ABSTRACT

Geckos were observed and collected around Gobabeb, the Namib Desert Research Station, during 5 – 10 August, 1971. Some specimens were taken alive to Jerusalem, Israel, for studies of pupillary responses and reproduction. *Lygodactylus capensis* is recorded for the area. *Rhoptropus afer* was the commonest reptile; it and *R. bradfieldi* are diurnal and their vertical pupils are remarkably insensitive to light. Pupils of *Pachydactylus laevigatus* and *P. punctatus amoenoides* are more, and of *Palmatogecko rangeli* most light-sensitive. *Ptenopus garrulus* was heard but not seen.

In captivity *Pachydactylus laevigatus* lay loose eggs measuring ca. 19 x 15 x 13 mm. Incubation lasts ca. 60 days at 29–30°C. Hatchlings measure ca. 65 mm (total).

These observations are discussed in comparison with available data on gecko biology elsewhere.

1 INTRODUCTION

Having taken a continued interest in deserticolous gekkonid lizards in Southwestern Asia (Werner, 1968, 1973) and having briefly observed them in the Sonoran desert of North America (Werner, 1972) and the Gibson desert in Western Australia (Werner, in Ms), I sought an opportunity for comparative observation in South Africa.

Thus, when my family and I were to return from a year in Western Australia to Israel, I directed our route through Gobabeb, the Namib Desert Research Station. Our party included my wife Nurit, our children Uri (6) and Sharon (4), all versed in the detection and capture of lizards; and, for part of the time, Mr. H. Finkelday of Windhoek, who kindly volunteered to introduce me to the local herpetofauna.

The visit to Gobabeb, 5–10 August 1971, was so brief that, despite the helpful cooperation of Mr. Finkelday, the station staff and the family, I could make only fragmentary observations on some of the local geckos. Nevertheless, the following presentation may add a little to previous records of gecko life in the Namib (quoted below). The moro so, since the permission I received to take certain animals with me, enabled me to extend the observations on two points: the response of the eye's pupil to illumination, in gecko species possessing different habits of diurnality or nocturnality; and reproduction of *Pachydactylus laevigatus* in captivity.

2 TECHNICALITIES AND METHODS

The Namib Desert Research Station (P.O. Box 953, Walvis Bay, S.W.A.) is administered by the Desert Ecology Research Unit (supported by the S.A. Council for Scientific and Industrial Research). The station comprises a weather station, laboratory, library and several convenient, permanent, family bungalows for resident stuff and visiting scientists. Transport facilities at the time included a light “dune buggy” Volkswagen that was useful on the dunes and a Landrover used over other surfaces and for longer excursions. My license to collect and export specified reptiles was issued by the Department of Nature Conservation and Tourism (Private Bag 13186, Windhoek). Only of one species, *Rhoptropus afer,*
was a considerable excess of animals caught, examined and released.

Most collecting was done at about a 5 km distance from the station, in all directions, because on the one hand removal of animals was prohibited within this radius from the station, and on the other hand the unavailability of detailed maps and the lack of marked trails limited the cruising range.

Standard herpetological equipment and methods were used but emphasis was on scouting, reversible rock turning, and digging in the sand in "likely" spots. Crowbarring of rocks and bark-stripping were kept to a minimum.

Photographs were taken in the field with a Leica camera equipped with 28, 50, and 135 mm lenses, on Kodachrome II and Kodak plus-x films. Field observations on pupillary opening and shape were augmented by photographic observations in the laboratory (Fig. 9), under illumination and neutral density filters using a Gossen "Lunaatix 3" photometer, as explained elsewhere (Werner, 1970).

Animals were initially identified by the keys of FitzSimons (1943, 1962) and Mertens (1971); and identifications of most was later kindly checked by Mr. W.D. Haacke. He also obligingly cared for the live animals for several days between our return to Pretoria and departure for Israel. Indeed, the majority reached Jerusalem alive when we arrived on 20 August.

In the laboratory animals were (and some are) kept in a suitable, air-conditioned reptile room, in wooden cages with a floor area of 27 x 27 or 47 x 37 cm. Summer day-time temperature is often around 30°C. The main food is house-made maggot. Water is available at all times. Survival times in captivity are appended to the comments on each species, as well as serial numbers in the Zoological Museum, the Hebrew University of Jerusalem (HUJ-R) for preserved specimens, or in the author's research collection (OK) which includes also live animals. The Latin expression caudalrem (rostrum-anus) signifies, where relevant, the snout-vent length of animals, in preference to the latter English expression (Werner, 1974). Taxonomical problems are commented on only when needed to clarify the extent of the relevance of my observations.

3 THE ENVIRONMENT

The Namib Desert stretches along 1 900 kilometres of the Atlantic coast of South West Africa from 12° to 15°S (depending on definition) to 31° 30'S but extends only up to some 145 km inland (Wellington, 1955; Logan, 1975). It is classified as a cool coastal desert (Logan, 1968) but it is one of the most extreme deserts of the world, being much more arid than the more famous neighbouring Kalahari "Desert" (Brain, 1962 b). The total annual precipitation averages only 12–50 mm, depending on location (Logan, 1975). The Namib Desert's landscapes include three basic formations: in the north, (a) flat gravel plains (Coetzee, 1969; Plate Ia; Haacke, 1974; fig. 5) and (b) rock outcrops, which are often similar; these are usually granite (Plate 1) but sometimes sandstone (Plate 2). In the south, (c) sand dunes (Plate 2; also Mertens, 1954; fig. 12; Louw & Hamilton, 1972: fig. 1). All these landscapes have in common a plant cover approaching utter barrenness (Kling, 1951; Wellington, 1955) except in restricted sites (Logan, 1960).

