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FIELD OBSERVATIONS ON THE BUSH LOCUST, *PHYMATEUS LEPROSUS* (FABRICIUS, 1793), IN THE GREAT KAROO, SOUTH AFRICA (ACRIDOIDEA: PYRGOMORPHIDAE)

G. KÖHLER[1], J. SAMIETZ[2] and G. WAGNER[1]

[1] Institute of Ecology, Friedrich-Schiller-University of Jena, Dornburger Str. 159, D-07743 Jena, Germany
[2] Applied Entomology, Swiss Federal Institute of Technology (ETH), Clausiusstr. 25 / NW, CH-8092 Zurich, Switzerland

The observations on host plants, body temperature and on local movements were carried out in March 1995. The population of immature locusts occurred on shrubs pertaining to 7 families, without a significant aggregation of individuals.The locusts exhibited a tendency towards vertical movements in the *Asclepias buchenaviana* shrubs, probably due to a complex of abiotic parameters; the evidence for the inverse correlation between the height of the locusts position in the shrubs and the solar radiation (670-1100 W/m^2) is presented. The thoracic temperatures of individuals were 0.1-9.5°C higher than the ambient temperatures. The evidence indicates that *P. leprosus* basks in the sun until a radiation threshold of ca 700 W/m^2, which corresponds to a thoracic temperature of 30°C approx. Above this threshold, the locusts tend to regulate their temperature by reducing their vertical position in the vegetation. The maximum daily distance covered by marked individuals amounted to about 50 m, and the total movement over five days to 101.50 m.

INTRODUCTION

The Stinking bush locust (*Phymateus leprosus* Fabr. 1793) is distributed in South Africa, Namibia, Zimbabwe, Zambia and Swaziland (JOHNSEN, 1990; JOHNSEN & FORCHHAMMER, 1978). Considering the large size and striking appearance of *Phymateus* species, several studies are hitherto available on their life cycles (BISHOP, 1940; DE LOTTO, 1951), food habits and hopper behaviour (KEVAN, 1949; CHAPMAN, 1962; ROFFEY, 1964; ROWELL, 1967; LE GALL & GILLON, 1989). Their hopper and nymphal stages remain gregarious throughout life, forming dense aggregations and bands of at least 100 individuals (KEVAN, 1949; CHAPMAN, 1962). Later, the immature adults tend to disperse, but once mature they reaggregate for mating and oviposition (ROFFEY, 1964; ROWELL, 1967). According to BISHOP (1940), *P. leprosus* has a biennial life cycle in South Africa, and the adults occur from January to November of the first year. Following this, the Karoo population studied obviously consisted of immature adults, mainly distributed along the drainage lines in the study area. This and some details on morphometry, colour morphs, and warning behaviour has been described by KÖHLER et al. (1999).

Our observations were made during a research mission in March/April of 1995, on a population of adult *P. leprosus* in the Great Karoo, Cape Province, South Africa. They focus on some aspects of host plant spectrum, body temperature, and local movement, hitherto poorly known in bush locusts.

METHODS

Field observations were conducted from 19 to 24 March 1995, near Prince Albert, on the south-eastern edge of the Great Karoo (33°10'S, 27°17'E). At this site, an average annual rainfall of about 167 mm and a mean annual temperature of 17.5°C occur (MILTON et al., 1992). For the stratification of the locusts (see Fig. 6), we used weather data (several temperature readings, relative humidity, wind velocity, rainfall) recorded hourly for the nearby Tierberg study site. The observations on host plants and the measurements of body temperature were made on a population near the Tierberg Research Centre (Fitzpatrick Institute, University of Cape Town) ca 25 km E of Prince Albert. This study site is situated at an elevation of 800 m above sea level, within the valley of the Sandrivier, about 80 km long and 5 km wide (for further details see MILTON et al., 1992). The *Phymateus* population occurred in a dry drainage line, running SSW (Fig. 1, plot 1), 5-10 m wide and about 1 m deep. On both sides shrubs of *Asclepias buchenaviana* SCHINZ (Asclepiadaceae) occurred at irregular intervals, along

