1	18.74 ± 1.27 b	42.5	30.2	34.86 ± 0.93 d	38.7	27.2	33.72 ± 1.01 c	39.1	30	35.63 ± 0.71 bc	30
12	Asending to night-roosting plants	16:09	18:47	35.1	29.2	31.26 ± 0.88 abcd	18.8	8.7	11.76 ± 2.62 bcde	36.4	28.7	31.44 ± 1.93 de	34.7	25.7	29.71 ± 2.09 cde	35.8	29	32.30 ± 1.46 cd	7

Air temperature, humidity, and ground temperature was recorded by a data logger.

Background substrate (ground or plants where locusts remained) temperature and locust body temperature was recorded by an infrared thermal camera.

Different letters after each value indicate significant differences at $P < 0.05$ from Tukey-Kramer HSD

Table 2. Parameters used in the ectotherm model for *Schistocerca gregaria* hoppers.

Parameter	Description	Unit	Value	Reference/remarks
CT_{max}	lethal maximum body temperature	°C	50	This study
CT_{min}	lethal minimum body temperature	°C	1	Lab observations
Tpref	thermoregulation target body temperature	°C	40	This study
T_F^{max}	maximum foraging body temperature	°C	43	This study
T_F^{min}	minimum foraging body temperature	°C	25	This study
T_B^{min}	minimum basking temperature	°C	15	This study

T_{RB}^{min}	minimum temperature for movement to basking site	°C	15	This study
burrow	can the animal move underground?		false	
climb	can the animal climb?		true	
shade_seek	can the animal seek shade?		true	
shape	body shape		cylinder	
W_w	wet body mass	g	5	overestimated*
%wet	fraction of body surface acting as a free-water surface		0.1	estimated
%eyes	fraction of eyes surface acting as a free-water surface		0	estimated

minshades	daily minimum shade values	%	0	study sites are semi-desert areas with vegetation
maxshades	daily maximum shade values	%	90	

* but at the lower limit of the model computation capacity

Table 3. Confusion matrix of the observed vs. predicted behaviors of hoppers with the ectotherm-microclimate model.

		predicted behaviors		
		inactive	basking	foraging
observed behaviors	inactive	37	0	2
	basking	0	5	90
	foraging	8	0	163

Figure legends

Figure 1. Various behaviors of gregarious nymphs of *Schistocerca gregaria* from night (a) to dusk over a 1-day period (l). (a) Night-roosting on tree, (b) nymphs moved to east side of night-roosting plant and descended to the ground, (c) ground basking, (d) basking posture: their body direction was perpendicular to the sun’s rays at cooler temperatures (< 40 °C), (e) feeding on low vegetation, (f) marching bands, (g) stilting on the hot ground, (h) lateral view of stilting locust: such stilting locusts remained on the ground and lifted their bodies to be distant from the ground surface, (i) locusts moved to the shade, (j) locusts perched on dried *Calotropis procera* when ground temperature was intolerably hot (> 50 °C), (k) ground-basking during the late afternoon, and (l) ascending to night-roosting tree around dusk.

Figure 2. Diel fluctuations in mean air temperature (○), ground surface temperature in

sunlight (●) and humidity (△) for 15 days (November 2016) near Akjoujt, north-west Mauritania. Error bars represent SE. Dark bar along the horizontal axis represents night-time.

Figure 3. Example of diel fluctuation in mean ground surface temperature exposed to sunlight (○) and under the shade of a spreading shrub or medium-sized tree, *Calotropis procera* (●), from 09:00 to 18:00, and grass surface temperature of *Indigofera argentea* of less than 10 cm height (▲) taken by an infrared thermal camera on Nov. 12, 2016 near Akjoujt, north-west Mauritania. Error bars represent SE. Gray-colored area is available temperature for locusts during the daytime in the field.

Figure 4. Relationships between various behaviors and mean air temperature (○),

background temperature (●), humidity (△), and locust body temperature (●) over 1-day. Note, locusts kept their body temperature close to 40 °C when it was hot (> 40 °C) during the daytime by displaying cooling-down behaviors. In comparison, locusts warmed-up by basking at cool temperatures during the morning and afternoon. Different letters above each bar indicate significant differences at $P < 0.05$ from Tukey-Kramer HSD for body temperature (°C). Numbers in the figure represent the sample size.

Figure 5. Thermal images of locusts displaying group basking during the morning (09:04) (a & b) or shading and perching on *Calotropis procera* at midday (14:05), taken by an infrared thermal camera. Arrows in the photos indicate the positions of locusts that were present.

Figure 6. (a) Relationships between background temperature (Ts) and locust body

temperature (*T*b) when locusts displayed roosting on plants at night (●), warming-up behavior (●: morning and afternoon basking), and cooling-down behaviors (▲:stilting, shading, and perching on plants). (b) Comparison between *T*s and *T*b for each thermoregulatory behaviors. N.S., $P > 0.05$; ***, $P < 0.001$, represent significant differences from the Wilcoxon-test.

Figure 7. (a) Relationship between background temperature (*T*s) and locust body temperature (*T*b) when locusts actively marched (●) or fed on plants (●) during the daytime. (b) Comparison between *T*s and *T*b for each thermoregulatory behaviors. N.S., $P > 0.05$, represent significant differences from the Wilcoxon-test.

Figure 8. Frequency of gregarious nymphs displaying warming-up (group-basking, *n* = 324) (a, b & c) or cooling-down behaviors (stilting, shading, and perching on plants, *n* = 262) (d, e & f) at various times of the day (a & d), air temperatures (°C)(b & e), and ground temperatures (°C) (c & f). Basking behaviors were mainly displayed during morning and late afternoon, while cooling-down behaviors were displayed at midday when it was hottest (a & d). Basking behavior occurred at cool temperatures, while cooling down behavior occurred at hot temperatures (b, c, e & f).

Fig. 9. Frequency of gregarious nymphs displaying marching (*n* = 335) (a, b & c) or feeding (*n* = 207) (d, e & f) behavior at various times of the day (a & d), air temperatures (°C) (b & e), and ground temperatures (°C) (c & f). Both behaviors were observed at any time during the daytime and wide range of temperatures; however, most behaviors occurred after 09:00 when the temperature rose. Most marching occurred after feeding.