Gobabeb station is located on the Kuiseb River some 97 km SSE of Walvis Bay at 23° 33’ 41.5”S, 15° 002’ 30.8”E (408 m above sea level), where the landscapes mentioned above meet.

The dunes, typical wandering dunes (Solger et al., 1910), advance from the south upon the gravel-and-rock penelope and, except near the sea, are stopped by the Kuiseb River (Coetzee, 1969: map; Louw & Holm, 1972: fig. 3) which is cleared by periodic floods (Logan, 1960). The superficially dry bed of the Kuiseb River, with its underground trickle of water, provides a contrasting green band of majestic trees (Coetzee, 1969: plate IIb), including many Acacia albida and A. giraffa, and a variety of shrubs (Logan, 1960). The Acacia albida trees, incidentally, are very much larger than any I have seen in Israel, at the northern extreme of this tree's distribution (Zohary, 1973: 18, 324, 544). A detailed report on the vegetation of the area is given by Gliss (1962).

The climatic conditions at Gobabeb, which has its own weather station (No. 649/37), have been summarized by Schulze (1969): Mean daily maxima of air temperature are about 32°C in summer (December – April) and about 27°C in mid-winter; mean daily minima are about 15°C in summer, 10°C in winter; the absolute observed maximum was 42.3°C, and the minimum, 2.1°C. Mean monthly relative air humidity varies from 60% in February to 36% in May. Sunshine hours in mid-summer average 80% of the possible, but in water over 90%, as clouds and fog are common in summer. The fog occurs in the night and morning; according to Logan (1975) the heavy dew is ecologically important in the coastal area. Rainfall occurs throughout the year but mainly around January–March; the mean annual precipitation is 24 mm.

Meteorological data during our visit are relevant to activity times of reptiles and may be summarized as follows. Sunrise, 0734–0731 h; sunset, 1842–1844 h. The moon, full on 5 August, rose late each night, moonrise shifting from ca. 1900 h to ca. 2200. Wind was, at the most, moderate throughout. Temperature and humidity data are presented in Table 1 as kindly provided by Mr. Alex Durr from the weather station's records. Some additional weather data recorded by me are mentioned in the text where relevant.

<table>
<thead>
<tr>
<th>Date and time</th>
<th>Air Surface</th>
<th>From dry</th>
<th>Total temperature</th>
<th>Ground Surface</th>
<th>From wet Surface</th>
<th>Overall temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td>5 August</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0800</td>
<td>9.8</td>
<td>8.6</td>
<td>83</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1400</td>
<td>22.0</td>
<td>3.0</td>
<td>34</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2000</td>
<td>18.4</td>
<td></td>
<td>59</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6 August</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0800</td>
<td>6.2</td>
<td>9.3</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1400</td>
<td>18.6</td>
<td>40.0</td>
<td>50</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2000</td>
<td>14.2</td>
<td>14.8</td>
<td>70</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7 August</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0800</td>
<td>7.4</td>
<td>6.0</td>
<td>93</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1400</td>
<td>24.0</td>
<td>42.8</td>
<td>26</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2000</td>
<td>18.6</td>
<td>17.5</td>
<td>24</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8 August</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0800</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1400</td>
<td>17.0</td>
<td>39.8</td>
<td>56</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2000</td>
<td>15.7</td>
<td>14.8</td>
<td>65</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9 August</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0800</td>
<td>6.1</td>
<td>5.0</td>
<td>103</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1400</td>
<td>23.6</td>
<td>44.7</td>
<td>32</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2000</td>
<td>17.1</td>
<td>15.3</td>
<td>53</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10 August</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0800</td>
<td>7.1</td>
<td>6.4</td>
<td>82</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1400</td>
<td>28.7</td>
<td>42.1</td>
<td>12</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2000</td>
<td>22.2</td>
<td>19.8</td>
<td>28</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
The reptile fauna of the Namib has been studied from the taxonomical and zoogeographical standpoints and illustrated (FitzSimons, 1943, 1962; Mertens, 1955, 1971; Haacke, 1965) with a certain emphasis on geckos (FitzSimons, 1943: plates 1–17; Loveridge, 1947; Mertens, 1971: p. 6; Haacke, 1975, 1976). However, knowledge of the biology of reptiles in the area remains scant, despite a small number of detailed recent studies (e.g. Haacke, 1969, 1974, 1975, 1976; Hamilton & Coetzee, 1969; Louw & Holm, 1972; Mertens, 1972).