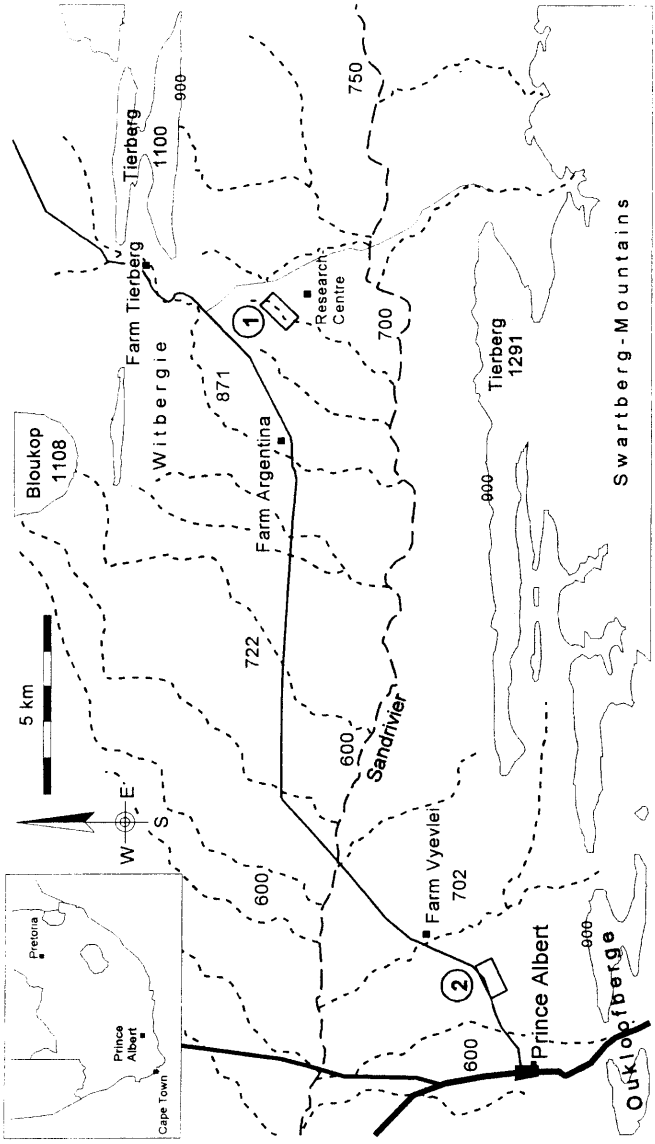

Fig. 1. Study area with the two main study plots (1 and 2) in the southeastern Great Karoo, Cape Province.

with some other shrub species and a few trees. The *Asclepias* shrubs reached a height of up to 3 m and their average diameter was 1-3 m (Fig. 2). For the locusts, we checked a section of 250 m along the drainage line for, whereas only few individuals occurred away from the drainage line in the lower shrubs.

Altogether 70 *P. leprosus* individuals were studied on 57 shrubs within the drainage line. Additional observations from a major drainage line nearby have also been considered. On 21 and 24 March between 2:00 and 5:00 p.m. we noted the sex and vertical position of each locust as well as the height and the identity of the host shrub (according to SHEARING & HEERDEN, 1994). To calculate the dispersion of the *Phymateus* individuals on the *Asclepias* shrubs, the Morisita's Index and the Standardized Morisita Index (KREBS, 1989) were used. We recorded on 24 March between 1:30 and 3:30 p.m., thoracic temperatures of 50 *Phymateus*-individuals (40 ♂, 10 ♀) sitting on sunny places on *Asclepias* stems on study plot 1. An electronic thermometer (Testoterm, Germany), with a high resolution thermocouple-probe (NiCr-Ni-thermocouple, resolution 0.1 degrees, 0.5 mm in diameter) was used. Within 5 s after taking the locust with gloves from the stem, the probe was inserted approximately 5 mm deep into the distal part of the thorax. A constant temperature was obtained after about 3 s and recorded. This "grab-and-stab" procedure has been successfully applied to gomphocerine grasshoppers (SAMIETZ & KÖHLER, 1998). In addition, we measured the ambient air temperature in the vicinity of each individual using a shaded thermocouple probe. The solar radiation energy (W/m^2), with a calibrated thermoelectric