Fig. 10. Percentage of gregarious nymphs displaying various behaviors at various times of the day. Field observations over 13 days were pooled. (Different locust groups, *n* = 1584). Note, locusts displayed various behaviors during a single daytime.

Fig. 11. Status of the foregut of gregarious nymphs that displayed night-roosting (06:00–09:00), basking (16:00–17:00), stilting (11:00–15:00), and marching (11:00–17:30) behavior. The foregut was grouped into five categories depending on size. Numbers above the bars represent the sample size.

Fig. 12. Effects of preferred body temperature on the digestive rate in gregarious nymphs on Nov. 24 2016. Just after feeding, locusts were exposed to either sun (a) or shade (b), and the state of their foreguts was recorded every 30 min from 13:00 to 15:00. *n* = 20 (10

females and 10 males) each.

Fig. 13. Effects of preferred body temperature on digestive rate in gregarious nymphs under laboratory conditions. Just after feeding, locusts were exposed to a heat lamp or no heat lamp of 32 °C and 20 °C, and the weight of their foregut was measured after 1 h exposure. *n* = 20 males each.

Fig. 14. Predicted surface temperature (a), air temperature at 2m (b), body temperature (c) and behavior (d) following the microclimate and the biophysical ectotherm models. The field observations are displayed in red.

Fig. 15. Predictions of hourly behaviors from the ectotherm model along the 2016 year for a) the study site near Akjoujt in Mauritania (19°23’N, 14°35’W) and b) the Draa

Waddy near Fam el Hisn in Morocco (28°39’N, 8°52’W). Color code: dark blue = night time (inactivity), light blue = basking, orange = foraging, and white = inactivity during light hours. The red rectangle in subplot (a) indicates the period of the field study in Mauritania.

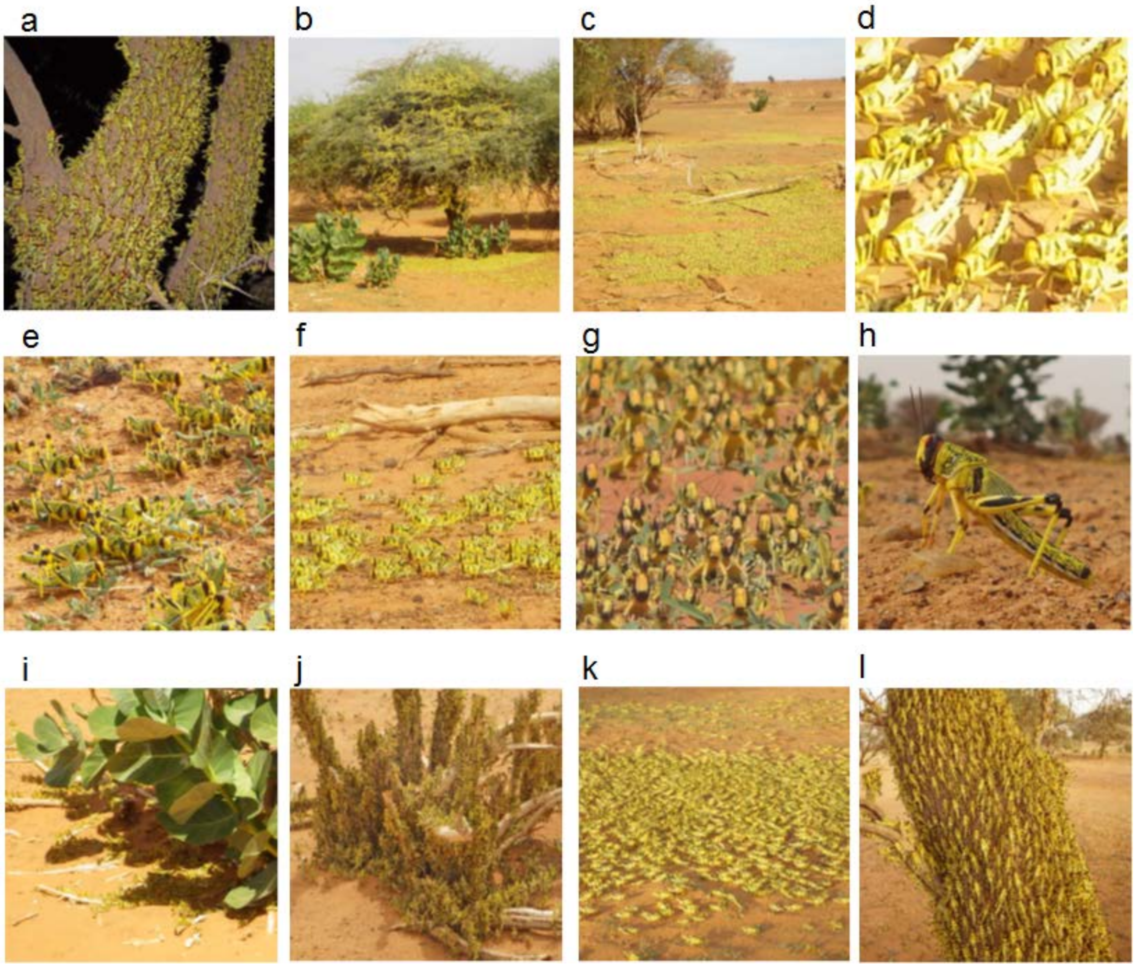


Fig. 1

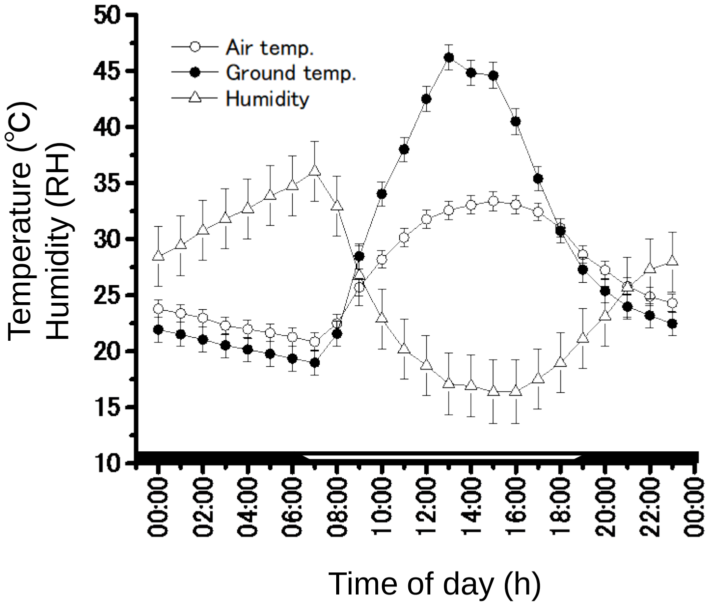

Air temp.
Ground temp.
Humidity
Temperature (°C)
Humidity (RH)
50
45
40
35
30
25
20
15
10
00:00
02:00
04:00
06:00
08:00
10:00
12:00
14:00
16:00
18:00
20:00
22:00
00:00
Time of day (h)