At Gobabeb reptile life seemed quite scant. Many man-hours were spent in futile search. The few reptiles which were seen besides the geckos reported, occurred almost exclusively on or near sand. Those secured, and thus identified, comprise *Merolea cuneirostris* (Strauch, 1867), adult male and juvenile, among Neris (Acanthosicyos horrida) bushes in the sands, active at 1100–1200 h on 6 August (HUI-R. 13283); *Aporosaura anchiatae* (Bocage, 1867), one caught by Alex Durr on the bare dunes, active at 1730–1800 h on August 9 (HUI-R. 11877); *Mabuya longiboca* (Methuen and Hewitt, 1914), on rocks next to sand, 1600–1700 h, on 7 August (HUI-R. 11878, 13246); and a snake, *Psammophis* sp., caught by Mr Finkeldey, active in the forenoon of 7 August, in a river bed (HUI-R. 8639). As observed, i.e., by Lawrence (1959), the two first named species, both lacertids, have fringed digits; they constitute two further examples of this convergent adaptation to life on sand, additional to those assembled by Buxton (1923: figs. 39–40). Niche separation between the two has been dealt with by Louw & Holm (1972: fig. 4). Of the two, *Aporosaura* has a *Scincus*-type snout and is the lacertid most extremely adapted to burrowing rapidly into the sand, as Mertens (1955) pointed out.
In addition, skink tracks were seen in the dunes (fresh at 1730–1800 h on 9 August). Where the animal obviously had moved under the surface, these resembled those of *Sphenops septoides* (Werner, 1968 b: fig. 2). However, the portion where the animal had moved upon the sand was not like *Sphenops* tracks, but continuously sinuoid. We failed to find the responsible animal. This, most probably was *Tyrphlops braminus* Haacke, 1964 (Lawrence, 1959: 235; Haacke, 1964: 5–7) for which these very dunes are the terra typica.

### 4 FIELD NOTES AND COMMENTS

#### 4.1 *Lygodactylus capensis bradfieldi* Hewitt, 1932
(Plate 8A)

**Field Notes:** 9 August 1971, ca. 1000 h (with Alex Durr and Uri). Kuiseb River bed, ca. 5 km E of station. Stripped bark off a large dead (standing) *Acacia* tree. Flushed one female *L. capensis* from under the bark of an arm-thick branch, ca. 1 m above ground. Captured after search and chase. When grabbed, it chipped. Thereupon removed much bark from this and adjacent dead trees, but found no more geckos. Under most of the dead bark there was a lot of the rotten sawdust-like material which is usually shunned by geckos.

**Comments:** This appears to be the first record of *Lygodactylus capensis* for the Gobabeb area.

**Pasteur** (1964) recognizes *bradfieldi* as a distinct species whereas **Loveidge** (1947) synonymizes it with *capensis*. I follow **FitzSimons** (1943) who regarded it as subspecifically distinct.

**The distors eel** (Frankenberg, 1975) of this animal when first seized is noteworthy in view of Kästle's (1964) observation that captive *Lygodactylus* behaved as if they were mute and communicated visually. This specimen, too, did not squeak again afterwards. I had the same experience with both *Phelsuma lineata* ? *chlorocellus* Mertens, 1962, and *P. bimaculata* (Kaunders, 1922) just east of Perinet, Madagascar, on 31 July 1971: when caught in the *Pananus* bushes (in which both species occurred together) the animals chipped. They also chipped soon after capture, when grabbed. But later on they could not be made to chip any more. This genus, too, has been described as mute, and communicating visually, by Kästle (1964). The phenomenon of chipping at the initial capture but not later appears to be common, at least among certain gecko species.

The animal, adult when caught, survived in Jerusalem till 7 August 1972 (one year less a day) (HUJ-R 12357).

#### 4.2 *Pachydactylus laevigatus laevigatus* Fischer, 1888
(Plates 6 & 8B)

**Field Notes:** 7 August 1971, ca. 1115 h (with the family and Mr Finkelday). In an open, bare riverbed ca. 5 km N of the station, an isolated, upright rock of exfoliating blackish sandstone, with a few small *Acacia* trees. Behind one of the thin vertical stone slabs found two adult female *P. laevigatus*, rather sluggish and easily captured. On the previously hidden rock face there were also oval whitish “scars”, each ca. 14 x 11 mm, where gecko eggs had previously adhered. Further search of this rock revealed no more geckos.

7 August, ca. 2330 h. On returning to our residential bungalow, found and captured a half-grown male (regenerating tail) on the white-washed concrete wall of the “patio”.

**Comments:** According to the experience of other collectors, too. *Pachydactylus laevigatus* occurs in houses as well as rock crevices (Loveidge, 1947: p. 399; Mertens, 1955: p. 46). However, FitzSimons (1956: p. 394) mentions a subadult found under the bark of a dry tree stem. This euryoeous parallel that of *Oedura marmorata* in the Australian deserts (Werner, in MS).

The vertical pupil is moderately sensitive to light, implying predominantly, but not strict, nocturnal habits (Plate 8B).

Of the three animals, the two females, caught as adults, meanwhile died in captivity: one (HUJ-R 13273) in summer 1975, the other (GK 748) on 16 January 1976, four years, five months and nine days after capture, when it probably had already been at least two years old. The male caught half-grown, still thrives after five years (GK 747: August 1976; ra 79 mm). Some details are presented after the field notes.

It is doubtful that the egg “scars” found with the two females belong to this species. We shall return to this point when discussing the eggs laid in captivity (p. 164).

