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Band movement and thermoregulation in *Schistocerca cancellata*

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Abstract:

At high density, juvenile locusts create marching hopper bands. Understanding the roles of temperature and vegetation on the movement of these bands shall allow to better forecast and control them. Following a hopper band in North Argentina in November 2019, we explored the thermoregulation behaviours of the South American locust, *Schistocerca cancellata*. Gut-content samples informed about the feeding status at different time of the day. Hoppers' body temperature was above cold air temperature in the mornings during basking and group-basking activities and before the onset of marching behaviour. Marching by walking or hopping was dominant at body temperatures close to 40°C. Jumping, stilting, shading and perching on plants were seen as thermoregulatory behaviours to avoid ground temperatures above 50°C. Feeding was observed throughout the day with continuous high gut contents despite an intermittent pattern of feeding-resting-marching. Speed and daily travelled distance of the front of the hopper band was depending on the type of encountered vegetation. Daily behavioural patterns, thermoregulatory behaviours, walking speed and daily travelled distances of *S. cancellata* were similar to the ones observed for the Desert locust, *S. gregaria*, in Africa. High air temperatures recorded during the observation times could explain the continuous feeding patterns. These species may have evolved behaviours of alternating consuming a bit and marching as a migration strategy to avoid staying where no food is available after the havoc left behind large hopper bands. Recommendations made for the control of Desert locust hopper bands can be extended to South American locust ones.

Keywords: behavioural thermoregulation, infrared thermography, locust, mass migration, Orthoptera, plant-animal interactions.

1. Introduction

Locusts are grasshoppers able to display two extreme phenotypes in response to population density: at low density, the solitarious locusts display cryptic and low activity behaviours; at high density, the gregarious locusts create mass migration and active behaviours (Pener & Simpson 2009). This extreme form of phenotypic plasticity is called phase polyphenism, and for some species, in addition to group movement behaviours, the changes are also morphological, physiological and affecting life history traits (Ayali 2019, Maeno et al. 2020). With their capacity to create large swarming groups of winged adults that can impact agricultural fields and pasture lands, locusts are amongst the most feared plant pests worldwide (Zhang et al. 2019). The understanding that actually the same species are behind these changes of behaviours was only unravelled a century ago by Uvarov (1921). However, since then, many scientific studies explored the processes behind the change of behaviour (e.g. Ellis 1963, Simpson et al. 2001, Rogers et al. 2014, Cisse et al. 2015), the mass migration phenomenon (e.g. Bazazi et al. 2012, Ariel & Ayali 2015) and the ecology of locusts in general (see review by Cullen et al. 2017).

The group movement of locust, for most species, can be displayed in two forms. The winged adults create swarms that can take columnar forms with thermic winds or horizontal clouds when insects are spread over large areas (see Uvarov 1977). Depending on the species, these swarms may move from few kilometres to hundreds of kilometres per day. The wingless nymphs, or hoppers, may also show group movement under the form of so-called hopper bands. These hopper bands can take different shapes (Dkhili et al. 2017), with typical locust species displaying crescent shape, with a high density of hoppers in the front and a decrease of insects towards the back of the band (Buhl et al. 2012). These band movements were understood in the lab as the result of local interactions among individuals that increase with density and eventually create a coordinated movement with a homogeneous direction of the group (Buhl et al. 2006). Recent further laboratory studies proposed a change of behaviour during band movement (Knebel et al. 2020). Some laboratory works proposed that locusts march to catch the ones in front in the search of cannibalising them (Bazazi et al. 2008, 2011). Field observations of band movements (Ellis & Ashall 1957, Lecoq et al. 1999) however rarely informed about cannibalism but explained how vegetation, hence food, actually modified band movement (through feeding). And laboratory experiments also showed that marching may not occur when locusts are well fed, and particularly just after feeding, during a so-called post-prandial period (Ellis 1951, Dkhili et al. 2019).

The local conditions of food availability, but also temperature, wind, and rain conditions were observed as influencing locust swarm and hopper bands movement (Ellis & Ashall 1957, Uvarov 1977). Understanding the interplay of these different factors together with the intrinsic behaviours of locusts may allow better forecasting the movements of these groups, and hence better managing them. The role of thermoregulation behaviour in relation to feeding and displaying different activities was investigated for Desert locust, *Schistocerca gregaria* (Maeno et al. 2021), the most destroying locust in the world. Maeno et al. showed that desert locust attempts to reach a body temperature close to 40°C to optimize its food assimilation. Several thermoregulation behaviours were identified to increase temperature as fast as possible in the morning (through basking and group-basking) and to avoid overheating during the hottest hours of the days (through stilting or shading). The identified optimal body temperature matched the optimal development range observed in laboratory conditions (Chapman 1965). The shape and extend of performance curves in relation to temperature as the optimal body temperature can be important in evolutionary processes (Huey & Kingsolver 1989). For example, high thermal tolerance may confer an advantage against predators (Chappell 1983). Hence, there are also interests in understanding the thermal tolerance and thermoregulatory behaviours of insects in general. However, as for many other knowledges on locusts, the desert locust is the most studied species, and little is known on other species (Latchininsky et al. 2016). On the same genus, *Schistocerca cancellata*, the South American locust was given much attention in the first half of the 20th century, but much less over the last 60 years.

The South American locust is nevertheless an economically important locust, with potential impact on the agriculture of 5 countries covering approximately four million km² at maximum invasion phase (Waloff & Pedgley 1986). During most of the first half of the 20th century, *S. cancellata* caused great economic losses through the damage of almost every crop. After the setting in place of preventive measures in 1954, the invasion periods decreased and eventually disappeared (Kohler 1962, Gaston 1969). However, since 2015, swarms and hopper bands of *S. cancellata* are seen again and harm agricultural lands of Argentina, Bolivia and Paraguay (Medina et al. 2017). This resurgence has impacted various types of pastures and annual and perennial crops as large swarms invaded the north of Argentina in 2017, 2019 and 2020.

Reproduction of *S. cancellata* is generally occurring from September to March, i.e. during the hot and wet austral spring and summer seasons (Waloff & Pedgley 1986). Years that present favourable rains until March may allow a third autumn reproduction and generation (Hunter & Consenzo 1990). During the winter months, the adult are in diapause until finding good conditions to breed in September-October. Hoppers hatch 18 to 36 days after the egg-laying events and develop through 5 instars for between a month and a half or two until the adult stage is reached (Hunter & Consenzo 1990). These development times and diapause conditions are temperature-driven. *S. cancellata* gregarious hoppers display typical marching band behaviours. In laboratory conditions, gregarious hoppers' grouping behaviour was seen as close to *S. gregaria* ones (Ellis 1962). The phase polyphenism expression was also documented recently for *S. cancellata* and seen comparable to *S. gregaria* (Pocco et al. 2019). However, very little was documented so far on the thermoregulatory and feeding behaviours of this species, nor on the speed of band displacement and vegetation influence.

The objectives of this study were two-folds. First, we wanted to verify if thermoregulatory behaviours of *S. cancellata* hoppers, such as those identified in *S. gregaria*, could be observed in natural conditions and if feeding activity was related to these behaviours. A second, more general objective was to document the characteristics of this species to march as hopper bands, particularly the walking speed in different types of habitats.