Fig. 2

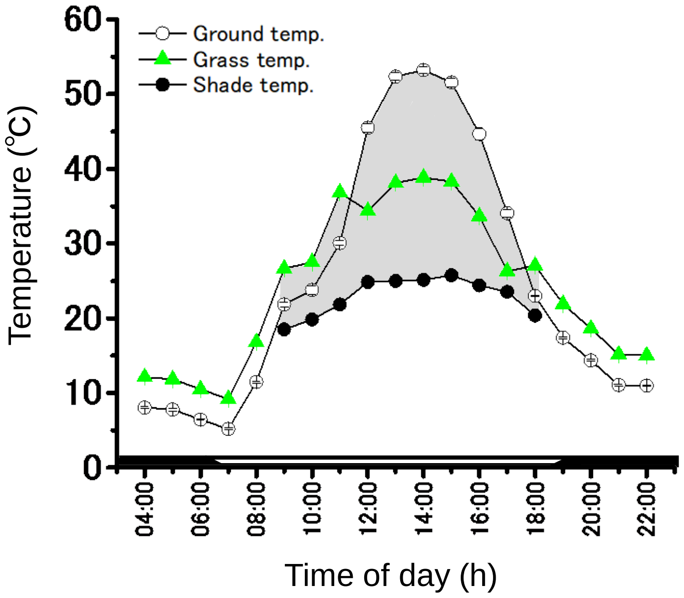

Ground temp.
Grass temp.
Shade temp.
Temperature (°C)
0
10
20
30
40
50
60
04:00
06:00
08:00
10:00
12:00
14:00
16:00
18:00
20:00
22:00
Time of day (h)

Fig. 3

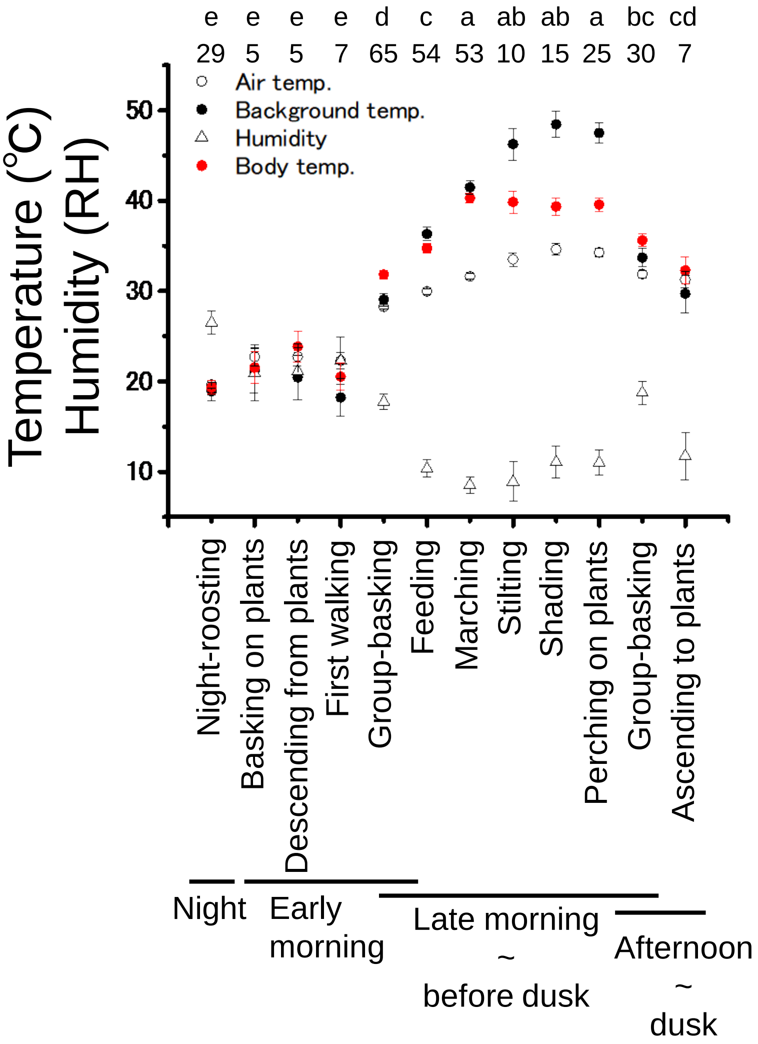

e e e e d c a ab ab a bc cd
29 5 5 7 65 54 53 10 15 25 30 7
Air temp.
Background temp.
Humidity
Body temp.
Temperature (°C)
Humidity (RH)
50
40
30
20
10
Night-roosting
Basking on plants
Descending from plants
First walking
Group-basking
Feeding
Marching
Stilting
Shading
Perching on plants
Group-basking
Ascending to plants
Night
Early morning
Late morning ~ before dusk
Afternoon ~ dusk