#### 4.3 *Pachydactylus punctatus amoenooides* Hewitt, 1935
(Plate 8C)

**Field Notes:** 7 August, afternoon (with Mr. Finkelday and the family), low rocks near riverbed ca. 8 km N of the station. One specimen was caught under exfoliating granite indistinguishable from that inhabited by *Rhapontopus afer* which abounded in the same place. A second specimen was dug up by Mr. Finkelday from a hole between stones in the soil, into which a snake had escaped (*Psammophis*, also captured).

**Comments:** Parker (1926: 130) and Loveidge (1947: 352–357) doubted the validity of any subspecies of *P. punctatus*, but the subspecies *amoenooides* was accepted by Fitz-Simons (1943: 73) and Mertens (1955, 1971), whereas Wermuth (1965) even regarded the form as a distinct species.

The vertical pupil appears to be about as light sensitive as in *P. laevigatus*, probably implying a similar degree of nocturnality (Plate 8C).

One animal died on the journey, but the other survived in Jerusalem till 2 April 1972 (238 days) (HUJ-R 12108).

#### 4.4 *Palmatogecko rangel* Anderson, 1908
(Plate 8D)

**Field Notes:** 9 August 1971, ca 2020 h (with Alex Durr). Dunes south of the station. I discovered in the light of the paraffin lux lamp one young *Palmatogecko rangel* with perfect tail, walking slowly on the wind-rippled, hard-packed sand in a shallow depression between dunes. It was walking normally semi-erect (Werner and Broza, 1969) and its webbed feet (Mertens, 1955: figs. 17–20; Haacke, 1976: Plate 1) were impressing no tracks in the sand. No plants were close by. At the time there was little wind and the air did not feel cold. The animal, however, felt cold to my hand.

**Comments:** In order to observe and obtain this bizarre species I spent in the same area several hours searching with
lights at night, in vain, both before and after I found the above-mentioned specimen. The nocturnal search comprised both several hours of moonshine and a completely dark hour of the moon eclipse (6 August, 2100–2200 h). The fruitless search, in which Mr. Finkelday and others participated, included also a morning (8 August, 1000–1200 h) when heavy fog made it likely that the geckos would indulge in digging—but we found no fresh holes.

The vertical pupil is by far more light sensitive than in the two Ptyodactylus species. This would accord with rather strict nocturnal habits (Plate 8D).

Brain (1958) drew attention to the fact that geckos of this species only rarely lose the tail, and if they do—they always from the base. Haascke (1976) confirms this phenomenon. An investigation of the comparable psammophile geckos of Southwestern Asia, Ptyodactylus and Ceramodactylus, revealed that in them only few vertebræ at the base of the tail are provided with fracture planes, and the latter are mostly incomplete (Werner, 1965, 1968). It may be expected, but still remains to be proven, that the same is true of Palmatogecko.

The Palmatogecko reached Jerusalem alive but survived only a few days.

4.5 Ptyopus garrulus maculatus Gray, 1865

Field Notes: 8 August 1971 (with the family). Drove to Zebra Pan, a grassy depression ca. 53 km NE of Gobabeb. Arrived before 1700 h, in full daylight. In the ground, between and at bases of grass clumps, saw many holes of various shapes and sizes. At 1800 h, with the sun low over the horizon, a chorus of Ptyopus calls gradually began. It became intense and continuous by sunset (1843 h) and remained so till 1940 h when the night became completely dark. It then abated abruptly and thereafter only little calling went on. We did not find the noise level deafening or disturbing as described by A. Smith (quoted in Brehm, 1893: 44).

While the chorus was on, there was a continuous background din, relatively high-pitched—the cumulative vocalization of many Ptyopus over a considerable area. Above this rose the occasional loud calls of nearby animals. Each single call consisted of an evenly spaced series of five clicks, rarely four or six, as is typical of this species in this area (Haascke, 1964, 1969, 1974). The near clicks sounded less loud and lower pitched than those of the Israeli Ptyodactylus. Each click sounded mettalic, like a low-pitched string organ. There was some qualitative variation among the calls. We tried consistently to locate and observe the calling animals with binoculars, and later also with electric torches, but failed completely. Not only was it very difficult to decide on the direction of a given call, but sometimes it seemed as if the source was moving fast (compare Haascke, 1969: 87). Often we had the definite impression of an organized chorus of animals responding to each other, or taking on from each other and carrying on.

Local air temperature was 16.5°C at 1900 h when the chorus was going strong. We left the place at 2000 h after calling became very sporadic and before the moon rose.

Comments: The validity of a separate subspecies maculatus (for the S.W. African population) has been denied by Brain (1962 a) but accepted by Mertens (1971) and confirmed by Haascke (1974, 1975) who presents detailed distribution maps.

The vocalizing activity of Ptyopus at this low temperature is not surprising, because geckos of this genus have been seen in the open even at 10°C (Brain, 1962 b).

The geckos of the genus Ptyopus were the subject of the first study of gecko vocalizations ever published, by Hascke (1964, 1969, 1974). Among other details, he described differences between and within species, and depicts animals calling from the entrances to their burrows. However the function of the calls is even more obscure than in the geckos of the genus Ptyodactylus (Frankenberg, 1974).

