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Ten Instars in the Leprous Grasshopper, *Phymateus leprosus* (Fabricius, 1793) (Caelifera: Pyrgomorphidae): Maximum Number Recorded in the Acridoidea

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Abstract. First instars of the pyrgomorphid *Phymateus leprosus* (Fabricius, 1793) were collected in the Great Karoo (South Africa). In the field about 190 hoppers were distributed in small groups over 1.5 m^2 during the day, but densely aggregated during the night. The hoppers reared in captivity, were fed with *Vincetoxicum*, *Euphorbia* and *Rubus*. The mortality of the first instar hoppers was 97 %, but few of those that survived reached adult moult. Ten juvenile instars of variable duration (2–8 weeks each) occurred in both sexes, which is the highest known stage number in the Acridoidea. Postfemur and body length measurements (exuviae) as well as short descriptions are presented for each instar. The juvenile development lasted about one year, and the phenology corresponded with long-standing field observations by Bishop (1940). One male and three female grasshoppers completed the biennial life cycle (April 2000 to January 2002). The adult lifespan amounted to 2–8 months, with mating attempts after three months, but no egg pods were produced. The ovariole numbers varied from 116 to more than 187. Fully developed eggs were found in females that died in July/August, but not in a female that died the following January. The few known reproduction parameters of the genus *Phymateus* are summarized.

Keywords. *Phymateus*, juvenile stages, biennial life cycle, reproduction, South Africa.

1. INTRODUCTION

The genus *Phymateus* belongs to the tribe Phymateini within the family Pyrgomorphidae (Kevan & Akbar 1964). It is distributed with eight species in continental Africa south of the Sahara and two species in Madagascar (distribution maps in Anonymous 1982). These giant and colourful Orthoptera are popularly known as bush grasshoppers or bushhoppers, sometimes (and erroneously) as bush locusts or milkweed locusts. They inhabit semi-deserts with Karoo vegetation, tree savannas, woodland, as well as gardens and other cultivated areas (Anonymous 1982, Johnsen 1990, Picker et al. 2002). They can cause damage in several crops (summarized by Uvarov 1977, Anonymous 1982, Sithole 1986). This initiated studies on their biology, dealing with life cycles (Bishop 1940, De Lotto 1951), food habits (Kevan 1949, Chapman 1962), and hopper behaviour (Roffey 1964, Rowell 1967). The chemical defence of the pyrgomorphids including *Phymateus* was summarized by Whitman (1990). Recently, the genus became a study object in biochemical and endocrinological research (e.g. Gäde & Kellner 1995, Gäde 2002), pharmacophagy (Seibt et al. 2000), and flight capability (Kutsch et al. 2002). Ephemeral studies dealt with local dispersion, thermoregulation, and short-term movement of adult bush grasshoppers (Köhler et al. 1999, 2001a). Despite of these research activities, few data exist about the complete life cycle in either the field or the laboratory. Information on hopper stages are available from only two *Phymateus* species (Bishop 1940, De Lotto 1951, Kaufmann 2000). Therefore, the present article focuses on the instars of *Phymateus leprosus* (Fabricius, 1793), particularly their number, morphometry and duration. The species, here popularly named as leprous grasshopper (according to Samways 2005), was reared over its whole life cycle in the laboratory, enabling us for the first time to observe an exact number and differences of the instars.

2. MATERIAL AND METHODS

In the afternoon of the 24th April 2000 a bulk of densely aggregated hatchlings of *P. leprosus* was found in the Eastern Great Karoo, South Africa, about 100 km N Port Elizabeth near a camp with typical Karoo vegetation (S.R.). With respect to an ovariole number >200 per female (see Table 2) and the same size and colour of hoppers within the bulk, it was very likely the complete offspring of one egg pod deposited nearby in the soil, but which was not found. Most of the hoppers were collected next morning in a plastic contain and, together with some not specified native plant species, transported to Jena/Germany. Later the adults were identified as *Phymateus leprosus* (Fabricius, 1793).