2. Material and methods

2.1 Study site

The study was conducted in an area situated in the North-West of the Salta province of Argentina (Fig. 1). According to Oyarzabal *et al.* (2018) this area belongs to the west part of the xerophytic woodland unit (semiarid Chaco) of the Gran Chaco phytogeographic region. The area was documented by SENASA (Servicio Nacional de Sanidad y Calidad Agroalimentaria, the public institution in charge of locust survey and control in Argentina) to have been the ground of a large-scale reproduction of a *S. cancellata* swarm in the beginning of October 2019. The estimated area of oviposition was up to 60 000 ha. This area was consequently a ground of monitoring for SENASA teams in November 2019 to find groups and bands of hoppers in order to control the population before another swarm would create.

The morning of the 12th of November 2019 two teams monitored a property of about 7000ha to find the largest groups possible. About 10 different N1 to N3 hopper spots were encountered and the largest one was located along an unpaved road coming out of an area of dry forest. This band was chosen for the observations as many hoppers were observed as marching at 11:00. The main part of the data collection started that same day at 14:00.

The site of observation of this chosen band was located between the coordinates 63°17’16’’ West, 22°06’09’’ South and 63°17’32’’ West, 22°06’45’’ South (Fig. 2). The elevation was 370m above sea level. Crop fields were in the fallow period and the spontaneous vegetation growing then was mainly constituted of *Amaranthus quitensis* and *Conyza bonariensis*. These species are considered as weeds by the farmers who grow soybeans or corn on these open fields during the rainy season. The original dry forest of this area, a Xerophytic woodland following the classification of Oyarzabal *et al.* (2018), typical of the Chaco area, was left on some corridors of about 30m wide to separate fields every 400m. At this specific location the largest patch of forest fringed a small temporary creek that crossed the unpaved road (Fig. 2). The main species of trees and bushes found in these forests were *Acacia caven, A. furcatispina, A. praecox, Acanthosyris falcata, Caesalpinia paraguariensis, Cercidium praecox, Cereus coryne, Chorisia insignis, Geoffroea decorticans, Opuntia quimilo, Pereskia sacharosa, Prosopis alba*, *P. nigra* and *Ruprechtia triflora*.

2.2. Data collection

The data collection consisted of 4 main activities during 3 days: 1) recording the positions of the band, 2) recording the main behaviours of hoppers, 3) measuring temperatures and 4) evaluating foregut contents of hoppers. The timing of observations was constrained by site accessibility and logistics but covered roughly the periods of 14:00 to 20:00 the 12th of November, 10:00 to 18:30 the 13th of November and 05:00 to 19:30 the 14th of November.

In order to follow the speed of the band and its trajectory, the position of the borders of the band was noted with GPS coordinates every 2 to 3 hours when not very active and up to every hour when notable marching was observed. We considered the borders of the band where densities went abruptly from almost no hoppers to more than 10 hoppers/m² (visually estimated). From these GPS coordinates, we extrapolated polygons of occupancy of the band using QGIS (v.3.4 LTR, QGIS development team 2018 http://www.qgis.org). A particular attention was set on the advance of the front of the band and marching speeds were estimated based on the positions of this front.

2.3. Behaviours notation

As reported by Ellis & Ashall (1957) and Maeno et al. (2021) for *S. gregaria*, hoppers of *S. cancellata* within the band displayed different behaviours among individuals. Hence, to characterize the behaviours, we noted regularly (at least every hour during the times of observation, sometimes up to every 15 minutes) the different displayed behaviours of visible hoppers with approximate proportions of occurrence (over hundreds of hoppers). Ellis & Ashall (1957) described 14 typical behaviours of *S. gregaria* and Maeno et al. (2021) used 12 of them. To simplify these ethological observations we focused on 10 different behaviours (see illustrations on Appendix 1): Feeding (including fighting over food), Night roosting (staying on plants during the night), Descending from plants after the night, Basking on plants, Basking on the ground (generally group-basking), Marching (walking), Jumping (hopping or long distances jump), Stilting (lifting the body up above the ground and alternating the legs touching it, also called Peering in Ellis & Ashall 1957), Shading under plants or within the plants and Ascending to plants for the night. The main activity (other than Feeding because it was always visible) at each time of observation was noted as the one the most displayed in the band and used for the selection of hoppers for temperature measurements and foregut content sampling (following sections).

2.4. Temperature measurements

Three thermo-hygro recorder (FI 84ED, Française d'Instrumentation®) were positioned at 14:00 the 12th of November in different areas of the study site: 1) at 1.5m above the ground to record air temperature; 2) on the ground in an open area to record ground temperature, and 3) on a bushy plant (at 1 m from the ground) to record vegetation temperature. The ground logger was removed at night to avoid losing it during eventual rain events.

Body temperature of hoppers was estimated using a FLIR one pro LT® thermal camera by shooting pictures of hoppers displaying the main activity at that time. Series of 2 to 3 pictures were taken approximately every 30 minutes. A total of about 300 pictures were taken. On the pictures where hopper body were clearly visible, the software FLIR Tools V5.13® was used to estimate the temperature at the position of at least 10 individuals of a series of picture for a given hour. A mean of these estimates was computed and was used as a proxy of hopper body temperature for that specific hour (see Maeno et al. 2021 and Appendix 2 for more details on the methodology). The hoppers in our study were of second and third instar and too small to obtain a precise body temperature for statistical analyses relating body temperature to environment temperature. Nevertheless, these estimates were interesting to relate the behavioural changes through the days in relation to the temperature experienced by the hoppers.

2.5. Foregut contents

To evaluate the feeding activities of *S. cancellata*, samples of 10 hoppers displaying the main activity at that time were collected and dissected in the field every hour the first day and every 2 to 3 hours the following days. The dissection consisted in cutting the tip of the abdomen and removing the muscles and exoskeleton starting between the rear of the head and the pronotum down to the end of the abdomen. This way, the digestive system was apparent and the foregut of the hopper was clearly visible. For each dissected hopper, a categorical note was given depending on the level of filling of the foregut: 0 for empty, 1 for traces of food, 2 for full foregut (food occupying the space but not distending the foregut wall), 3 for extended foregut (food filling the foregut with a slight distention of the foregut wall) and 4 for fully extended foregut (clearly distending the foregut wall displaying a protuberance). These notes were used and illustrated by Maeno et al. (2021) on *S. gregaria* as a methodology adapted from Ellis (1951). Maeno et al. (2021) show that at preferred temperature, the fully fed hoppers (category 4) digest and empty their foregut in two hours (reaching an average category 1). At lower temperature, they show that the digestion is slower but starved hoppers for 24h are generally of category 0.

2.6. Analyses

The percent of behaviours of hoppers at each observation time were used to compute weighted averages of the experienced temperatures (air, vegetation, ground and proxy of body temperatures) for each activity type.

The behaviours of hoppers were summarized by hours of observation through the three days to obtain a typical daily pattern of activity. However, as feeding was observed throughout the three days, the percentage of activity was recomputed without feeding.

The foregut content index was also synthetized by activity period, grouping together the times when the main activity was basking (basking on plant or basking on the ground) and avoiding heat (jumping, stilting or shading behaviours). These syntheses were conducted to evaluate how thermoregulatory behaviours may impact feeding and digestion activities.