4.6 Rhotropus afer Peters, 1969

(Plates 3, 4 & 8E)

Field Notes: These were the commonest reptiles near the station, and we must have seen several scores during our stay. They were basking on, and scampering over, the boulders (Plates 1 & 4), flat rocks (Plate 2) and gravel (Plate 3) throughout all or most of the sunshine hours. I have actual records of their activity in the open at these times:

6 August: 1600–1700 h; 1800 h
7 August: 1030–1240 h
10 August: 1000–1130 h; 1515 h

All but the last of these records are from the immediate vicinity of Gobabeb. The last (1515 h) is from the weather station between Gobabeb and Rooibank. This animal, a male, was on a gravel plain with few scattered, small to medium, loose stones. These geckos did not seem particular about the substratum, occupying sandstone outcrops (Plate 2), granite rocks (Plates 1 & 4) and flat gravel areas (Plate 3), and even small, more or less isolated flat rock outcrops in the sands (Plate 2). However, they appeared not to inhabit the few cliff-like rocks along the Kuiseb riverbed (Coeetze, 1969: Plate III).

We found some under stones or exfoliating rock slabs, in daytime, under circumstances that convinced us that it had not been our approach that made them hide there. Obviously they had to shelter from the sun occasionally to avoid overheating.

Depending on the hues of the rocks, the geckos were often camouflaged excellently (Fig. 4).

When running, Rhotropus afer always kept adpressed to the surface (Werner and Broza, 1969), with the limbs spread widely aside, regardless whether this surface was vertical or horizontal.

It was conspicuous that most R. afer we saw were adult males. Of the 18 animals caught and measured, 9 were males of 50–53 mm ra, and one a male of 46 mm ra. There were few juveniles (N=4; 36–44 mm ra) and females (N=5; 50–53 mm ra); the latter usually (N=3-4) pregnant. Despite the abundance and activity of these geckos, we heard no calls, in contrast with the usual experience with, e.g., the vociferous Ptyodactylus (Werner, 1965; Frankenberg, 1974).

Comments: The habits of R. afer are remarkable in two ways. First, the animal has a vertical pupil (Plate 8E), as in predominantly nocturnal geckos (Walls, 1942), but appears to have fully diurnal habits. In agreement with this, the pupil is extraordinarily insensitive to light so that in average daylight it is broadly elliptical.

Second, its relatively narrow fingers and toes do possess digital pads, as in properly climbing species. Yet most R. afer inhabit horizontal or inclined rock surfaces, or even flat
gravel, and few occur in rocks with limited vertical surfaces. Even over horizontal surfaces they locomote as if they were climbing, in the adpressed posture, rather than in the semi-erect posture of proper ground-dwelling geckos (Werner & Broza, 1969).

Upon comparison with R. bradfieldi (below) it is tempting to suggest that R. afer represents a relatively recent ecological radiation and evolution, from an originally climbing stock, to occupy the daytime niche of horizontal and near-horizontal non-sandy desert ground. Presumably this niche was free and inviting at a certain time. During my visit, I only once saw a lizard other than R. afer in the daytime in this biotope around Gobabeb.

The specimens brought to Jerusalem survived only a few weeks. Mr. Haacke has also told me that this species is particularly difficult to keep in confinement (HUJ-R 11880—85).

4.7 Rhoptropus bradfieldi Hewitt, 1925
(Plates 5 & 8F)

Field Notes: This species, slightly larger and somewhat darker, occurred only on the vertical cliff-like rocks along the Kuiseb River (Coetzee, 1969: Plate IIb), and on other rocks in the immediate vicinity of the cliffs. In this area it occurred on both the blackish, soft, layered sandstone and on the light-colored granite (Plate 5). It always locomoted, of course, adpressed.

R. bradfieldi appeared to be just as diurnal and sun-loving as R. afer but due to its occurring in a restricted area, I have actual records of activity, including basking, for these times only:

7 August: 1530—1745 h
9 August: 1215 h (air temperature 24.5°C)

Most animals caught or observed were adult males. Adult females were rare, and only one juvenile was found.

In the rocks inhabited by R. bradfieldi, two egg-laying sites were uncovered behind vertical slabs of exfoliating sandstone on north-facing rocks (the sunny direction). The covering stone slabs were thin, only 1—2 cm thick in one case. The "scars" where eggs had adhered to the rock were not in pairs as in Pyodactylus (Werner, 1965: Fig. 8) and many other geckos, but single. Each "scar" was elongate about 15 x 9 mm. In one site the scars were numerous and in several layers, implying repeated use of the site for years as in Pyodactylus, (Werner, 1965: Fig. 6). Of course, it is only a surmise that these egg-laying sites belong to Rhoptropus bradfieldi.

Comments: The vertical pupil (Plate 8F) is about as insensitive as in R. afer, and this, again, would appear to relate to the diurnal habits, which are mentioned also by Haacke (1965). The ecological relationship of the two Rhoptropus species is considered in the Discussion (p. 165).

Of the specimens brought to Jerusalem, one survived for two years and three months but was preserved on 7 November 1973 when it appeared moribund (HUJ-R 12735; the others are HUJ-R 11879, 13242).
Plate 4. Rhipropus after basking on a granitic rock, the colour of which it matches well. (Near Gobabeb, 7 August 1971, early afternoon.)