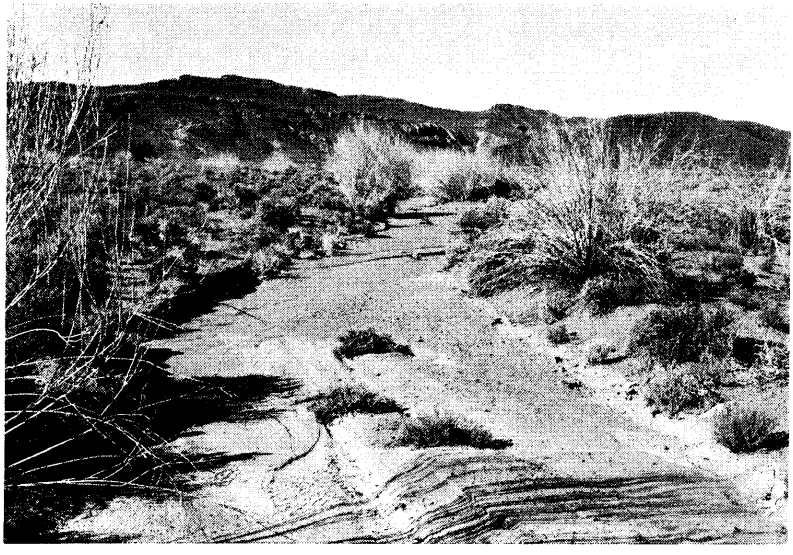

Fig. 2. Study plot 1 near the Tierberg Research Centre; a drainage line with bushes of *Asclepias buchenaviana.*

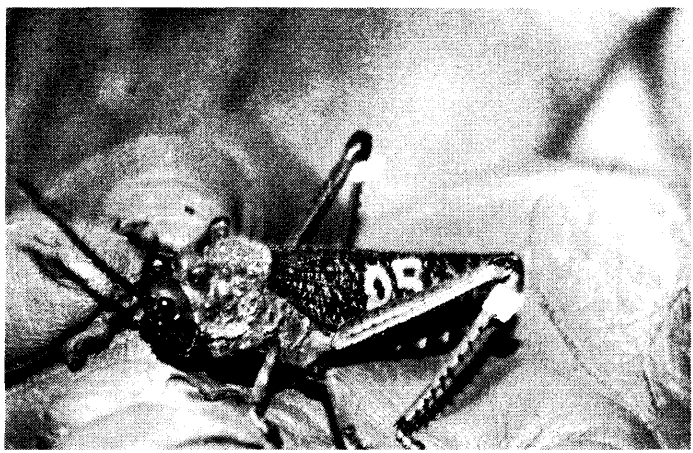

Fig. 3. Individually marked female of *P. leprosus*, with reflective tapes on the hind tibiae.

pyranometer (Thiess, Germany), was recorded every 10-20 minutes. During this time, sunny phases changed with cloudy ones, with temperatures of 23-28°C, relative humidity of 30-35%, and wind speed of 1.0-1.5 m/s.

The individual movements were recorded near the Vyevlei Farm, about 2 km E of Prince Albert (Fig. 1, plot 2), from 19 to 24 March. On 19 March, 5 females and 2 males were individually marked by a number written on their tegmina with a blue Edding paint-marker. In addition, each individual was marked with small pieces (4 × 8 mm) of self-adhesive reflective tape (3M Scotchlite 7610 high gain) on both hind tibiae (Fig. 3). This made it easy to locate the marked individuals at night, as they were visible up to a distance of about 50 m in the light of a head lamp. The marked individuals were released in a 225 m line of *Asclepias* shrubs along the southern side of a road, with one locust per shrub. After marking them, we conducted four night surveys and one survey in daylight. The locations of each locust were recorded on a detailed map of the study plot. The daily distances covered by each individual, the maximum activity radius (from the release point), and the total movement over the study period were measured.