All analyses were conducted with R v3.5 (R Development Core Team 2019).

3. Results

The estimate of the band size was quite variable and went from about 0.25ha during the night-roosting of the 12-13th of November to more than 2ha at the largest extent during the day of the 14th of November (Fig. 2). Night roosting places were the dry forest for the 1st night, along the edge of the field with a part still on the dry forest the 2nd night and entering another forest stripe the 3rd night. Given an average local density of about 350 hoppers/m² at that time (of largest extension), we estimated that this band was about 7 million individuals. Note that density was impossible to evaluate while the band was in the dry forest with hoppers climbing up to several meters high and falling all over.

During the three days of observation, the air temperature varied between 20°C and 45°C with an expected diurnal pattern (Fig. 3). The vegetation temperature was buffered and never went higher than 40°C. On the contrary, ground temperature could reach locally more than 60°C in the sun and average hourly ground temperature reached 53°C. The hopper body temperature was equal to air and vegetation temperature during night (Figs. 3 & 4). In early morning, before the hoppers went down off the vegetation to bask, their body temperature was eventually lower than air temperature (Fig. 3). As soon as they started basking in the plants or descending to the ground to heat up, their body temperature was above air temperature (Fig. 4). The hopper body temperature stayed closer to ground temperature than air temperature until around midday (Fig. 3). From 7:00 to midday, group basking on the ground occurred (Fig. 5) in different spots with different sizes of groups but usually not for longer than 1 hour per group. Around 9:00, when hopper body temperature was above 30°C (Fig. 3) some hoppers started marching (Fig. 5). Marching became generalized around 10:00, when air temperature reached 30°C (Fig. 3) and stopped when hoppers went back to their night roosting plants (Fig. 5). Marching frequencies displayed two main peaks: from 10:00 to 13:00 and 15:00 to 18:00 (Fig. 5). During the marches, body temperature was generally above air and vegetation temperatures but below ground temperature (Fig. 4). Jumping happened also across most of the day (Fig. 5) but during the hottest hours of the day, jumping was observed as a way of avoiding heat, particularly hot ground temperatures (Figs. 3 & 4). The main heat-avoidance behaviours of stilting or shading happened respectively between 13:00 and 16:00 or 12:00 and 17:00 (Fig. 5) at air temperatures around 40°C and ground temperatures that could reach more than 55°C (Fig. 4). During the ascending phase between 17:00 and 20:00 (Fig. 5), the body temperature was higher than air, ground or vegetation temperatures (Figs. 3 & 4).

The feeding activity was observed throughout the day during the three days of sampling. Hence, the temperatures associated to this activity were not very different from overall mean temperatures (Fig. 4). The analyses of the foregut contents of 124 individuals showed continuously full guts (Fig. 6) implying a consistent continuous feeding process. The only time that some individuals were found with little or no food in their foreguts was in the morning during basking or marching times (Fig. 6). The cyclic behaviour of marching, climbing on small plants, feeding, resting, jumping down, marching, etc. was frequently observed and corresponded to the resulting pattern of all levels of foregut content observed for the marching individuals (Fig. 6). All the insects found on plants, either to avoid heat, to climb up for night roosting or actually during the night were observed with full, extended or very extended foreguts, illustrating also the fact that they were continuously feeding when green plants were available (Fig. 6). The relative mild temperature during nights (above >20°C, Fig. 3) was probably favouring this continuous feeding behaviour (but we did not sample between 21:00 and 5:00).

Despite the continuous feeding, the marching band was overall quite fast. The front of the band covered 800m in 3 days (Fig. 2), with some speed peaks up to 200m/h on the 13th of November early afternoon while marching on the side of the unpaved road. The band was moving at about 20m/h when progressing within the dry forest on the 13th of November morning (Fig. 2). In the weed fields, the band was moving at very different speed at different times (see also Appendix 3). The morning movements were quite slow with front speed almost null on the 14th of November. On the contrary, at the end of that same day, the front could cover 50m/h in the weed fields (Fig. 2).

On the evening of the 13th of November, around 17h, we observed that the southern wind was so strong that the hoppers that were still coming out of the dry forest were blown away when they tried to cross the unpaved road (Fig. 2). These strong winds hindered these late individuals to regroup with the major part of the band that had already passed on the other side of the road and continued southward. This event created that two separate roosting sites were used during the night of 13-14th of November. The next morning, the small band that roosted on the dry forest was basking latter than the rest of the band (that was ideally exposed to the morning sun). Once these delayed individuals started walking, they actually followed the same path of move than the rest of the band the previous day. The walk was then following some paths within the weed field on the western side of the road (but not walking much on the road). Until the end of daylight the 14th of November the delay of these regrouping individuals was noticeable with some hoppers actually walking much faster at the end of the band than at the front.

4. Discussion

4.1. Thermoregulation of S. cancellata

As expected, we could observe that *Schistocerca cancellata* displayed clear thermoregulatory behaviours. These behaviours allowed the hoppers to reach body temperatures higher than air temperature early in the morning. It is only when they reached a body temperature above 30°C that they started marching in a coordinated direction. On the contrary, we could observe that over-heating avoidance drove some shading, stilting, jumping and climbing behaviours. These results are concordant to the observations of identical types of behaviours for *S. gregaria* (Maeno et al. 2021, Ellis & Ashall 1957) and previous observations on different grasshopper species (e.g. Yule & Lloyd 1959, Lactin & Johnson 1998). We observed relatively high body temperature with a trend to reach 40°C on the morning but to avoid 50°C during the hottest hours. This could mean that the optimal body temperature for *S. cancellata* is circa 40°C as for *S. gregaria* (Maeno et al. 2021), which is supposed to enhance the digestive rate (Clissold et al. 2013). The activity of hoppers was low but still feeding during the night and early morning when air temperature was below 25°C, so it is reasonable to believe that *S. cancellata* may have an activity threshold around 20°C as *S. gregaria* (Maeno et al. 2021). Further studies may find a slightly lower activity threshold for South American locust as it was found to fly in swarms at lower temperature (18°C, Hayward 1934) than desert locust (generally believed to fly when air temperature >20°C, Rainey & Waloff 1951). We did not here attempt to evaluate lethal body temperature, but the thermoregulatory behaviours of *S. cancellata* that we observed tended to keep body temperature as close as possible to 40°C and avoiding to have a body temperature reaching 50°C, as the lethal temperature identified by Maeno et al. (2021) for *S. gregaria*. The cumulative and punctual effects of different high temperatures leading to mortality as proposed by Rezende et al. (2020) would also be interesting to study for different species of *Schistocerca.* Indeed, different species of *Schistocerca* may have different adaptation to hot arid environments.