Fig. 4

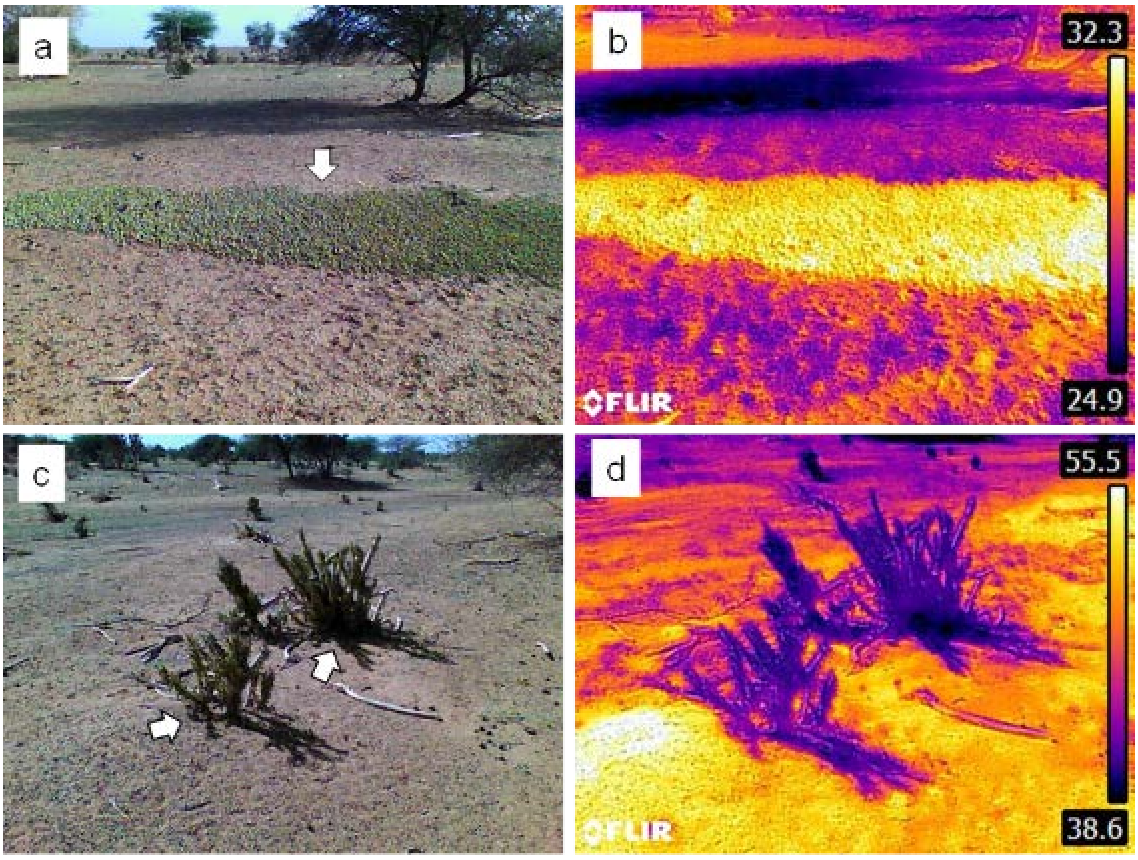


Fig. 5

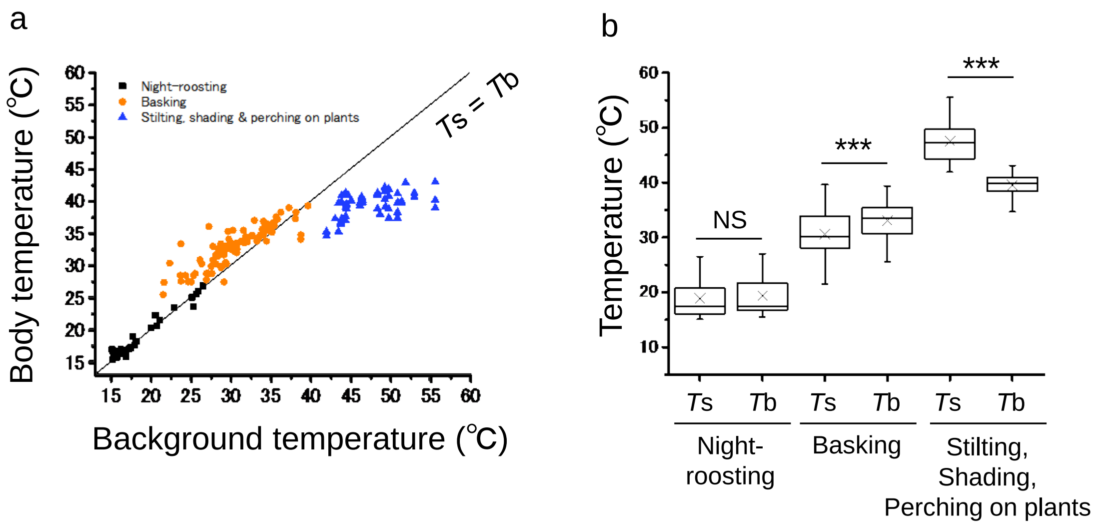

a
Body temperature (℃)
Background temperature (℃)
60
55
50
45
40
35
30
25
20
15
15 20 25 30 35 40 45 50 55 60
■ Night-roosting
● Basking
▲ Stilting, shading & perching on plants
Ts = Tb
b
Temperature (℃)
60
50
40
30
20
10
NS
***
***
Ts Tb Ts Tb Ts Tb
Night-roosting
Basking
Stilting, Shading, Perching on plants

Fig. 6

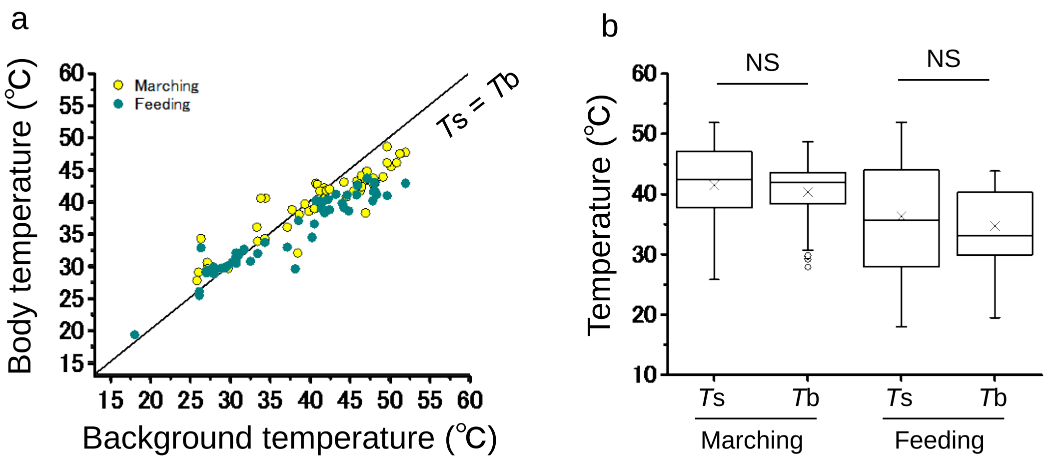

a
Body temperature (℃)
60
55
50
45
40
35
30
25
20
15
Marching
Feeding
Ts = Tb
15 20 25 30 35 40 45 50 55 60
Background temperature (℃)
b
Temperature (℃)
60
50
40
30
20
10
NS
NS
Ts
Tb
Ts
Tb
Marching
Feeding