RESULTS

DISTRIBUTION ON HOST PLANTS

The observations in the area of the Tierberg Research Centre of the Great Karoo suggested a concentration of bush locusts on mountain milk bush, *A.*

buchenaviana Schinz, sitting on the straight, thin, vertical grey-green stems of the shrub up to a height of 3 m. In study plot 1, *P. leprosus* occurred mainly on four plant species (Fig. 4). Most of the observations (73.5%) were made on *A. buchenaviana*, and only about 10% each on *Rhigozum obovatum* Burch. (Bignoniaceae) and *Acacia karoo* Hayne (Fabaceae). Only a single locust was found on *Grewia robusta* Burch. (Tiliaceae). In a neighbouring locality this species also occurred on *Rhus undulata* Jacq. (Anacardiaceae). A somewhat different host plant spectrum could be detected in study plot 2, including individuals found during the night within the mark-recapture experiment (Fig. 4). Here we found only about 40% of the locusts on *Asclepias* and the same proportion on *Rhigozum*. The other individuals settled on *Euphorbia* sp. (Euphorbiaceae) and *Lycium oxycarpum* Dunal (Solanaceae).

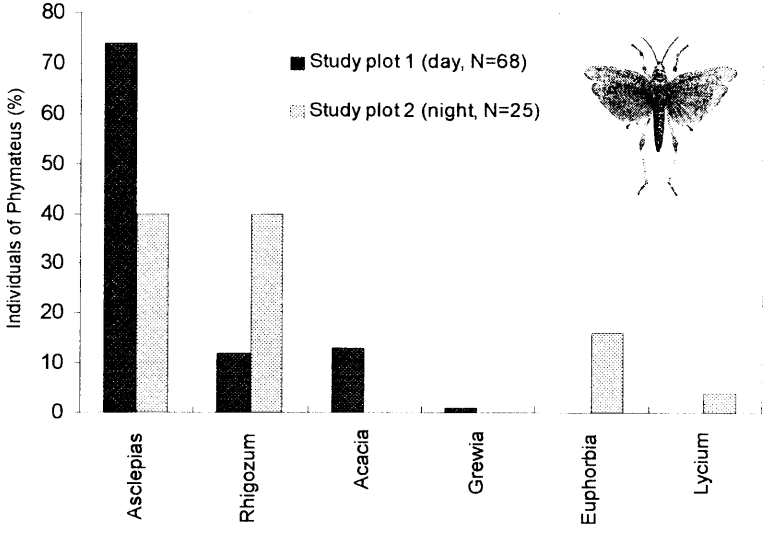

Fig. 4. Host plants of *P. leprosus* in the two study plots.

The numerical distribution of *Phymateus* individuals on *Asclepias* shrubs is shown in Figure 5. Thus, 54% (31 shrubs) were found without any locusts. Further 19% of the plants had a single locust, while 12% and 11% of the shrubs, respectively, were found with 2 or 3 individuals. In two cases

(each 2%), we even found 4 and 6 individuals per shrub, respectively. The male assemblages were particularly remarkable. From seven shrubs with 2 and six shrubs with 3 individuals, five of each were only settled by males. In total, at least three times more males than females could be found. Using Morisita's Index of Dispersion (0.498) for all individuals, the chi-square distribution shows no significance for aggregation. Furthermore, the 95% confidence of the Standardized Morisita Index of Dispersion (-0.606) indicates uniform distribution. The latter index, calculated for males only (-0.079), indicates a random distribution.

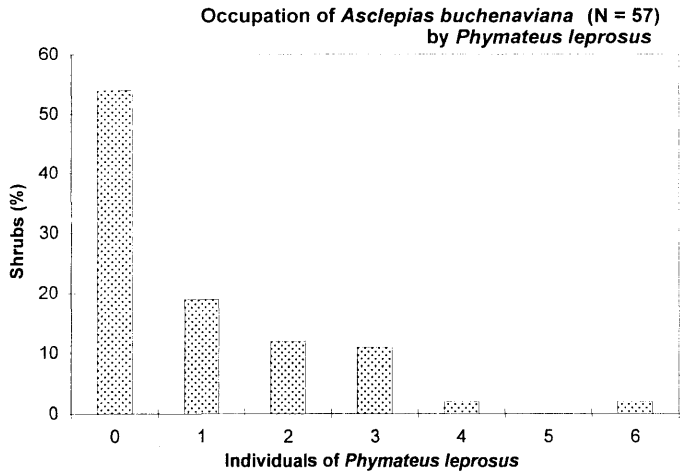

Fig. 5. Occupation of *Asclepias*-shrubs by immature *P. leprosus* on study plot 1.