4.2. Feeding patterns

During the three days of observation, the air temperature was always above 20°C. This probably favoured the continuous feeding behaviour observed in our hopper band. The night feeding observed here was also found in different locust species (Ellis & Ashall 1957, Simpson 1982). With low night temperature, Maeno et al. (2021) did not observe *S. gregaria* feeding continuously. However, they did observe intermittent feeding activity during the day, and even when group marching occurred (Maeno et al. 2021). This also corresponds to the reported effects of dense vegetation slowing down band movements (Ellis & Ashall 1957). Yule & Lloyd (1959) observed continuous feeding of *Nomadacris sceptemfasciata* hopper bands while migrating. Lecoq et al. (1999) also observed alternating behaviours of feeding and jumping/marching in *Rhammatocerus schistocercoides* hopper bands moving through grassland vegetation. These observations correspond also to the pattern of feeding-resting-marching cycles of behaviours proposed by Dkhili et al. (2019) based on laboratory experiments on *S. gregaria*, and the general pattern of alternating phases of feeding summarized by Simpson (1990). When crossing vegetated areas, bands of hoppers of *S. cancellata*, as *S. gregaria* ones, alternate their feeding activity with resting times (post-prandial periods, Ellis 1951) and walking or hopping moments to progress through the band and the environment. On open grounds, with temperature below 45°C, we could observe that hoppers would walk and hop with a pause-and-go type of motion (Ariel et al. 2014), with short pauses and long moves that are typical of relocation behaviours (Bazazi et al. 2012). However, in complex vegetated areas, the pause-and-go motion was visible only in the small bouts of walking periods between moments of feeding and resting. The patterns observed in vegetated versus open areas correspond to the two behavioural modes of local search and relocation behaviour proposed by Bazazi et al. (2012). The latter mode would correspond to the recent proposition of a specific state of mass-migration of individuals once they start marching and do not encounter food for a long time (Knebel et al. 2020). However, we also observed that hoppers would walk (or hop) even if some food was still available behind them.

Farrow (1990) proposes that if emigration from a favourable habitat happens, this indicates that the migration is obligatory. The hopper bands of *S. cancellata* that we could follow moved through vegetation but did not deplete it completely everywhere they passed. This was also observed in *S. gregaria* (Kennedy 1939). This fits also with the observation of Dkhili et al. (2019) who showed that hoppers of *S. gregaria* restarted marching even if some food was still available when previously fed enough. This let believe that marching in *S. cancellata* and *S. gregaria* is an obligatory behaviour once they are gregarious. The intermittent feeding and marching pattern observed during the days together with this obligatory migration may be an adaptive response to anticipate the lack of food that may arrive if the band stayed too long in the same place. It may have evolved under the selective pressure of plague periods, when the massive population build-up may deplete the resources. As individuals do not know the size of the band they are into, it is likely that this migration strategy of alternating consuming a bit and walking is more adaptive than consuming vegetation until no food is available and then decide to migrate (Clark & Mangel 1984). Future evolutionary studies would be interesting to explore this hypothesis.

4.3. Band characteristics

As with *S. gregaria* (Ellis & Ashall 1957), we observed the highest activity of marching behaviour during two periods of the day: morning and late afternoon. The stilting and shading behaviours at the hottest hours of the day clearly displayed a heat-avoidance period between the two activity peaks. However, the dominant activities were not always synchronous across the entire band, particularly when the band was split in two parts. As basking could be done much earlier on the front part of the band the last day of observation, this part started marching earlier than the rear part of the band that spent overnight in the small forest. Hence, band shape, structure and density gradients that characterize locust hopper bands (Dkhili et al. 2017, Buhl et al. 2012) were actually depending on many factors varying locally: micro-climate, exposition to sun rays, vegetation presence and height, and recent history.

The overall shape of the band was not crescent, but more frequently with a crescent-shape front followed by a long elongated strip. As our band was mainly following the borders of an unpaved road, this may have created the elongated shape. Indeed, Lecoq et al. (1999) observed that roads tended to extend the shape of *R. schistocercoides* hopper bands. Ellis & Ashall (1957) also reports that open grounds alter bands coming out of bushes for *S.*

gregaria. Also, our measurements of walking speed of the front on bare ground, on the road or nearby, were faster than when the front was in dense vegetation. Actually, the speed of the front was clearly lowest in the densest vegetation, i.e. the forest. Hence, it is probable that the hoppers still walking within the forest were much slower than the front when it came out in open area. This structurally explains the elongation of the band the following two days.

During the third day, when the front was evolving through a weed field, we could see a wide crescent front spreading on the sides through vegetation. This is consistent with many observations of locust hopper bands of different species (Lecoq et al. 1999, Yule & Lloyd 1959, Ellis & Ashall 1957). Within this crescent-shape front, a density gradient was also observed (but not measured) with higher number of hopper on the front line than 100 meters behind. These observations also correspond to many locust band characteristics of other species (Buhl et al. 2011, Ellis & Ashall 1957). However, as illustrated with our study, the shape and distribution of hoppers within the band may be strongly influenced by local vegetation structure. Amichay et al (2016) showed that changing topography was not influencing much the coordinated march of *S. gregaria* in laboratory conditions. They also showed thigmotaxis and a tendency to spread out to fill available space. But the locusts are not fed during these laboratory experiments and feeding and thermoregulatory behaviours should be taken into account in further studies to be able to upscale from individual behaviour to marching band structure and speed.

We observed varying speed of the front of the band depending on vegetation. The fastest speed was observed on bare grounds with up to 200m/h. This is quite fast (5.5cm/s) compared to the potential walks of individuals measured for *S. gregaria* nymphs of third instar in laboratory conditions (e.g. fastest around 1cm/s in Dkhili et al. 2019, 3 to 4cm/s in Buhl et al. 2006). However, this is comparable to desert locust hopper bands moving on empty areas of sand measured in Mauritania in 2013 (Sory Cissé, personal communication) and to the punctual walking speed of third-instar individuals (up to 10cm/s) reported in Ellis & Ashall (1957). Field conditions with body temperature potentially reaching the optimal temperature probably favours high walking speed. In vegetated areas, the speed of the front of our *S. cancellata* band (between 20 and 50m/h) is comparable to documented third-instar *S. gregaria* bands (Ellis & Ashall 1957, their Fig. 6 reported from 10 to 75m/h). Overall, the daily distance travelled by the front of our band (around 300m/day) is the result of one day travelling 500m on low vegetation along the road and another one travelling 150m in weed field. These variations are similar to the vegetation effects measured by Ellis & Ashall (1957) for *S. gregaria* (for third instars: 159m/day in dense vegetation vs. 638m/day in sparse vegetation, summarized in Coppen 1999). These variations are also similar to other locust species (e.g. for *D. maroccanus* between 50 and 600m/day (Latchininsky & Launois-Luong 1992)), but much higher than for some other (e.g. 36m/day for *N. septemfasciata* (Yule & Lloyd 1959)).

4.4. Implications for controlling S. cancellata hopper bands

The thermoregulatory behaviours as well as the band marching behaviours of *S. cancellata* that we could document here are finally relatively similar to those known for *S. gregaria*. Further studies may find some slight differences, such as the activity rate at low temperature or the walking speed in different vegetation settings. However, parallels between the two species are numerous. Waloff & Pedgley (1986) have already shown that in comparable environmental settings of southern Africa, *S. gregaria flaviventris* display relatively similar outbreaking dynamics than *S. cancellata* in South America. The lower frequency of large outbreaks of the South American locust compared to the desert locust in its northern range of distribution could be explained by the interaction between the spatial settings of the outbreak areas (concentrated in one area for *S. cancellata* while spread in many places for *S. gregaria*) and the decreasing attention of the preventive management system (Gay et al. 2020, in press). On biological aspects, the gregarization process and phase polyphenism expression in laboratory settings has been analysed recently for *S. cancellata* by Pocco et al. (2019) and showed to be relatively similar to the ones of *S. gregaria* (see also Ellis 1962).