About one week after collection the hoppers were reared in a terrarium (l 34 x w 18 x h 46 cm) in the Institute of Ecology (G.K.), placed on the sunny window directed to SSE. During field-work in the Great Karoo the adults of *P. leprosus* were mostly found on *Asclepias* bushes (KÖHLER 1999, 2001a). And BISHOP (1940) mentioned a frequently attacked *Euphorbia* species. Therefore we offered food plants of the same families, *Vincetoxicum hirundinaria* (Asclepiadaceae) and *Euphorbia cyparissias* (Euphorbiaceae), from the surroundings of Jena from May to October 2000. Because these plants were not available in winter of 2000/2001, leaves of *Rubus* sp. (Rosaceae), a generally accepted food plant for herbivorous insects, were provided during further captivity. According to ANONYMOUS (1982) and our field observations grass is not eaten by the species.

In regular intervals the exuviae of the hoppers were collected and preserved dry. Later the length of the left hind femur and the body length from these exuviae were measured with an Electronic Vernier Calliper (Helios-digit, accuracy 0.02 mm). The formation of wing pads was noted. For measuring the early instars a stereoscope (x10) was used. The exuviae of all instars are deposited in the Institute of Ecology at the University of Jena. The culture was maintained until the death of the last adult. Immediately after death, the females were dissected for classifying the ovarian development according to the terminology (I–IV) of PHIPPS (1949) and for counting the ovarioles resp. eggs.

Later the preserved and mounted adults were also measured (body length, pronotum, postfemur, forewing). For not stressing the few individuals, no photos or line drawings were made. The sex ratio was determined from the dead first instar hoppers, and from those that survived. To do this, the hardened hoppers were softened with water vapour. Despite the black colouration the sex of most individuals was identified by the shape of the external genitalia of the terminal abdominal segments (subgenital plate in male, upper and lower ovipositor valves in female – as described in UVAROV 1966).

3. RESULTS

3.1. Offspring, mortality, and hopper aggregation

From the aggregated bulk in the field (Fig. 1), altogether 172 first instar hoppers had been sampled, whereas about 5–10 % had escaped. Thus, about 180–190 hoppers should have hatched from this obviously one egg pod. The sex ratio of the bulk could be confirmed as nearly equal, with altogether 84 male and 80 female first instar hoppers, and 8 of unknown sex. These first instar hoppers suffered from a very high mortality, perhaps to a lower extent by the transport stress and after that mainly by the habituation to new food plants in the culture (*Vincetoxicum, Euphorbia*). Otherwise, from the potential native food plants given into the plastic contain only few were eaten during the transport. After one week of transport, 30 dead hoppers were found in the plastic contain, resulting in a mortality of 17 %. During the following two weeks in the terrarium nearly all individuals of the surviving bulk also died, so the total first instar mortality amounted to 97 %. Only five hoppers moulted in early May to the second instar, but these five survived to adult moult, with *Vincetoxicum*, *Euphorbia* and *Rubus* as food plants.

Fig. 1. Bulk of first instar hoppers of *Phymateus leprosus* (body size about 6 mm) showing aggregation behaviour in the late afternoon. Eastern Great Karoo, South Africa, late April 2000. Photo: S. Roth.

The field observations in the Karoo showed that in the afternoon (24.04.2000, about 20°C, some clouds) the individuals were distributed over an area of about 1.5 m^2 mostly in small groups of five to ten hatchlings sitting at a height of 30–40 cm on high shrubs and grasses. With decreasing evening temperature and during the relatively chilly night (8–10 °C) all individuals gathered into a single dense bulk occupying about 0.15 m in diameter (Fig. 1). The aggregation behaviour was also observed in the following days within the plastic contain: dense aggregations during the night and looser ones during the day.