Plate 5. A dark Rhipropus Bradfieldi conspicuous against the whitish rock on which it basks. (Kaiserb River near Gobabeb, 9 August 1971, forenoon.)
5 REPRODUCTION OF PACHYDACTYLYUS LAEVIGATUS IN CAPTIVITY

5.1 Eggs and Oviposition

(Plate 6)

The two females and the young male (not identifiable as a male at the time) reached Jerusalem in good condition on 20 August 1971 and were placed in a wooden cage of ca. 27 x 27 cm floor which received the afternoon sun. The cage had about 3 cm of a sand-soil mixture on the bottom and was furnished with two diagonally leaning pieces of roof tiles. The animals were henceforth fed almost exclusively on housefly maggots, replenished every 2–3 days. For variety, grasshoppers were given every few weeks. During the succeeding months of September–October each female appeared to be pregnant at least twice. No eggs could be discovered and it was presumed that the eggs were eaten by the geckos, perhaps in relation to having been infertile.

However, during 1972 several eggs were discovered. By this time both the females and the male, now evidently mature, measured ca. 75–78 mm (ra).

All the eggs were nearly ellipsoid but somewhat flattened with three different diameters. The dimensions of seven eggs averaged 19.18 x 14.89 x 13.47 mm and the observed ranges were, respectively, 18.0–20.3; 14.4–15.8; and 12.9–14.2.

Most eggs were buried in the ground, the rest were deposited on the ground. All eggs were discoloured by sand and soil particles stuck to the shell, obviously because the eggshell had been soft and sticky at the time of oviposition. This encrustation with sand occurs also in Polychrotos loxosceles (Haacke, 1976) but I have seen it in no other gecko species, including (i.e.) all the Israeli gecko genera that oviposit in the ground or under stones: Alsophylax (Bunzpur), Ceranechus, Cryptodactylus, Heniadactylus, Stemodactylus and Tropidostola. Many of the eggs were deformed by a depression or indentation at some spot — further evidence of their soft state when laid. This, of course, is the normal condition in species that stick the eggs to the substratum, and it remains to be seen how the Pachydactylus oviposits, when given a variety of artificial rock crevices that more closely resemble natural ones. It thus remains an intriguing open question whether the remains of eggs that were found sticking to the rock where the females were caught, did belong to this species.

Because in captivity most eggs were buried there remains a varying degree of uncertainty about the dates of oviposition and even about the eggs' arrangement in clutches, despite frequent inspection of the females and the ground. From the inspection of the females it was obvious that a clutch normally consisted of two eggs. The two females were not marked individually and it is not known which eggs were laid by what female; however, both females appeared similarly productive. Eggs, once discovered, were put in small glass jars in an incubator room at 29.5 ± 1°C.

Oviposition was first recorded on 31 August 1972, between inspections at 1400 and 1630 h. However, in the ground there were three eggs. One was broken accidentally; the other two hatched, one between the mornings of 12 and 13 October, and one between the mornings of 28 and 31 October. The second probably represents the full incubation period of ca. 59 days, whereas the first (42 days or more) probably implies an earlier oviposition in mid-August. Three additional clutches were laid by the middle of November, and a sixth, last of the season, was laid on 2 or 3 January 1973. (For none of these later clutches is the hour of oviposition known.) Hence each female (apparently) laid three clutches during the season August–December. Of two clutches each, only one egg was recovered, and in one of these cases the other egg was probably eaten, as the mother had been pregnant with two eggs.

5.2 Incubation

Of the ten eggs recovered, one was broken (as mentioned) and six hatched. Of those incubated at 29.5°C throughout (four), the longest incubation period was 61 days, and this was an egg almost certainly discovered within a day of oviposition. The second longest incubation lasted 59 days. Hence if this species has a uniform incubation period (that of Gekko gecko, for example, appears to be highly variable — Brodky, 1959), this would seem to be ca. 60 days at this temperature.

The last (January) clutch hatched only after 80–81 days but during this time the incubator was unstable and at least for one 3-day period the temperature sank to 22°C. This delayed hatching occurred on 23–25 March 1973, but prior to this, the last hatching was during 2–3 January 1973.

5.3 Hatching and Neonati

(Plate 7)

The time of day when hatching occurred is unknown for most eggs, because usually eggs were inspected only once daily. However, one egg is known to have hatched on 5 December 1972 between 0900 h and 1600 h, and another hatched on 25 March 1973 between 1400 and 1450 h. Thus, at least some of the hatchlings occurred in daytime.

The hatching process, in the one case on which some information is available, was rather quick. On inspection on 25 March 1973 at 1400 h, one egg in the incubator displayed a slight crack. Wishing to photograph the hatching process, I inspected the egg at 5 min. intervals. No change was visible by 1445 h. However, by 1450 h the neonates had hatched and was found resting next to the eggshell with only the tail still inside. This was in contrast to the procedure common in geckos and other lizards, wherein the hatching lasts for a while after extruding its head and before emerging completely (depicted for Gekko gecko by Brodky, 1959: Fig. 10).

The measurements of four normal hatchings averaged 35.9 mm ra (range 35–37) and tail, 26.8 mm (range 25.5–28).

In two other instances hatching appeared to be premature, though spontaneous, and the neonati carried a remnant of the yolk sack. In the first case, an unusually small neonatus hatched on 5 December 1972, carrying a yolk sack (yolk volume about 1/6 that of the head); it looked otherwise healthy and climbed about in its jar. The yolk was not absorbed but dropped off and shrivelled after four days. On the 12 December this animal measured only ra ca. 32 mm and tail, 24 mm. During a severe cold spell, 15–17 January 1973, this animal was the only one of its species that died (together with two Hemidactylus mabouia, out of a collection of many geckos of over twenty species, several of them from deserts or the tropics).