Fig. 7

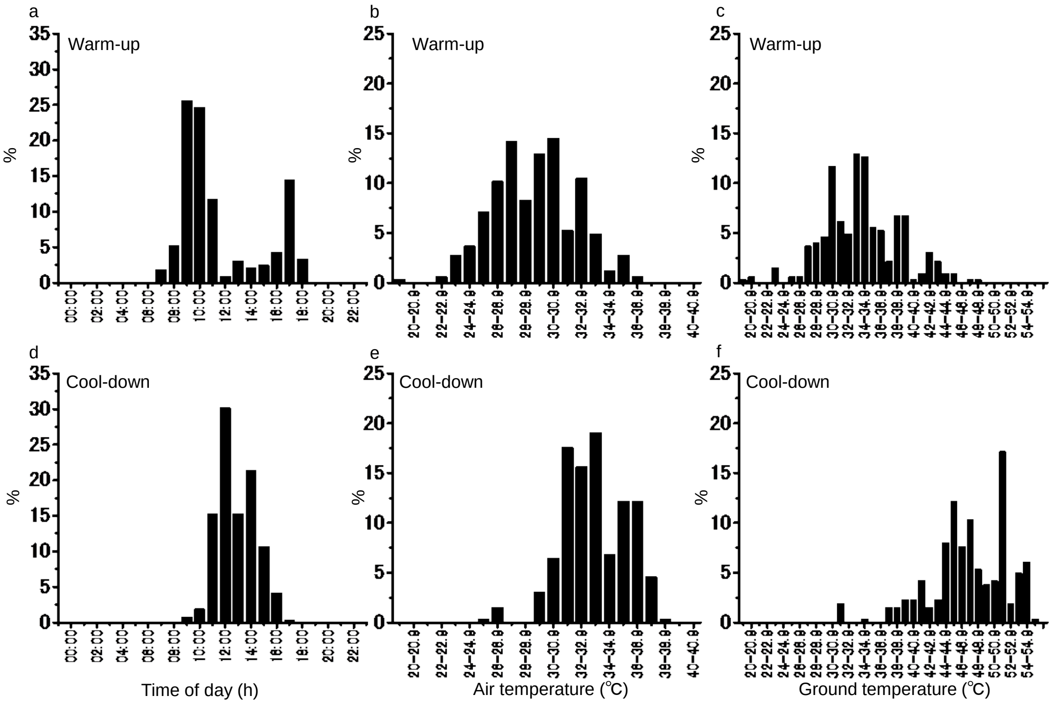

a
Warm-up
b
Warm-up
c
Warm-up
d
Cool-down
e
Cool-down
f
Cool-down
%
0
5
10
15
20
25
30
35
00:00
02:00
04:00
06:00
08:00
10:00
12:00
14:00
16:00
18:00
20:00
22:00
20–20.9
22–22.9
24–24.9
26–26.9
28–28.9
30–30.9
32–32.9
34–34.9
36–36.9
38–38.9
40–40.9
42–42.9
44–44.9
46–46.9
48–48.9
50–50.9
52–52.9
54–54.9
Time of day (h)
Air temperature (℃)
Ground temperature (℃)

Fig. 8

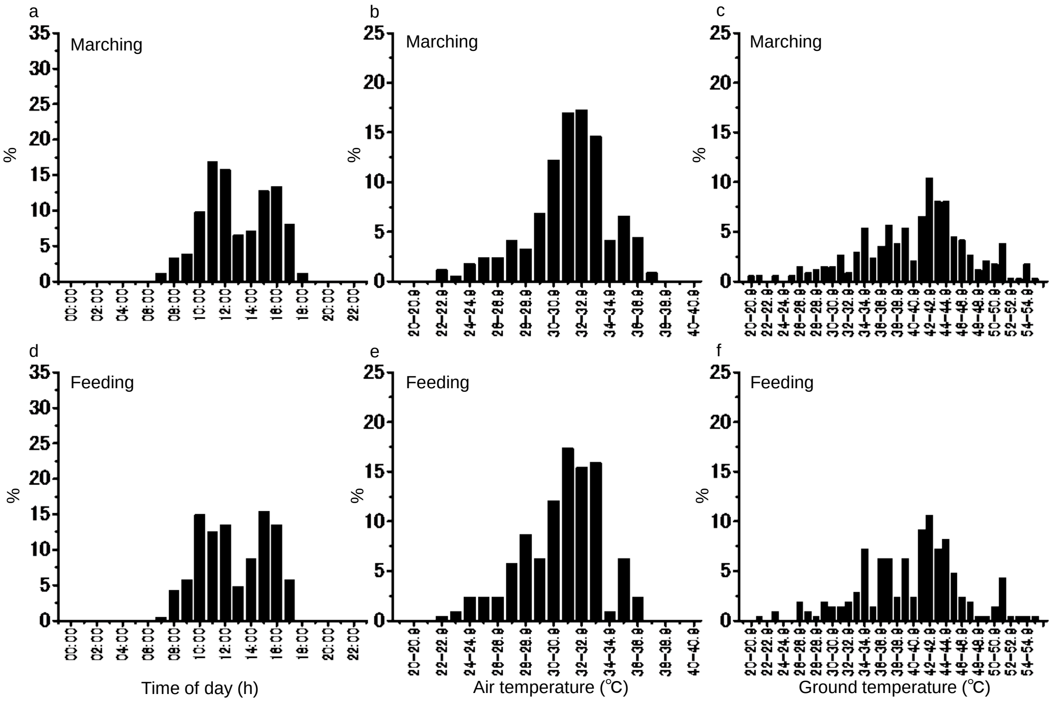

a
Marching
b
Marching
c
Marching
d
Feeding
e
Feeding
f
Feeding
%
35
30
25
20
15
10
5
0
00:00
02:00
04:00
06:00
08:00
10:00
12:00
14:00
16:00
18:00
20:00
22:00
20–20.9
22–22.9
24–24.9
26–26.9
28–28.9
30–30.9
32–32.9
34–34.9
36–36.9
38–38.9
40–40.9
42–42.9
44–44.9
46–46.9
48–48.9
50–50.9
52–52.9
54–54.9
Time of day (h)
Air temperature (℃)
Ground temperature (℃)