3.2. Number, colouration and duration of instars

Both hind femur and body length of exuviae originating from successive moults showed ten size classes with al-

Table 1. Morphometrical parameters of all developmental stages of *Phymateus leprosus* (Fabricius). Measurements: in juveniles – exuviae, in adults – dry mounted specimens. One male and four (juv.) resp. three females (ad.). In brackets – length influenced by shrinkage.

Parameter	Postfemur length (mm)		Body length (mm)	
instar / sex	male	female	male	female
1	2.9	2.9–3.0	6.8	6.2–6.7
2	3.9	3.9–4.3	8.4	7.1–8.0
3	5.0	4.7–5.0	10.1	8.8–9.6
4	5.8	5.8–6.6	10.7	10.2–11.8
5	7.4	7.3–8.3	12.7	11.8–13.7
6	9.0	8.5–10.7	16.0	13.8–16.1
7	11.5	10.9–13.2	[15.5]	16.8–17.8
8	14.9	13.1–16.4	19.1	20.1–25.1
9	17.7	18.1–19.7	24.9	27.1–34.7
10	23.3	23.1–25.8	42.8	42.5–42.8
adult	30.0	30.0–33.0	[50.0]	58.0–62.0

Fig. 2. Last instar nymph of *Phymateus leprosus* (body size about 40 mm). Great Karoo (S.A.), Tierberg Research Centre. Photo: J. Samietz.

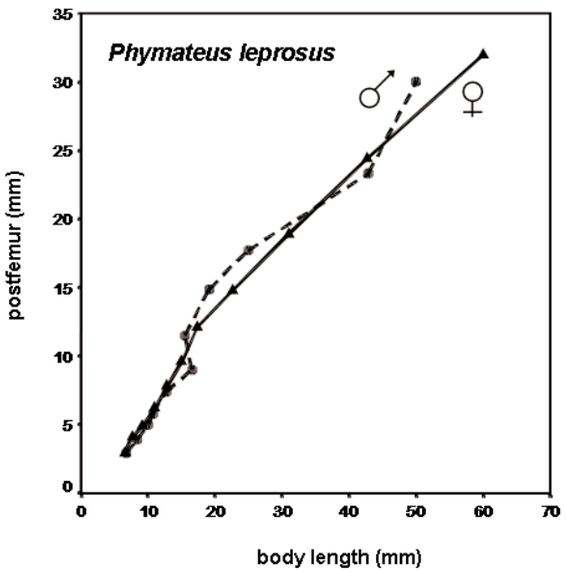

Fig. 3. Isometric growth in juvenile development of both sexes in *Phymateus leprosus*. Male (n = 1), females (n = 3). See also Table 1.

most no overlap in the male and females of *P. leprosus* (Table 1). According to the location of the wing pads, there are eight hopper (L1–L8) and two nymphal stages (L9–L10; Fig. 2). There is an isometric growth between body and postfemur length (Fig. 3). The body size of both sexes was largely identical over the entire juvenile development, but showed considerable differences in the adult stage (Table 1, Fig. 3).

The instars one to three were mostly black with several small yellowish or orange markings (Fig. 1). Two light spots were on the frons. On the upper and lateral pronotum as well as along the margins there were yellowish markings. On each of the first eight abdominal segments there was a lateral drop-shaped to trapezoid spot, whereas dorsally a fine creamy stripe occurred. Ventrally the thorax had four lateral spots near the coxae of the first and third pair of legs, while the antenna and legs were completely black. In the female hoppers the markings appeared slightly larger than in the male hoppers. Beginning with instar four the lighter portions (more or less of a bright green) extended successively, beginning on the tibiae of the hind and median legs, followed by the pronotum and other parts of the body (Fig. 2). In both sexes, the antennal segments increased from eight (instar 1–4) over eleven (instar 5–6) and 15 (instar 7) to 18–20 (instar 8–9) and 21 (instar 10 – Fig. 2), and in the females they varied