In the second case, on 25 March 1973, the neonati carried a smaller yolk remnant (which similarly dropped off), and body size conformed to the minimal size of normal neonati (ra, 35; tail, 25 mm). This animal still thrives (August 1976: ra, 71; tail, 53 mm).
6 DISCUSSION
6.1 Interspecific Relationships

As in the deserts of southwestern Asia (Werner, 1973) and Australia (Planka, 1972; Planka & Planka, 1976; Werner, in MS), so in the Namib the gecko fauna is rich, including a variety of climbing and ground-dwelling species. The following comments are restricted to the species actually observed. The nocturnal ground-dwelling forms are practically excluded from this category as our searches at night (with lamps) were nearly futile (p. 161). This may be due in part to the full moon at the beginning of our visit. The effects of the moon and its phases on animal activities have been investigated mainly in aquatic invertebrates (Sollberger, 1965) but Klauber (1939:50) presented data suggesting that the full moon depresses the activity of desert snakes. Casual observations on psammophile nocturnal reptiles in Israel appear to point in the same direction. Interestingly, the one dark hour of full moon eclipse we spent on the dunes was not more fruitful (p. 161).

At first it appeared remarkable that two congeneric species, Rhoptropus afer and bradfieldi, of similar size, and similarly diurnal, should inhabit rocks in the same area. However, closer observation showed that they occupy two distinct niches with very little overlap: R. bradfieldi, a slightly heavier animal, with "normally broad" digital pads, lives in vertical rocks as befits an honest climbing species; FitzSimons (1943:117) termed it "essentially rupicolous". R. afer, with rather narrow digital pads, occupies smaller boulders and, especially, horizontal surfaces of rock or gravel (as previously noted by FitzSimons, 1943:115) that would normally be expected to harbour typical ground-dwelling lizards. But R. afer is revealed as originating from climbing stock by always locomoting adpressed as if climbing, rather than semi-erect (Werner and Broza, 1969). From the scarcity of proper diurnal ground lizards in this habitat, it would seem that the free niche "invited" R. afer to radiate into it, perhaps concurrently with competitive pressure from the slightly heavier R. bradfieldi. According to Mertens (1954), niche separation between these two species (at Rössing, only some 100 km to the north of Gobabeb) is based on their different colourations, which match different rocks. This was not the case at Gobabeb.

On the other hand, each of the two diurnal Rhoptropus species appeared to occur in the same spatial niche together with a predominantly nocturnal species of Pachydactylus: R. afer coexisted with P. punctatus amoenooides, which, however, is much smaller than R. afer. R. bradfieldi would seem to share its habitat with the much larger P. laevigatus. Besides the temporal division of the habitat between the Rhoptropus and the Pachydactylus species, the two members of a coexisting species-pair presumably eat partly different sizes of food organisms, in accordance with the geckos' different body sizes (and head sizes), as shown by Planka and Planka (1976) for Australian desert geckos.

It is noteworthy, that P. punctatus has somewhat narrower digital pads than P. laevigatus, in parallel with the (greater) difference between R. afer and R. bradfieldi.
6.2 Specific Diel Cycle and Pupillary Response
(Plate 8)

The gecko species observed appear to differ considerably in their diel cycles, although my scant observations provide no conclusive proof of the details. In the completely diurnal species, Lygodactylus capensis, the pupil of the eye is round (Plate 8A; Pasteur, 1964). Among the species with a vertical split pupil, we may expect a correlation between light-sensitivity and the normal diel cycle, so that under uniform illumination the pupil would be more widely open in the species with the stronger inclination towards diurnality. Indeed, observations on Israeli geckos confirm this (Frankenberg, in press).

Among the Namib geckos observed, the two Rhoptropus species appear to have completely or predominantly diurnal habits. In agreement, their vertical pupils were partly open in nature, even in full daylight. Their relative insensitivity is further demonstrated by the controlled laboratory observations (Plates 8E & F). On the other hand, the two Pachydactylus species were found at times and places compatible with a supposition that they are crepuscular or nocturnal. Their pupillary responses were by far more light-sensitive (Plates 8B & C). The most extremely sensitive pupil was that of Palmatogecko (Plate 8D), which would appear to be as completely nocturnal as the ecologically comparable Israeli psammophile geckos Ceramodactylus doriae and Stenodactylus petril.

6.3 Annual Reproductive Cycle of Pachydactylus laevigatus

In Israel, geckos oviposit mainly during June–August (werner, 1965, 1966a, b). This generally holds true for Israeli geckos kept in my reptile room. The Pachydactylus laevigatus, ovipositing mainly during September–November, clearly failed to conform to their new environmental cycle, more than a year after their transfer. I am not sure that they kept fully in pace with their original reproductive cycle. I suspect, however, that they may have done so, because in August when they were caught, female Rhoptropus in the same habitat were commonly pregnant.