During the study, the locusts were resting near the base and at the top of the *Asclepias* stems (Fig. 6). There was no clear evidence as to the preferred strata, although a measurement of the same population in the same shrubs three days later yielded somewhat different results, suggesting individual movements within the shrubs. On 21 March in the afternoon, the locusts settled distinctly higher (median: 100 cm) than on 24 March in the afternoon (median: 60 cm), visible also in the distribution (Fig. 6 a, b). The difference in the median values between the two days is highly significant (Mann--Whitney-rank sum test: $p<0.0001$). During the mark-release observations in the evening hours (mean temperature of 16.3°C), the locusts (on *Asclepias* only) occurred in the middle and lower strata (Fig. 6c).

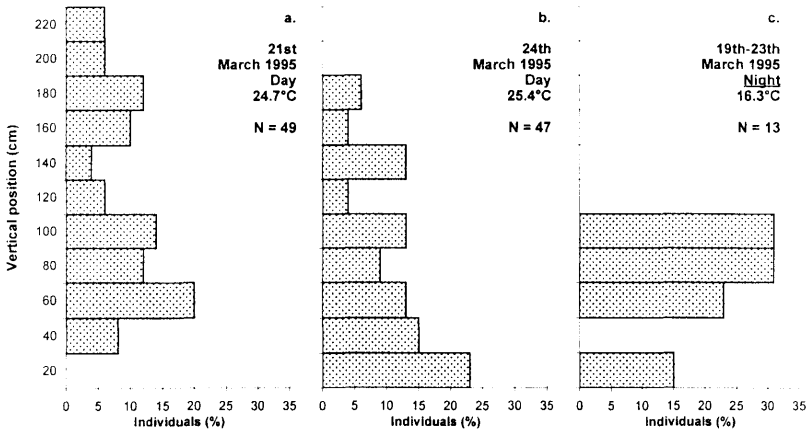

Fig. 6. Vertical distributions of *P. leprosus* in shrubs of *Asclepias buchenaviana* at study plot 1 (a, b) and 2 (c).

BODY TEMPERATURE

The measurements of thoracic temperature in immature *P. leprosus* showed considerable differences between the ambient and the thoracic temperature (Fig. 7). The temperature difference (dT) ranged from 0.1 to 9.5°C, and the thoracic temperature of about 65% of the individuals was 3-5° higher than the surrounding air temperature (mean 5.1, median 5.2°C). The distribution did not differ significantly from the expected pattern of a normal distribution (Kolmogorov-Smirnov-normality test, $p = 0.2708$). The mean temperature of the males differed with respect to the ambient air temperature, and that of the females by 6.5°C. The difference by 4.9° between the values for males and females was not significant (T-test, $p = 0.064$). The Mann-Whitney-Rank sum test showed no difference between the sexes with respect to solar radiation ($p = 0.206$), ambient air temperature ($p = 0.719$), and vertical position ($p = 0.766$).