Our results, together with these other parallels, allow reassigning many recommendations of controlling techniques applied to *S. gregaria* for *S. cancellata*. For example, the recommendations concerning hopper band controls using barrier treatments, which are highly dependent on walking speed and feeding behaviours (Coppen 1999) could be used. Holt & Copper (2006) mentioned that typical barrier width of 50m should be used for *S. gregaria* mainly on small instars or in dense vegetation. This is due to the walking speed of *S.*

gregaria on sparse vegetation that is higher than a maximum of 160m/day for greatest mortality. Given that we observed that *S. cancellata* walks at least as fast as *S. gregaria*, and sometimes faster than 160m/day in third instar on open grounds, this recommendation hold also for *S. cancellata*. The computation of Coppen (1999) or Holt & Copper (2006) could be further explored with more precise and multiple measurements of front travelled distance per day of *S. cancellata* bands. The inter-barrier distance for example, could be recomputed for different settings of vegetation cover and age of the bands. Meanwhile, the recommendations for desert locust could be used for the South American one.

Concerning total cover treatments, the recommendations of FAO to control desert locust (Dobson 2001) may also be extended to *S. cancellata*. For example, a recommendation to spray in the early morning is valuable: we saw that activity and marching behaviours are less in the early morning for *S. cancellata*. Finally, as we observed that *S. cancellata* hoppers also climbed trees to spend the night, the ideas of Maeno & Ould Babah Ebbe (2018) to use roosting trees as traps for environment-friendly control techniques could be explored for the South American locust.

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Figures

Figure 1. Maps of localisation of the study site in Argentina and areas of invasion, recession and permanent breeding of *Schistocerca cancellata* following Waloff & Pedgley (1986).

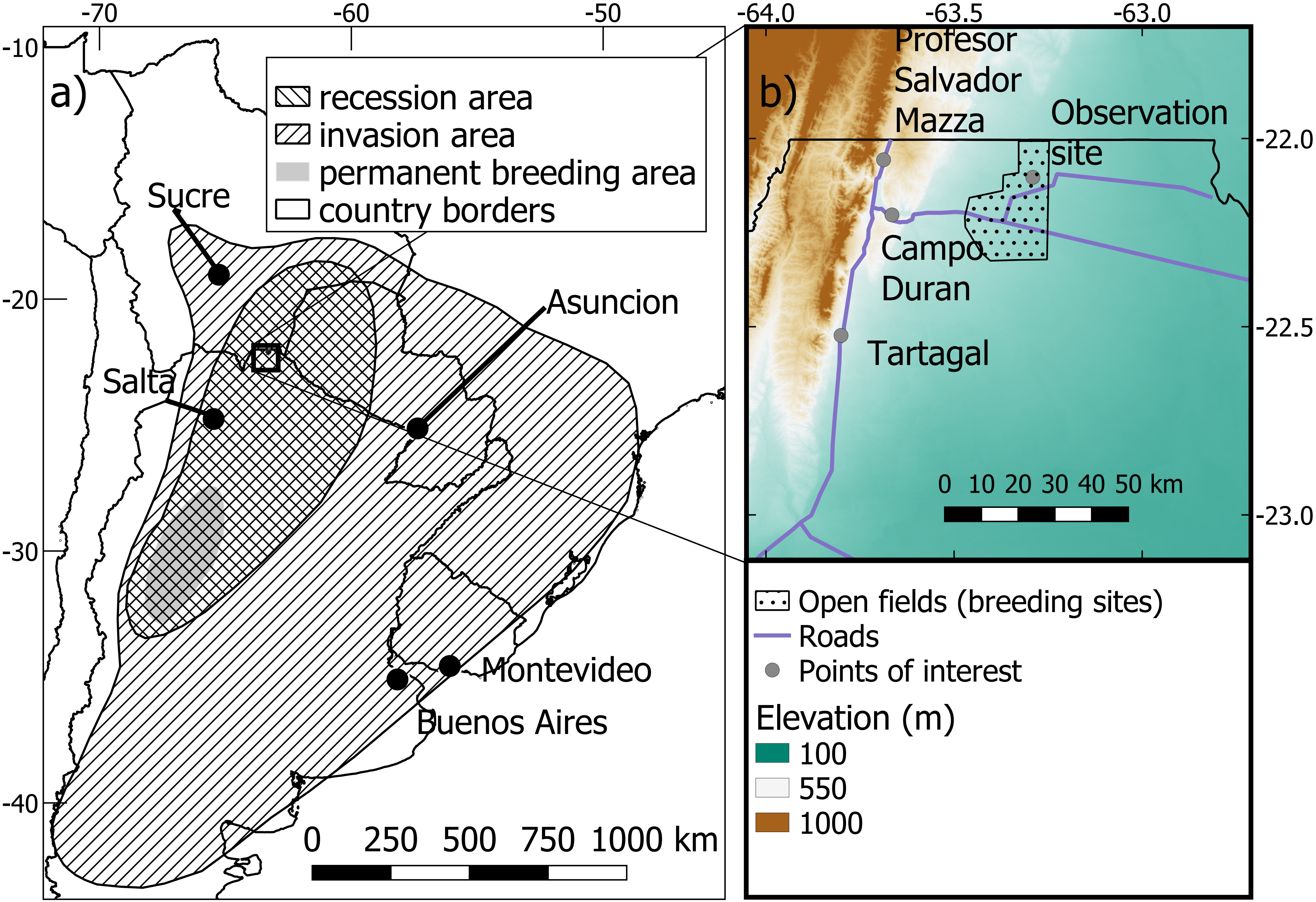
Figure 2. Maps of progression of the hopper band of *S. cancellata* followed between the 12/11/2019 and the 14/11/2019. Weed fields were cultivated lands during a fallow period (end of winter time) with a mixture of mono- and dicotyledonous plants.