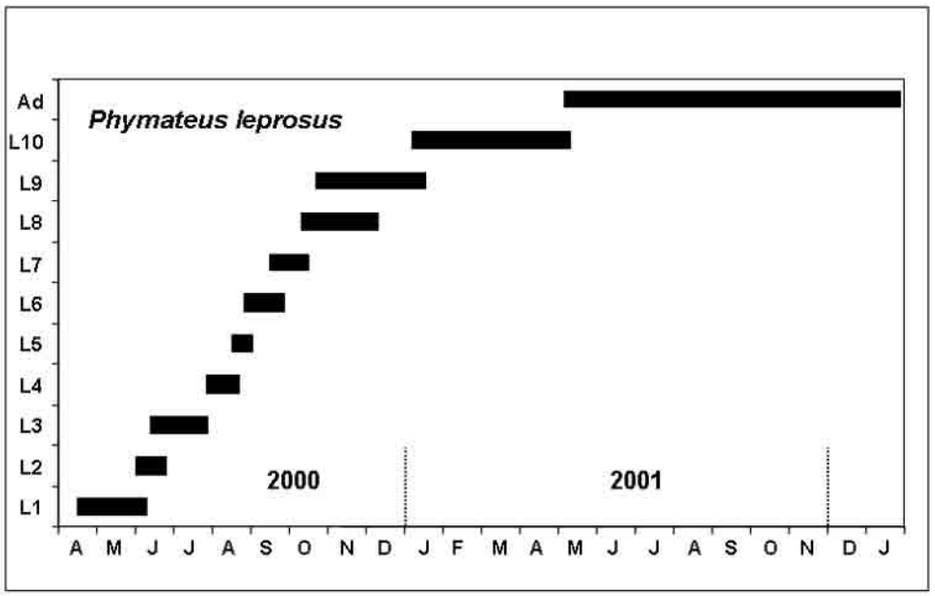

Fig. 4. Biennial life cycle of laboratory-reared *Phymateus leprosus*, starting with hatchlings, collected in late April in the Eastern Great Karoo (S.A.) and brought to the laboratory at Jena University.

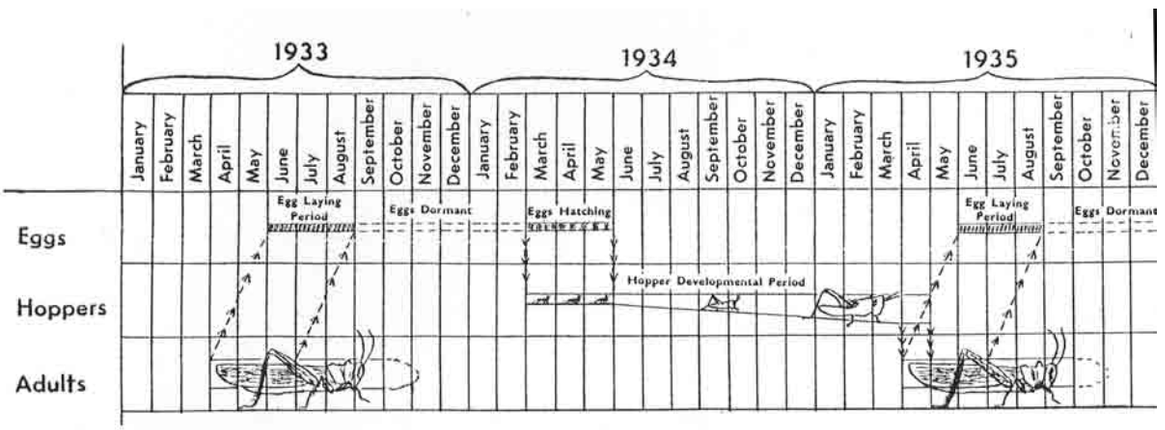

Fig. 5. Biennial life cycle of *Phymateus leprosus* in the field in the Eastern Cape Province, South Africa (detail from BISHOP 1940).

slightly within an instar (exuviae). According to our observations, the two prominent tubercles on the pronotum separating *P. leprosus* from other *Phymateus* species are distinctly visible from the 9th instar.