The temperature difference (dT) can be related to ambient air temperature, the amount of radiation energy, and vertical position of *P. leprosus*, as shown in two interpolated graphs (Figs 8, 9). It is noticeable that they vary very little along ambient temperature axis in both plots. On the one hand, one would expect the ambient temperature to correlate positively with the thoracic temperature (Spearman: $r_S = 0.587$, $p < 0.001$),

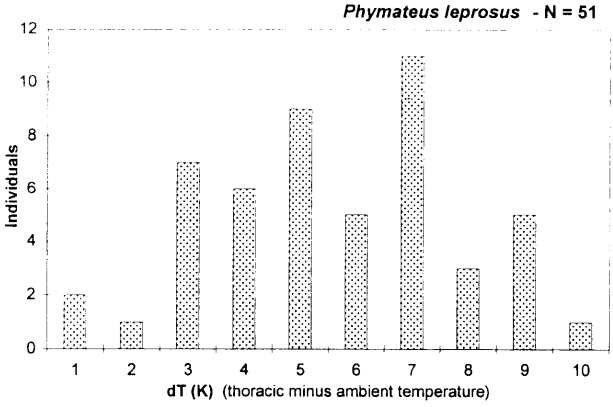

Fig. 7. Differences between thoracic and ambient temperature (dT) in the population of *P. leprosus*.

but it has only a small effect on the increase in thoracic temperature (dT) in *P. leprosus* within the range of 23-29°C. On the other hand, this temperature difference showed a distinct pattern along the radiation axis in Figure 8. The temperature difference (dT) increased with the radiation energy. At about 700 W/m², the maximum difference amounted to roughly 5°C. The thoracic temperature of the locusts in this range reaching about 30°C. When the radiation increased above 700 W/m², then dT decreased (Fig. 8). In the same range, there was also a highly significant decrease in the thoracic temperature of the locusts with increasing radiation (r_S = -0.385, p = 0.009). This decrease in the temperature difference corresponded to a decrease in the vertical position of *P. leprosus* in the shrub. For solar radiation between 670 W/m² and 1100 W/m² there was a highly significant negative correlation with the vertical position of *P. leprosus* (r_S = -0.455, p = 0.002; Fig. 9). After that, the ambient temperature did not seem to have an influence on the vertical position of the locust for temperatures between 23-29°C (r_S = -0.158, p = 0.290).

LOCAL MOVEMENT

The individual movement of females over five days (Tab. I) varied considerably in regard to the daily distance covered (0.00 m - 50.00 m), the

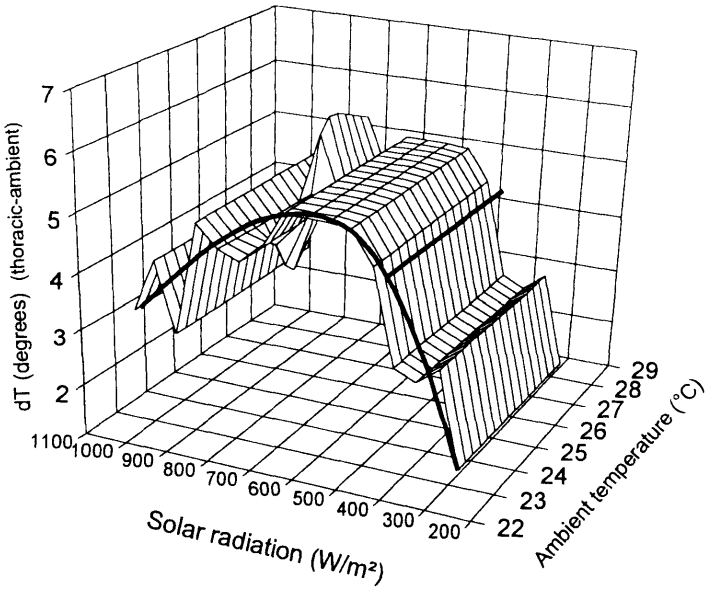

Fig. 8. Relation between solar radiation, ambient air temperature, and difference between thoracic and ambient temperature (dT) of *P. leprosus* in *Asclepias* shrubs. N = 45, interpolated by Sigma Plot.

maximum activity radius (1.20 m - 63.00 m), and the total movement (2.75 m - 101.50 m). The two males could be observed for only three days with daily distances of 0.00 m and 13.50 m, an activity radius of 10.70 m and 13.00 m, and total movements of 20.70 m and 28.00 m, respectively (Tab. I). Obviously, some females covered a greater distance than the males during the same period. Other females however, were rather stationary, and one of them (05; cf. Fig. 3) remained in the same *Asclepias* shrub during the whole period. The shrub's size may also had an influence, since this stationary female was released in the largest shrub.