Fig. 9

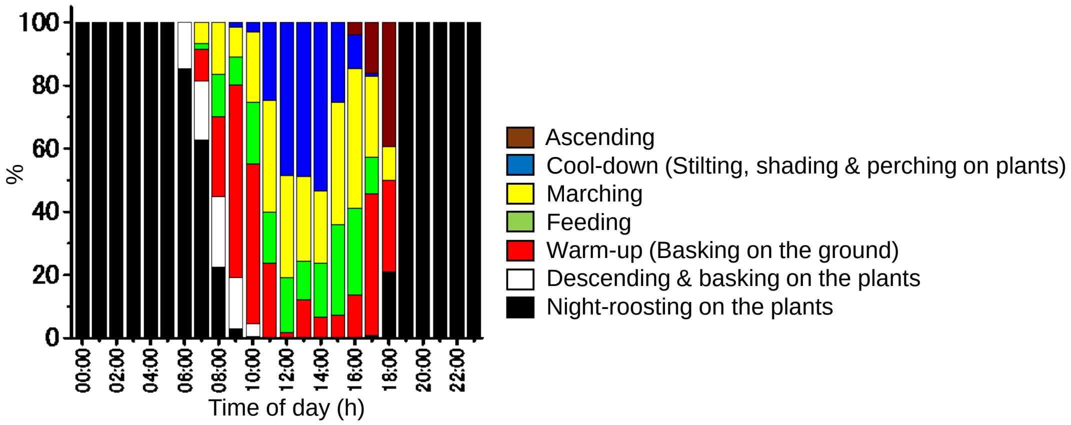

100
80
60
40
20
0
%
00:00
02:00
04:00
06:00
08:00
10:00
12:00
14:00
16:00
18:00
20:00
22:00
Time of day (h)
Ascending
Cool-down (Stilting, shading & perching on plants)
Marching
Feeding
Warm-up (Basking on the ground)
Descending & basking on the plants
Night-roosting on the plants

Fig. 10

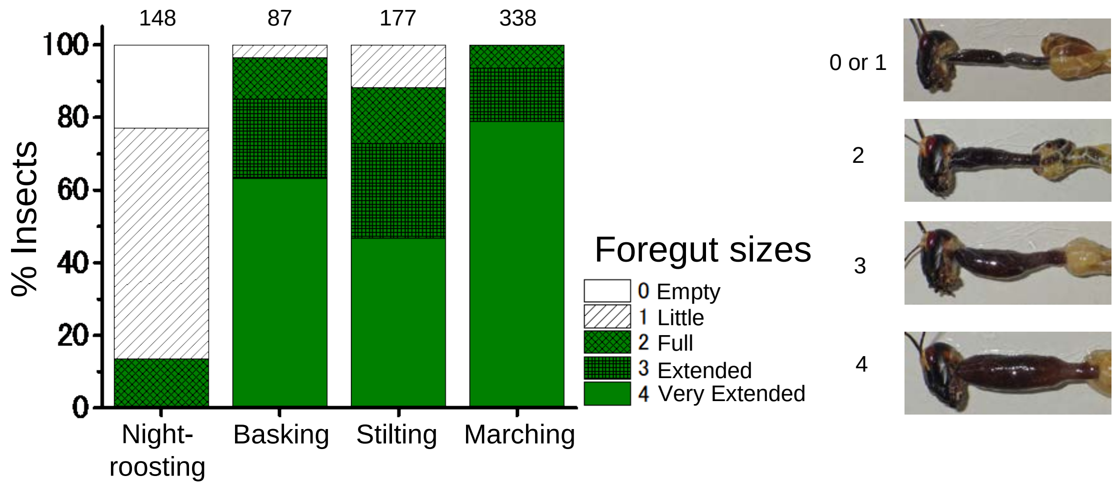

148
87
177
338
100
80
60
40
20
0
% Insects
Night-roosting
Basking
Stilting
Marching
Foregut sizes
0 Empty
1 Little
2 Full
3 Extended
4 Very Extended
0 or 1
2
3
4