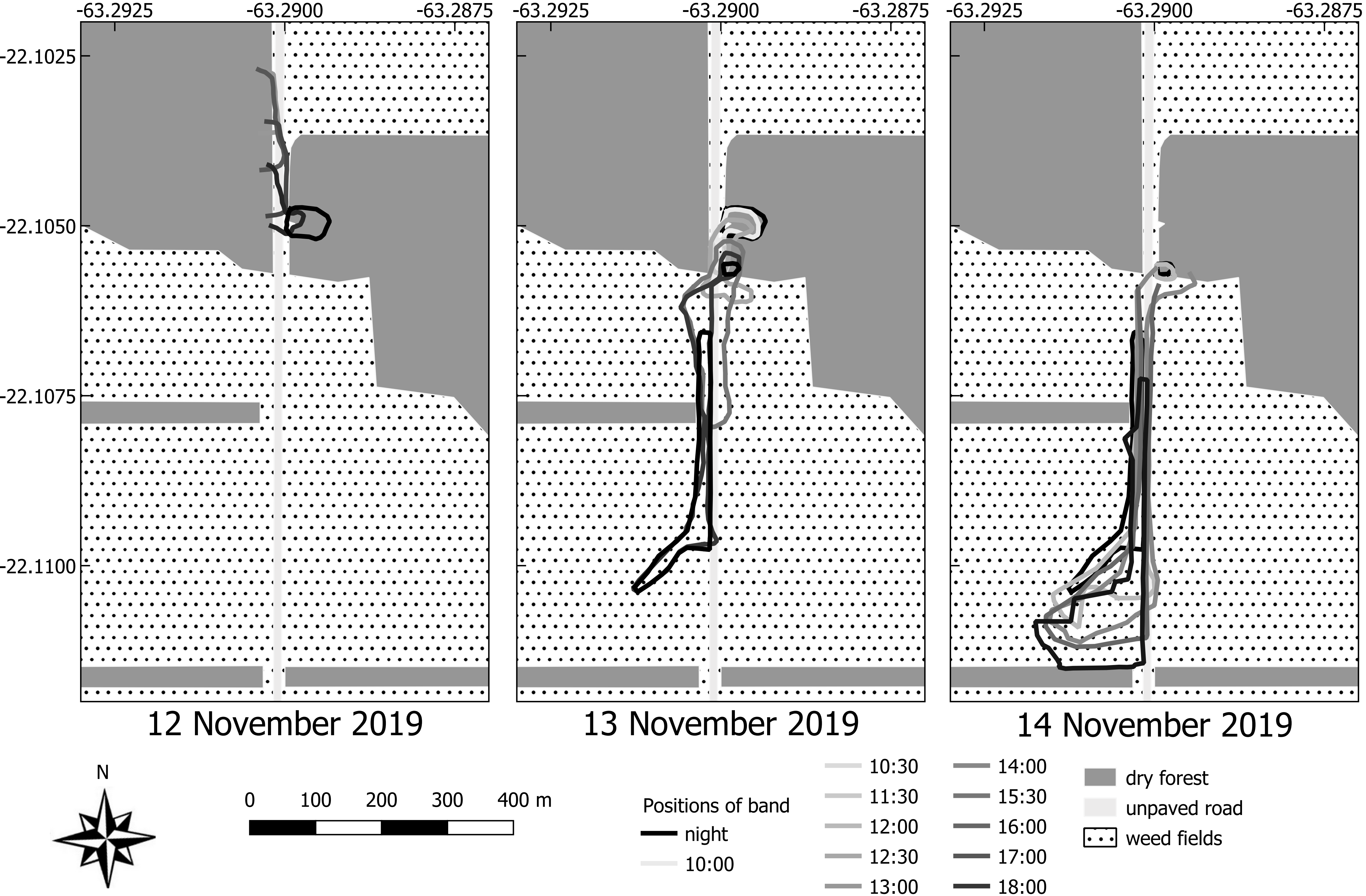
Figure 3. Average hourly temperatures over the three days of observation at the study site. Empty blue circles = Air temperature. Empty downward green triangles = Vegetation temperature. Black upward triangles = Ground temperature. Filled red circles = Estimates of hopper body temperature. Error bars represent standard deviations around the mean of the minute based recording of loggers (empty symbols) or of the picture based evaluation of temperature at hopper positions (filled circles).

Figure 4. Weighted average air, vegetation, ground and body temperatures at the time of observations of different behaviours. The weighted average were computed using the approximate percent of locusts displaying the given behaviour as weights. Empty blue circles = Air temperature. Empty downward green triangles = Vegetation temperature. Black upward triangles = Ground temperature. Filled red circles = Estimates of hopper body temperature. Error bars represent standard deviations around the mean of the minute based recording of loggers (empty symbols) or of the picture based evaluation of temperature at hopper positions (filled circles).

Figure 5. Circadian pattern of hopper behaviours during the days of observations (12-14 Nov. 2019). The N values on top of each bar indicate the number of observations per hour.

Figure 6. Index of presence of food in the foregut of N2 and N3 hoppers depending on the displayed main activity of the band at the time of collection (disregarding feeding behaviour). The N values on top of each bar indicate the number of hoppers dissected for each behaviour.

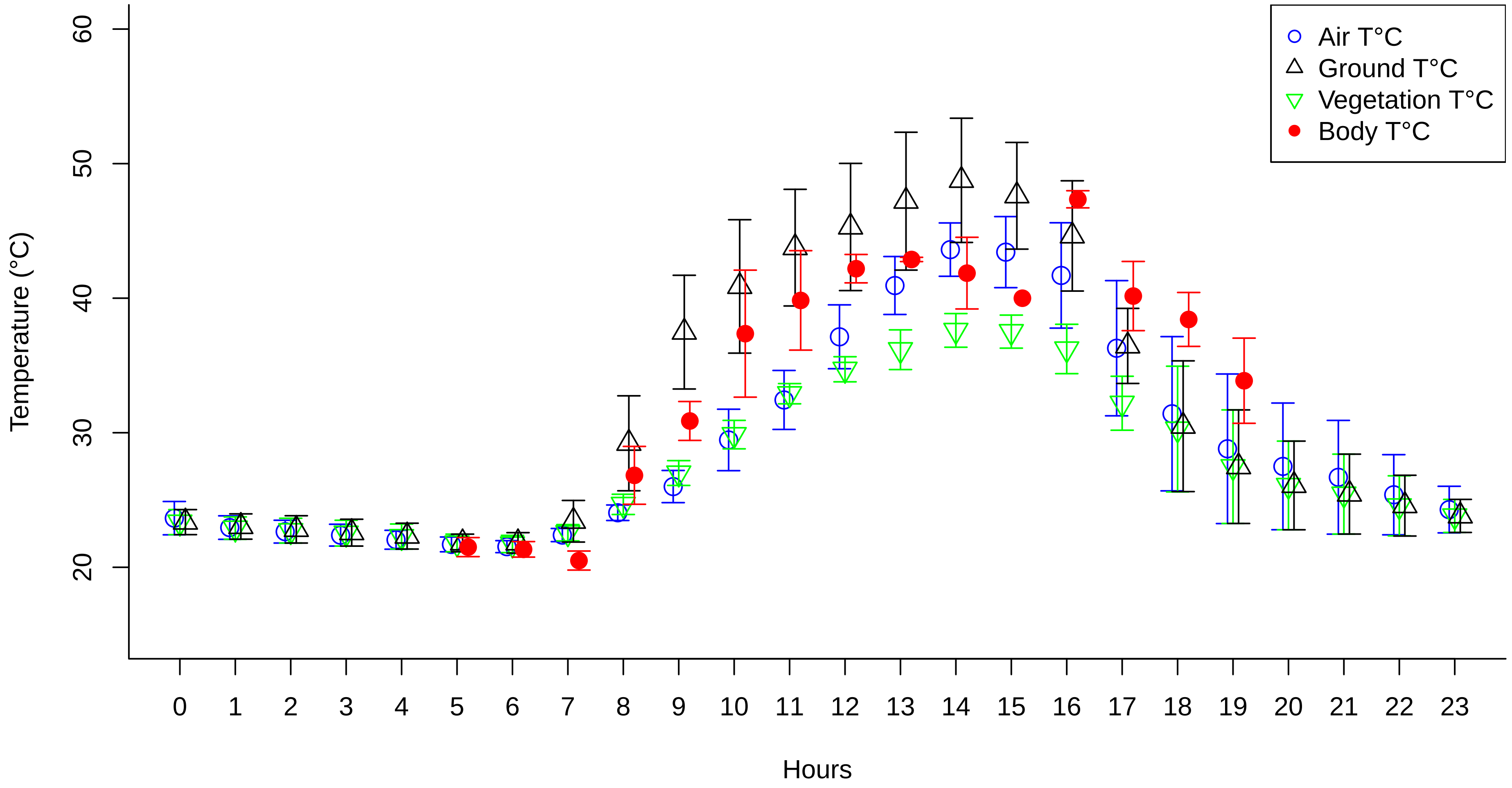

a)
recession area
invasion area
permanent breeding area
country borders
Sucre
Salta
Asuncion
Montevideo
Buenos Aires
0 250 500 750 1000 km
-70
-60
-50
-10
-20
-30
-40
b)
Profesor Salvador Mazza
Observation site
Campo Duran
Tartagal
0 10 20 30 40 50 km
-64.0
-63.5
-63.0
-22.0
-22.5
-23.0
Open fields (breeding sites)
Roads
Points of interest
Elevation (m)
100
550
1000