The locusts never crossed the sandy gravel road, 6-8 m wide, even though the same vegetation structure prevailed on the other side. This may indicate a preference for movement through vegetation, perhaps to avoid predators or extreme heating. We believe that these small-scale movements were the result of locusts walking on the ground, since we never observed any

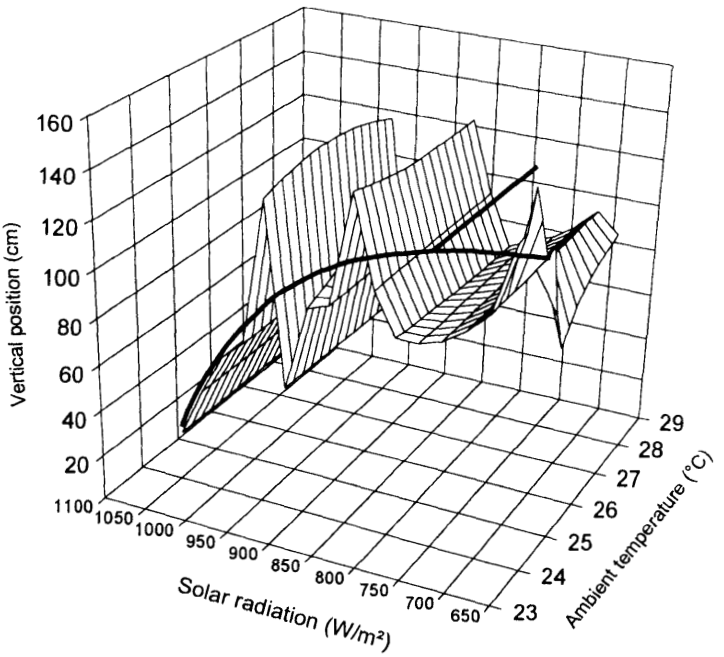

Fig. 9. Relation between solar radiation, ambient air temperature, and vertical position of *P. leprosus* in *Asclepias* shrubs. N = 45, interpolated by Sigma Plot.

Phymateus flying (either by day or by night). Furthermore, in study plot 1, in the major drainage line, we took a *P. leprosus* female from an *Acacia karoo* and put it on the sandy soil at a distance of 15 m from the tree. Within 15 minutes, the locust walked directly to the *Acacia* and climbed a twig on the same tree.

DISCUSSION

Assuming that the host plants are also the food plants of the locust, *P. leprosus* must be characterized as a rather polyphagous species, since the seven recorded plant species belong to seven different families. This agrees with what we know of the other Pyrgomorphidae in general and of *Phymateus* species in particular, which are polyphagous on forbs, as shown by analyses of the crop contents (CHAPMAN, 1962) and the faeces (LE GALL & GILLON, 1989). According to KEVAN (1949) there is a marked

Table I
Individual based activity radius and host-plant use in *Phymateus leprosus* between 19 and 24 March 1995 near Prince Albert/Great Karoo