Fig. 11

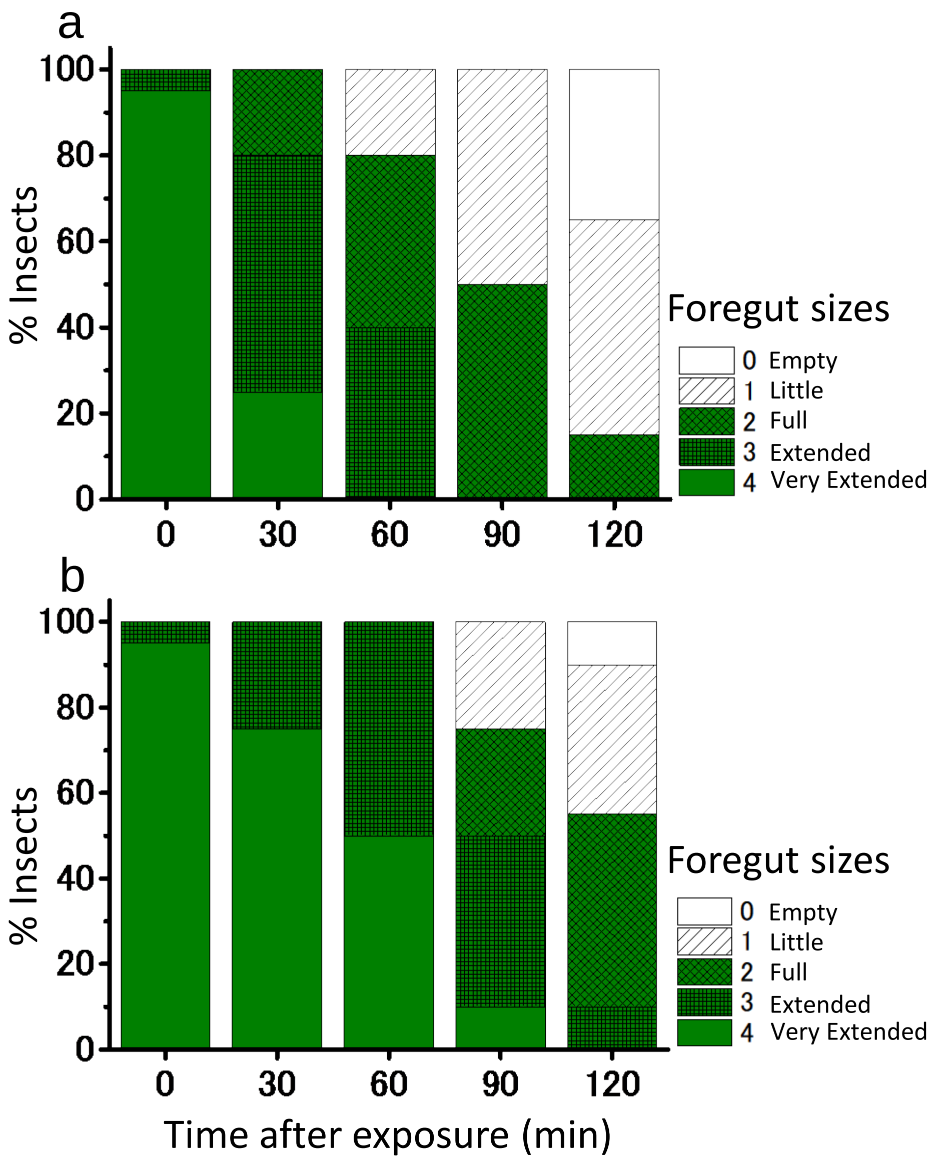

a
% Insects
100
80
60
40
20
0
0
30
60
90
120
Foregut sizes
0 Empty
1 Little
2 Full
3 Extended
4 Very Extended
b
% Insects
100
80
60
40
20
0
0
30
60
90
120
Foregut sizes
0 Empty
1 Little
2 Full
3 Extended
4 Very Extended
Time after exposure (min)

Fig. 12

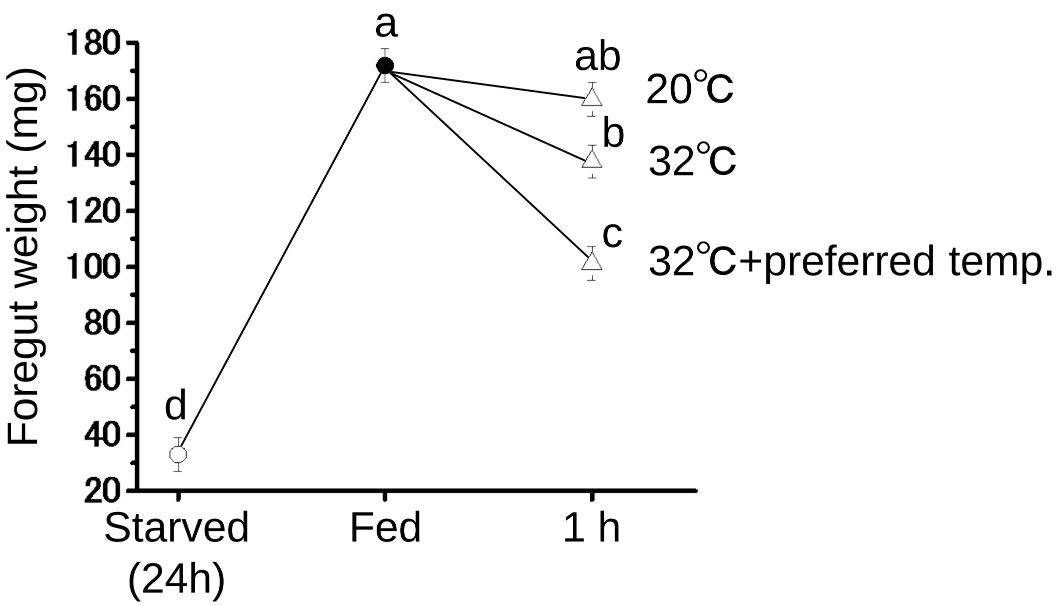

Foregut weight (mg)
180
160
140
120
100
80
60
40
20
Starved (24h)
Fed
1 h
a
ab
b
c
d
20℃
32℃
32℃+preferred temp.