There is a major change in colouration after adult moult to a mainly green or red morph, briefly described in KÖHLER et al. (1999). In the green morph the head, pronotum, tegmina and legs are olive-green or greyish-green, whereas in the red morph these parts are dark red (except some individuals with a green pronotum). As far as we know, the red morph of *P. leprosus* seems to occur mainly in the Southern Great Karoo, whereas the green morph is distributed from the Eastern Cape (and the coast) to Transvaal.

The juvenile development extended over one year from 24. April 2000 (hatchlings collected in the field) to the beginning of May 2001 (adult moult in the laboratory) (Fig. 4). Despite the sunny place in the window and warm temperatures caused by a radiator (15–25 °C) development of the instars 8 to 10 retarded somewhat in the European winter months (Fig. 4). The duration of the instars varied from 4–6 weeks in instar 1–2 (May–June), 2–3 weeks in

Table 2. Reproduction parameters in *Phymateus species*. Mean (min–max).

Species	Origin	Ovarioles	Eggs in a female	Eggs per pod	Source
P. leprosus	S. Africa		340, 367		Bishop (1940)
	S. Africa	360, 480			Köhler et al. (1999)
	S. Africa	116, >187	157		present ms
P. viridipes	Eritrea		287 (233–335)		
			[n=12]	135 (108–151)	
				[n=6]	De Lotto (1951)
	Ghana			282	Chapman (1962)
	Kenia	200±10			
		[n=?15]		162 (60–231)	
				[n=?15]	Kaufmann (2000)
	Malawi	>146			present ms
Phymateus sp.		393			Uvarov (1966; cit. Phipps)

instar 4–7 (July–September), 4–6 weeks again in instar 8–9 (October to January) and finally about eight weeks in instar ten (February–April). This phenology nearly perfectly fits with field observations over five years (1933–37) in the Eastern Cape Province by Bishop (1940) and with observations of adults in the Karoo (Köhler et al. 2001b) (Figs 4 and 5).

3.3. Adult development

One male and four females survived to adult moult, but one female died during the adult moult. After final moult, two females developed with somewhat scrambled tegmina and alae, only the male and one female had more or less normally folded wings. The adults eclosed in early

Fig. 6. Mating *Phymateus leprosus* in the field. Blyde River Canyon, N-Transvaal, South Africa, January 1995. Photo: K. Reinhardt.

May 2001, the last female died on 28. January 2002, resulting in a maximum adult lifespan of about eight months (Fig. 4). Two other females died on 9. July and 31. August 2001, reaching only two resp. four months of lifespan, which was not related to wing folding failure. The adults obtained were all of the green morph and in the four body parameters measured (length, pronotum, postfemur, forewing) smaller than individuals from the wild in the Southern Karoo near Prince Albert (P.A., KÖHLER et al. 1999). The only reared male reached about 50 mm body length (P.A. 53–62 mm) and 30 mm postfemur length (P.A. 27–34 mm), and the three reared females reached body lengths of 58–62 mm (P. A. 67–83 mm) and postfemur lengths of 30–33 (P.A. 32–40 mm).

Between 6. August and 10. September 2001 on six days it was observed that the male settled on the back of the female with the normal developed wings, although without actual coupling of the genitalia. This behaviour was seen mostly in the morning between 8:45 and 9:30 hours, on one occasion extending to 14:00 hours, and one case was seen only around 15:00 hours (Fig. 6).

On 3. August 2001 a plastic cup with a mixture of garden soil and fine sand was put into the terrarium, but no egg pod found on 11. December 2001. During these months no egg-depositing behaviour was observed nor were egg pods found on another medium.