7 CONCLUSIONS

1 Concerning Gobabeb Station in August:

1. Lygodactylus capensis occurs on trees along the Kuiseb River at Gobabeb.
2. Lygodactylus capensis, although reputedly mute, chirps when seized (based on one case).
3. At Gobabeb, Rhoptropus afer occupies horizontal habitats and small rocks whereas R. bradfieldi occupies larger steep rocks; there is little overlap between the two.
4. Pachydactylus punctatus amoenoideus appears to coexist with Rhoptropus afer in the same habitat.
5. Rhoptropus afer and bradfieldi are diurnal, and their vertical pupils are relatively insensitive to light.
6. The pupils of Pachydactylus laevigatus and P. punctatus amoenoideus are much more light-sensitive than those of Rhoptropus, and both species appear to be crepuscular or nocturnal.
7. The pupil of Palmatogecko is more light-sensitive than those of the Pachydactylus species.

2 Concerning Pachydactylus laevigatus in Captivity:

8. In captivity, Pachydactylus laevigatus lays eggs deposited loosely in the ground, that are initially soft and sticky.
Plate 8. Heads of geckos of six species from the Gohaleh area, to show the condition of the pupil under comparable levels of illumination. All photographs enlarged so that head length appears as 50 mm; where possible, 1 cm of a ruler originally photographed with the animal is included.

(A) & (B) Light intensity of ca. 20 lux (Jerusalem, 13 May 1972):
(A) Lygodactylus capensis bradfieldi.

(B) Pachydactylus laevigatus laevigatus.

(C) - (F) Light intensity ca. 30 lux (Jerusalem, 23 August 1971):
(C) Pachydactylus punctatus amoenolides.

(D) Palmgecko rangei.
(E) Rhapsopus afer.

(F) Rhapsopus bradfieldi.
9. Each female lays ca. 3 clutches of 2 eggs each during August—November.
10. Eggs measure ca. 19 × 15 × 13 mm.
11. Incubation appears to last ca. 60 days at 29.5°C.
12. The neonate measures ca. 36 mm, head and body; and 27 mm, tail.

8 ACKNOWLEDGEMENTS

I wish to emphasize my gratitude to my many colleagues at the South African Museum ( Pretoria), Namib Desert Research Station (Gobabeb) and S.W.A. Museum (Windhoek); to the S.W. African Administration officials; and to Mr. H. Finkelday, whose kind help made this report possible. I am also indebted to my family for cooperation in what seemed a Wild adventure, especially to Werner for her passive cooperation.

For taking care of the animals in Jerusalem I am obliged to Röni Engel, S. Levy, and Z. Yona and especially to Esther Moskovits who volunteered for the task in the long winter of 1973/74. For the preparation of the photographs for the press I thank A.B. Niz.

Finally, I doubt when this report could have been written, had not Corporal M. Swiriniski understandingly lent me her desk during part of the 1973 war.

9 REFERENCES

BUXTON, P.A.

BRAIN, C.K.

BREHM, A.E.

BRODSKY, O.

COETZEE, C.G.

FITZSIMONS, T.R.M.

FRANKENBERG, E.

GIESS, W.

HAMILTON, W.J. III and C.G. COETZEE

HAACKE, W.D.

KÄSTLE, W.

KING, L.C.

KLAUBER, L.M.

LAWRENCE, R.R.

LOGAN, R.F.

LOUW, G.N. and W.J. HAMILTON III

LOUW, G.N. and E. HOLM

LOVERIDGE, A.

MERTENS, R.

PARKER, H.W.

PASTEUR, G.

PIANKA, E.R.
PIANKA, E.R. and H.J. PIANKA
1978: Comparative ecology of twelve species of nocturnal lizards
(Gekkonidae) in the Western Australian desert. *Copeia* 1978 (1):
125–142.

SCHULZE, B.R.
38: 5–12.

SLOGER, F.P., GRÄBNER, J., THIENEMANN, P., SPEISSER and
F.W.O. SCHULZE

SOLLBERGER, A.
& New York.

WALLS, G.L.
1942: "The Vertebrate Eye and its Adaptive Radiation," Cranbrook
Institute of Science, Illl. no. 19.

WELLINGTON, J.H.
Geography." Cambridge University Press.

WERMUTH, H.

WERNER, Y.L.
1965: Über die israelischen Geckos der Gattung Psammodactylus und ihre

96.

1966b: "The Reptiles of Israel. Introductory lectures for students
in the course ‘Introduction to the Knowledge of the Fauna of
Israel,’" Department of Zoology, the Hebrew University of
Jerusalem. (In Hebrew, mimeo.)

1968a: Regeneration frequencies in geckos of two ecological types

1968b: Distribution of the Saharan *Sphenops reticulata* (Reptilia:

1970: Extreme adaptability to light, in the round pupil of the snake

1972: Observations on eggs of eublepharid lizards, with comments on

1973: "The Reptiles of the Sinai Peninsula. Introductory notes for
students in the course ‘Introduction to the fauna (Fishes, Amphibians
and Reptiles).’" Department of Zoology, the Hebrew University of
Jerusalem. (In Hebrew with English abstract, mimeo.)

1974: Some suggestions for the standard expression of measurements.

In MS. Ecological comments on some Gekkonid lizards of central
Western Australia.

WERNER, Y.L. and M. BROZA
1969: Hypothetical function of elevated locomotory postures in geckos

ZOHARY, M.
Fischer Verlag, Stuttgart; and Swets & Zeitlinger, Amsterdam.