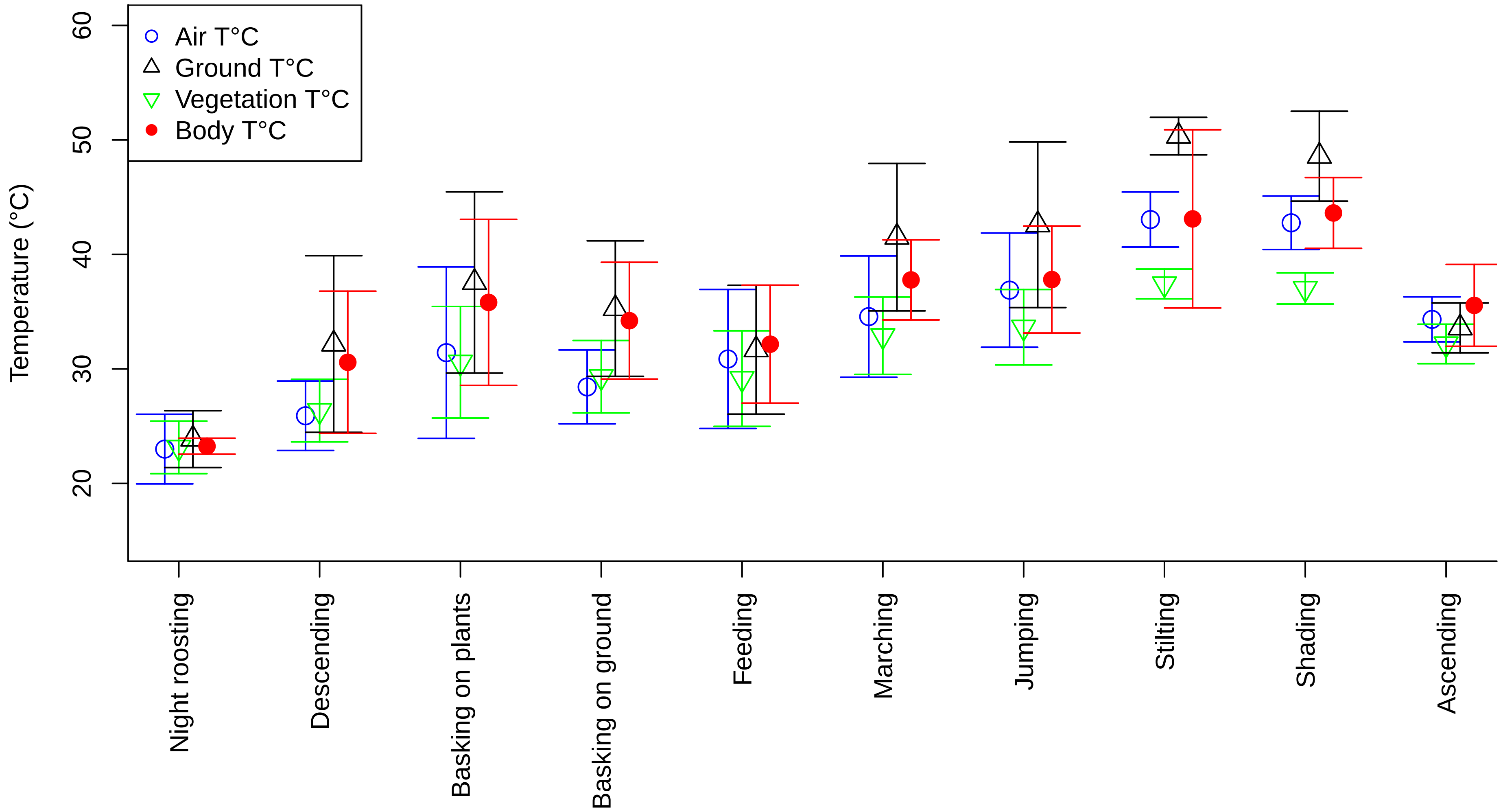


12 November 2019

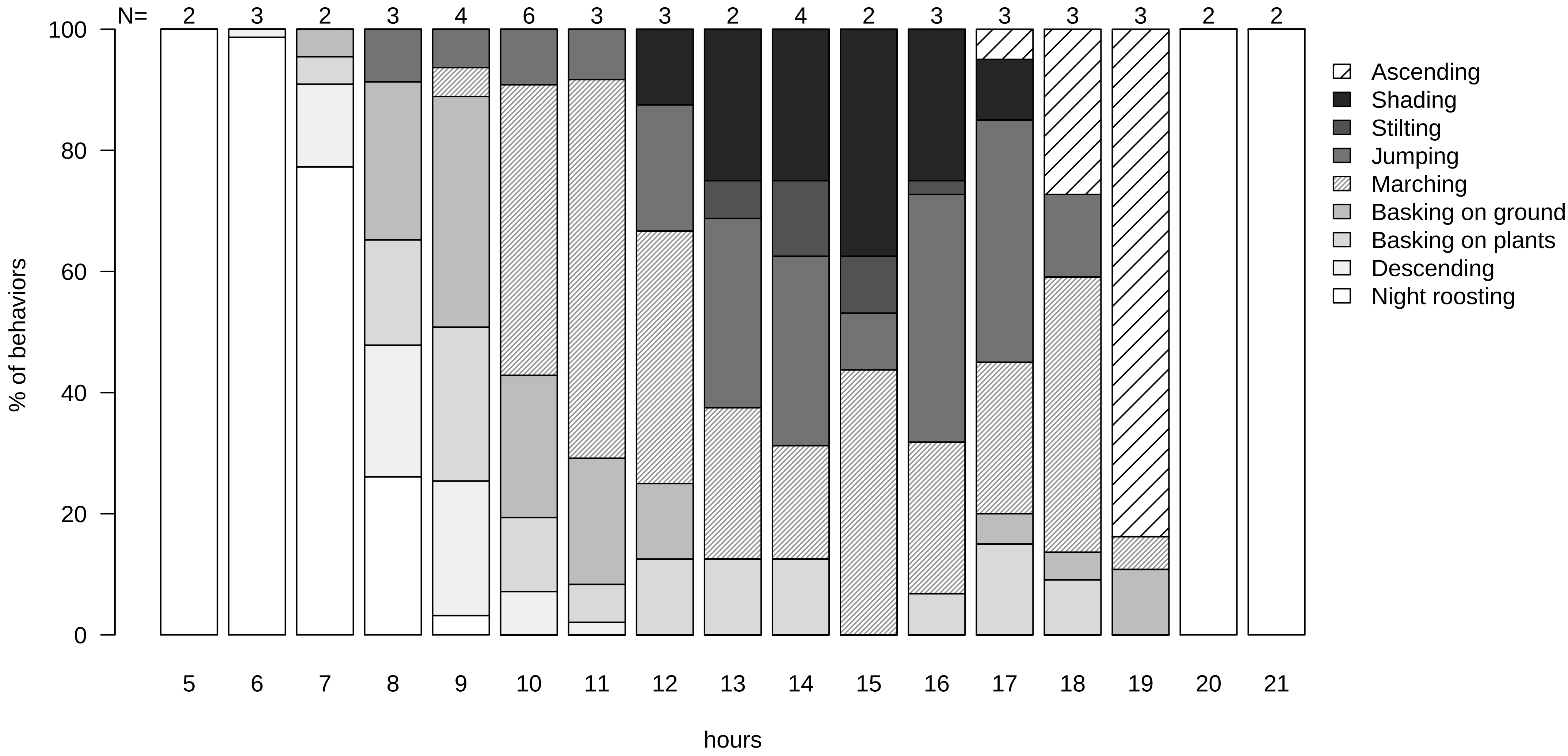
13 November 2019

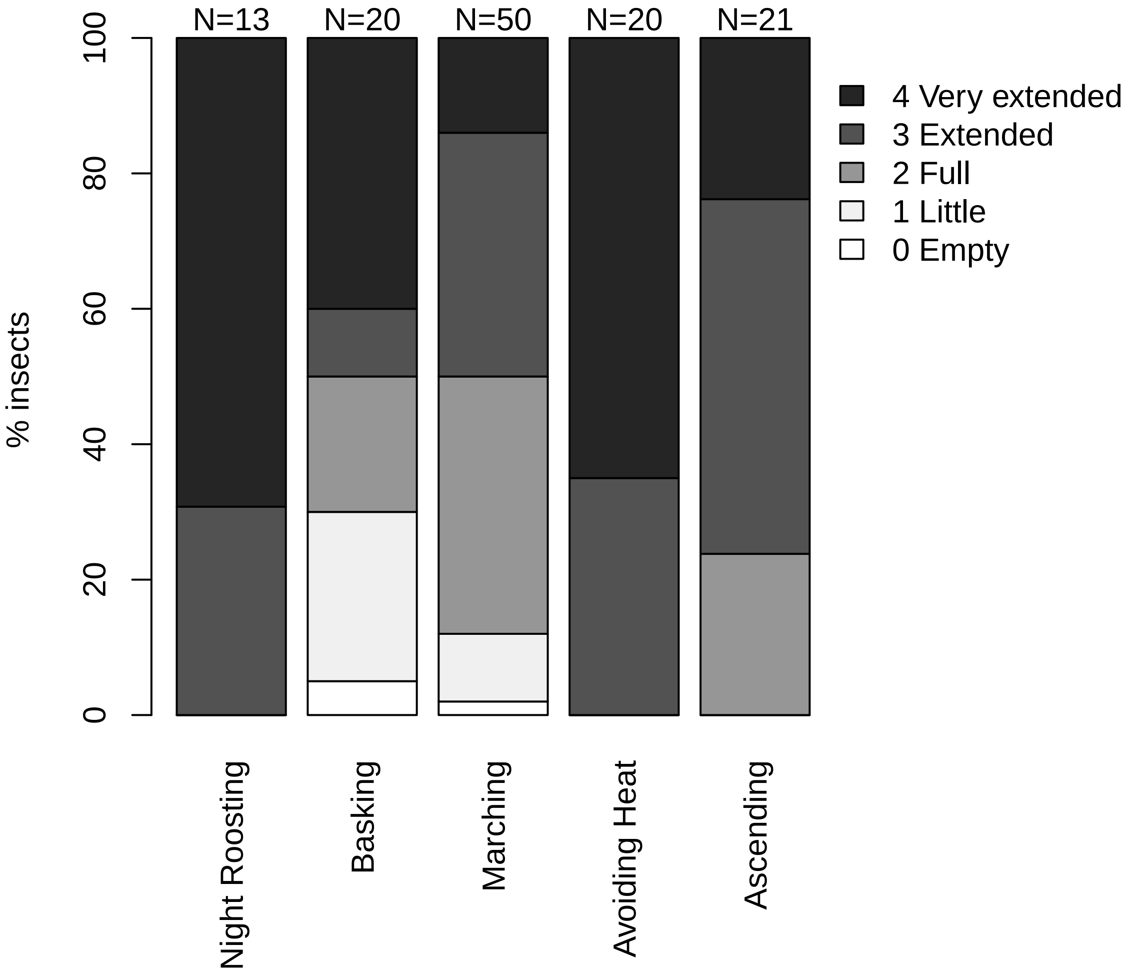
14 November 2019

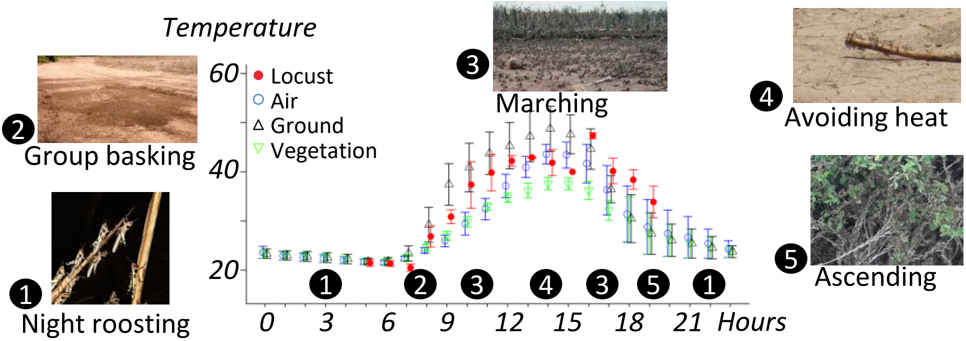

Temperature (°C)
60
50
40
30
20
Hours
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
○ Air T°C
△ Ground T°C
▽ Vegetation T°C
● Body T°C



Air T°C
Ground T°C
Vegetation T°C
Body T°C
Temperature (°C)
20
30
40
50
60
Night roosting
Descending
Basking on plants
Basking on ground
Feeding
Marching
Jumping
Stilting
Shading
Ascending


N=
2
3
2
3
4
6
3
3
2
4
2
3
3
3
3
2
2
100
80
60
40
20
0
% of behaviors
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
hours
Ascending
Shading
Stilting
Jumping
Marching
Basking on ground
Basking on plants
Descending
Night roosting


N=13
N=20
N=50
N=20
N=21
% insects
0
20
40
60
80
100
4 Very extended
3 Extended
2 Full
1 Little
0 Empty
Night Roosting
Basking
Marching
Avoiding Heat
Ascending


Temperature
Locust
Air
Ground
Vegetation
60
40
20
0
3
6
9
12
15
18
21
Hours
1 2 3 4 3 5 1
2 Group basking
1 Night roosting
3 Marching
4 Avoiding heat
5 Ascending