The dead female from 9. July 2001 was in a reproductive stage (III) with 116 fully developed terminal oocytes (6.0 mm long, 1.5 mm in diameter). The female, which died on 31. August 2001, was around the ovulation (IV) and had 157 light brown eggs. The third and oldest female, which died on 28. January 2002, was in the pre-reproduction stage (II) and had still poorly developed ovarioles with more than 100 on the left and more than 87 on the right (not clearly separated). Similarly, a female *P. viridipes* collected on 14. September 2001 (Mulanje Mountains, Malawi, K.R.), also had very thin, undeveloped ovarioles (stage II) with at least 75 and 71 on either side. Summarizing the few available exact reproduction data from the genus, a broad variability has been detected reaching in reared *P. leprosus* from 116 to >187 ovarioles resp. eggs per pod and in wild females from 340–480. In *P. viridipes* these numbers vary mainly between 100 and 300 (Tab. 2).

4. DISCUSSION

Because of their occasional economic importance, the distribution and biology of the ten *Phymateus* species are summarized in the "Locust and Grasshopper Agricultural Manual" (ANONYMOUS 1982). In addition to its considerable body size, members of the genus *Phymateus* exhibit at least five common characteristics: polyphagous on trees and shrubs, hopper aggregation behaviour, slow juvenile development, late adult maturation, and complex defence strategy of the adults. In *P. leprosus*, four of these characteristics are treated in the present paper, whereas the complex defence behaviour of this species was described as early as 1940 in BISHOP (1940) and recently in KÖHLER et al. (1999), but it is well-known in *Phymateus* species in general (DE VILLIERS 1985, WHITMAN 1990).

4.1. Food plants and rearing

The biology of *P. leprosus* has been studied only once nearly 70 years ago by BISHOP (1940) in the Eastern Cape Province, South Africa, where this species became very abundant in 1933 near Coega, Port Elizabeth district. It invaded farmlands, causing considerable damage by feeding on pumpkins and other crops, and in a citrus nursery. In general, pyrgomorphid grasshoppers are non-graminivorous (GANDAR 1982). However, all *Phymateus* species use a wide range of food plants, including toxic families like Euphorbiaceae, Asclepiadaceae, and Apocynaceae, as well as many crop species and garden plants with preferences for trees and shrubs (ANONYMOUS 1982, SITHOLE 1986). In the milkweed (genus *Asclepias*) the cardiac glycosides proved to be phagostimulants in *P. leprosus* (SEIBT et al. 2000).

Despite this, there are few rearing attempts and therefore the juvenile and adult development is rarely documented, possibly because of the high early mortality and because it is time-consuming to follow the very extended life cycle. There are two studies in *P. viridipes* (DE LOTTO 1951, KAUFMANN 2000), one in *P. morbillosus* (REYNEKE 1941) and one in *P. leprosus* (BISHOP 1940) that report successful rearing of laboratory populations over their complete life cycle. For *P. leprosus* BISHOP (1940) used mass and single rearing, but failed to ascertain the exact number of and the differences between the instars due to continuous high hopper mortality. Our hoppers suffered from a very high initial mortality, possibly caused by the unusual food plants, despite them being from the same families, Asclepiadaceae and Euphorbiaceae, as those eaten in the field (BISHOP 1940, KÖHLER et al. 1999). Finally, our rearing showed that after a period of habituation a complete development of the leprous grasshopper up to the adult stage is also possible with non-native food plants. As secondary plant compounds, *Vincetoxicum arundinaria* contains bitter glycosides, whereas in the milk of *Euphorbia cyparissias* some phenolic substances were found (HEGNAUER 1962–2001). Our successful rearing with *Rubus* spec. as food plant from instar 8 to the death of adults suggests that leaves of *Rubus* alone are sufficient for *Phymateus* in captivity.