	Maximum activity radius	Date	Hour	Distance covered (m)	Occupied plant (genus)	Vertical position (cm)
Female 01	4.5 m	19-III-1995	16:30	0.00	*Asclepias*	20
	(19/24-III)	19-III-1995	21:30	4.00	*Rhigozum*	100
		20-III-1995	21:00	4.50	*Asclepias*	70
		21-III-1995	21:30	0.50	*Asclepias*	80
		23-III-1995	22:45	0.50	*Asclepias*	80
		24-III-1995	18:00	0.50	*Asclepias*	20
Female 02	31.3 m	19-III-1995	16:30	0.00	*Asclepias*	80
	(19/24-III)	19-III-1995	21:30	22.50	*Euphorbia*	45
		20-III-1995	21:00	0.00	*Euphorbia*	50
		21-III-1995	21:30	8.50	*Rhigozum*	50
		23-III-1995	22:00	0.00	*Rhigozum*	50
		24-III-1995	17:30	8.50	*Euphorbia*	20
Female 03	63.0 m	19-III-1995	17:00	0.00	*Asclepias*	20
	(19/24-III)	19-III-1995	21:45	6.50	*Euphorbia*	50
		20-III-1995	21:15	45.00	*Lycium*	100
		21-III-1995	21:45	50.00	*Rhigozum*	120
		23-III-1995	22:15	0.00	*Rhigozum*	125
		24-III-1995	17:45	0.00	*Rhigozum*	50
Female 04	10.4 m	19-III-1995	17:30	0.00	*Asclepias*	10
	(19/23-III)	19-III-1995	22:00	10.40	*Rhigozum*	150
		20-III-1995	21:30	0.00	*Rhigozum*	130
		21-III-1995	22:00	0.00	*Rhigozum*	135
		23-III-1995	22:30	2.00	dead on ground	
Female 05	1.2 m	19-III-1995	17:45	0.00	*Asclepias*	0
	(19/24-III)	19-III-1995	22:15	0.50	*Asclepias*	50
		20-III-1995	21:45	0.50	*Asclepias*	60
		21-III-1995	22:15	0.00	*Asclepias*	100
		23-III-1995	22:45	0.75	*Asclepias*	100
		24-III-1995	18:00	1.00	*Asclepias*	20
Male 06	13.0 m	19-III-1995	18:00	0.00	*Asclepias*	0
	(19/21-III)	19-III-1995	22:30	5.00	*Asclepias*	100
		20-III-1995	22:00	9.50	*Rhigozum*	120
		21-III-1995	22:30	13.50	leg on ground	

Male 07	10.70 m	19-III-1995	18:15	0.00	*Asclepias*	15
	(19/21-III)	19-III-1995	22:45	0.00	*Asclepias*	50
		20-III-1995	22:15	10.70	*Lycium*	45
		21-III-1995	22:45	10.00	*Rhigozum*	100

preference in *P. aegrotus* for certain Euphorbiaceae and perhaps other latex--producing plants. Although the host plant choice of *P. leprosus* is expected to depend on the available shrub species in the Tierberg area (which were not surveyed), this locust obviously preferred *Asclepias buchenaviana*, a latex-producing Asclepiadaceae.

The thoracic temperature was in *P. leprosus*, on average, about 5°C higher than the ambient temperature. This is much less than has been found in comparable North American desert dwelling grasshoppers, such as *Dactylotum bicolor* (11.5°C; PARKER, 1982) or *Taeniopoda eques* (16.6°C; WHITMAN, 1987). Although the sampling period was short, our results suggest that thermoregulation might take place in immature *P. leprosus* by movements within the shrubs, a familiar phenomenon in the black desert grasshopper, *Taeniopoda eques* (WHITMAN, 1987), or in *Dactylotum bicolor* nymphs in the deserts of New Mexico, USA (PARKER, 1982). We consider that *P. leprosus* may actively bask in the sun up to a solar radiation of approximately 700 W/m², corresponding to a thoracic temperature of approximately 30 °C. Above this threshold the locusts may decrease their temperature excess by reducing their vertical position in the *Asclepias* shrubs. In that way they may hide from the insolation and regulate their thoracic temperature according to the ambient air temperature.

During the study of local movement, no locusts walking on the ground or flying in the air could be observed. This does not mean that this species is unable to fly, because another giant species, *P. viridipes*, was observed to fly long distances without interruption and swarms in thousands despite its sluggish behaviour (ESBJERG, 1976; DE VILLIERS, 1985; JOHNSEN, 1990). Our observations on mobility indicated considerable daily movements of some individuals. This gives evidence of nocturnal movements, perhaps as a predator-avoiding strategy. Few chitinized remains of marked *P. leprosus* refer to ants as important predators, whereas the poisonous locusts are protected from vertebrate predators. Perhaps the individual preferences at lower strata in *Asclepias* shrubs during the evening hours are the result of a beginning nocturnal dispersal. Considerable distances covered are known in nymphal *Zonocerus variegatus* bands, 500-

-800 m during the entire nymphal period (VUILLAUME, 1954) and as much as 50 m in one day in single individuals (CHAPMAN et al., 1986).

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