Fig. 13

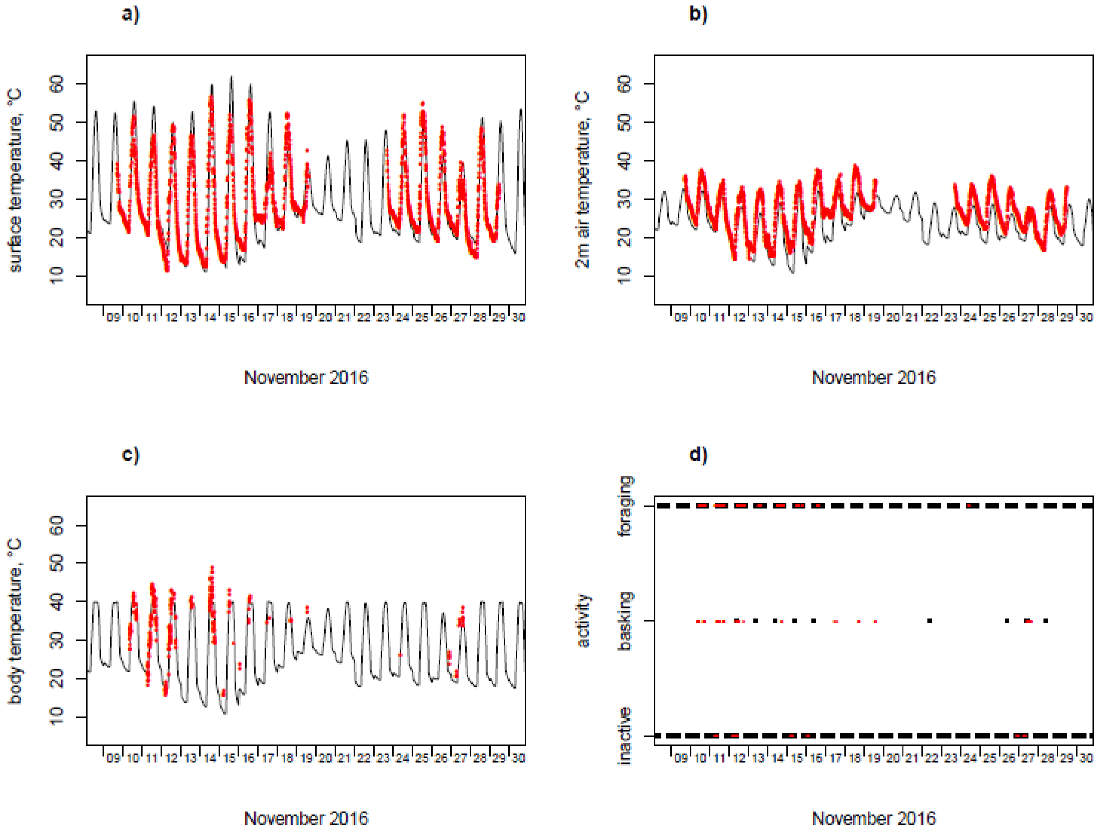

a)
surface temperature, °C
10
20
30
40
50
60
09 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
November 2016
b)
2m air temperature, °C
10
20
30
40
50
60
09 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
November 2016
c)
body temperature, °C
10
20
30
40
50
60
09 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
November 2016
d)
activity
foraging
basking
inactive
09 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
November 2016

Fig. 14

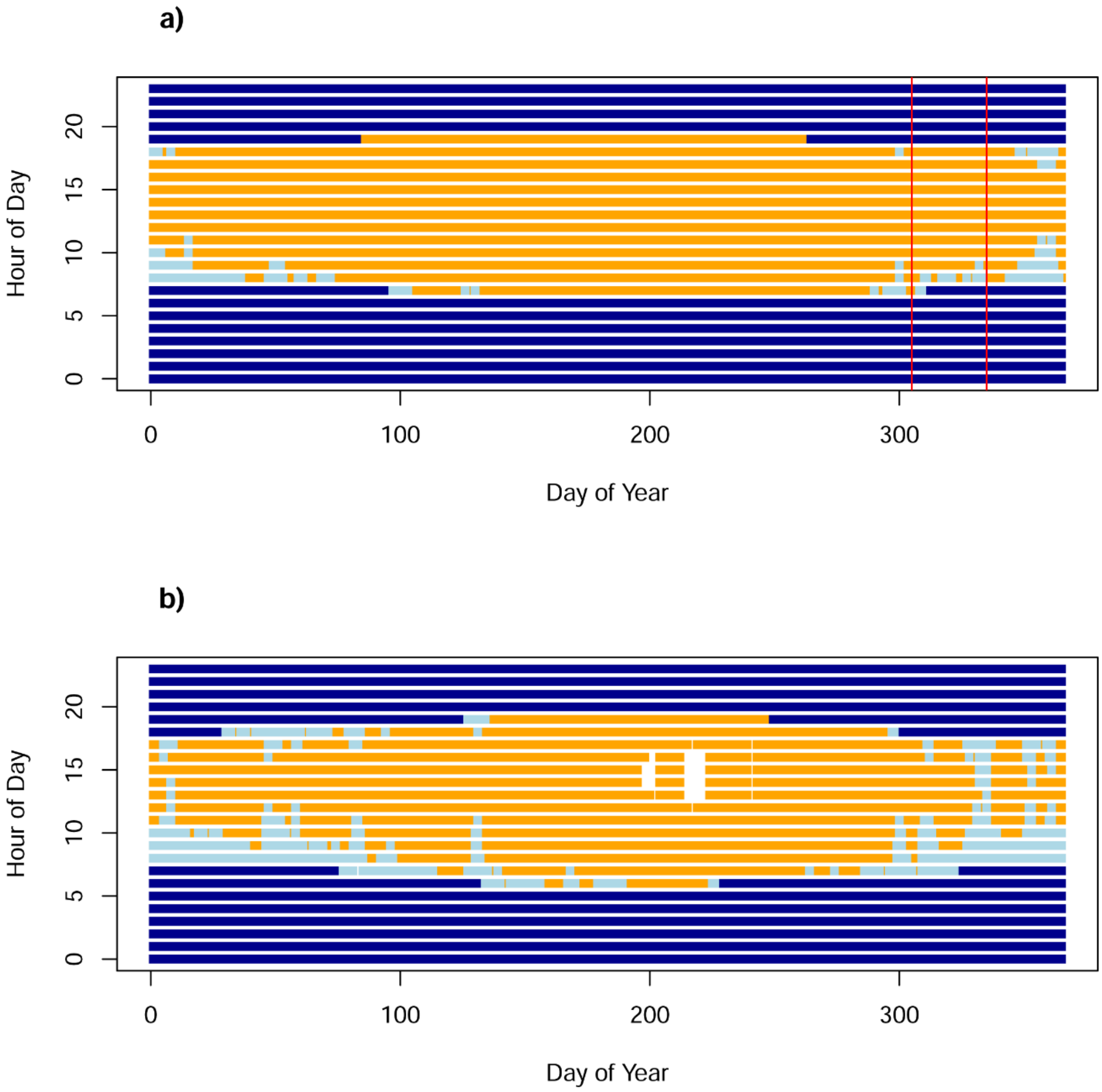

a)
Hour of Day
0
5
10
15
20
0
100
200
300
Day of Year
b)
Hour of Day
0
5
10
15
20
0
100
200
300
Day of Year

Fig. 15