4.2. Hopper aggregation

Several species of Pyrgomorphidae (and of Romaleinae) are typically gregarious as hoppers, but not as adults, a phenomenon named as juvenile gregariousness by UVAROV (1977). In the *Phymateus* species hitherto studied at most the young hopper stages remain gregarious forming dense aggregations on the food plants and bands of at least hundred individuals moving on the ground (e.g. *P. morbillosus* – REYNEKE 1941, *P. aegrotus* – KEVAN 1949, *P. viridipes* – DE LOTTO 1951, CHAPMAN 1962). In later instars the tendency to aggregate becomes weaker (UVAROV 1977), and immature adults tend to disperse, but reaggregate to some extent for mating and oviposition (ROFFEY 1964, ROWELL 1967). In *P. leprosus* this aggregation behaviour, as here observed for a bulk of first instar hoppers, was already described by BISHOP (1940) occurring immediately after hatching in the field and also in captivity. He observed that after any disturbance (even the shadow of the observer) the hoppers scattered in all directions in search of dense vegetation, and later they reaggregated again. This suggests that dispersion rather than aggregation is an anti-predator behaviour. In the same manner the hoppers behaved when collected in the field and brought into a plastic contain (S.R.). According to observations of DE LOTTO (1951) on *P. viridipes* and the few observations presented here on *P. leprosus*, aggregation is also affected by the circadian light-dark-regime. This suggests that hopper aggregation seems to have a thermoregulatory function.

4.3. Instar number and phenology

Apparently, the hoppers of all *Phymateus* species are very similar in colouration and morphological details and hard to distinguish, something that already KARNY (1910) had to confess. So BISHOP (1940) described juvenile stages of *P. leprosus*, which resemble considerably those of *P. viridipes* from Eritrea, described in detail and with fine drawings by DE LOTTO (1951).

In *P. leprosus* BISHOP (1940) estimated from mass rearing at least six juvenile instars in both sexes. In *P. viridipes* seven instars (DE LOTTO 1951), or six (males) and seven instars (females) were exactly observed (KAUFMANN 2000). Differing from both studies, we found altogether ten instars in males and females, which is the highest number presently known in the Acridoidea. Previous maxima reached up to seven to eight also in the Pyrgomorphidae, and nine instars in both sexes of one species, the Bombay locust, *Patanga succincta* (RAMSAY 1964, UVAROV 1966). The instar number in Caelifera is relatively stable (despite unfavourable rearing conditions), so in several acridoid species variability by one instar has been shown with geographic origin or food quality (RAMSAY 1964, UVAROV 1966), but never three or four additional instars as observed here.

Because of their long juvenile and adult development *Phymateus* species have a biennial life cycle with reproducing adults occurring every two years. The onset of the cycle may vary geographically (UVAROV 1977, ANONYMOUS 1982). According to BISHOP (1940), *P. leprosus* from the same region as our individuals, occurs in the wild from June to March as eggs in the soil with a dormancy period of at most six months (September to February). From March to next March the hoppers and nymphs develop, and from March to November the adults are present. Because of an extended egg-laying period over three months a considerable overlap of all stages from two to three months occurs in the field (compare Fig. 5). Such long duration of juvenile and adult period in the field corresponds closely to our rearing results, although the cycle is slightly delayed compared to that presented by BISHOP (1940). When the hoppers were brought to Central Europe, the altered temperature and photoperiod may have had some influence on the developmental period. This is apparent both in the variable duration of the instars and in the development of the adults. Our first adults moulted in May, whereas BISHOP (1940) mentioned April, and in 1995 a Karoo population of immature adults occurred even in mid-March with still poorly developed ovaries in the females (KÖHLER et al. 1999, 2001b). The ovarian maturation should last about two months, so we found in captivity females with fully developed eggs in July/August, but not in January. Apparently, no egg pod of *P. leprosus* has, as yet, been found in the field. In addition, females in captivity never laid eggs, despite a large number of reared adults (BISHOP 1940) and a few observed mating attempts in our culture. So the information about egg numbers was reached by dissecting gravid females (BISHOP 1940, KÖHLER et al. 1999). The few known reproduction parameters in the genus *Phymateus* show for *P. leprosus* and *P. viridipes* a considerable variation in ovariole number, eggs in a female and eggs per pod (Table 2). This can be explained by a broad local and yearly variation of climate, influencing the population dynamics and food plant availability of the biennial bush grasshoppers.

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