

Thermal ecology and habitat utilization of *Rhacodactylus leachianus* from New Caledonia (Squamata: Diplodactylidae)

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Abstract. Five specimens (2 ♀, 3 ♂) of the gecko species *Rhacodactylus leachianus* were radio-tracked for 14 days on Île de Bayonnaise, New Caledonia. Using thermo-sensitive transmitters, specimens were mapped continuously every hour. All movements, behavioural expressions and core temperatures were manually recorded, while data loggers simultaneously recorded the temperatures of microhabitat structures. In an additional trial, all geckos captured on the island were marked with Passive Integrated Transponders (PITs): Twenty-two adults (13 ♀, 9 ♂) and one subadult were marked in total. The mapping of *R. leachianus* on this island was repeated during 2005, 2007 and 2013. Average core temperatures of 23.4°C (♀) and 24.1°C (♂) were recorded ranging of 18.2–32.0°C (♀) and 18.0–32.2°C (♂), respectively. No sex-dependent differences were noted, but a clear relation to the local air temperature was found. Gravid females showed higher core temperatures (by up to 3°C) during oviposition. The test for equality of variances showed differences between the core temperatures of both sexes and the air temperature, indicating the ability of both sexes for active thermoregulation. Although no strict territorial borders were noted, males were observed marking their territories vocally. The females showed no territorial behaviour. Home ranges varied between 551 and 3,464 m² for all specimens. Areas within which the geckos were active averaged around 5 m per night, with some rare instances of movements over up to 200 m in one night. We observed that females often left their preferred home ranges for nesting, usually laying their eggs in coastal dunes. We presume that this occurred in search of higher, more stable soil temperatures.

Key words. Gekkota, Île de Bayonnaise, life history, PITs, radio tracking, thermoregulation.

Introduction

Reptiles of tropical regions are known for employing two models of thermoregulation. Some exhibit behavioural thermoregulation similar to most species of temperate zones and determine preferred temperatures actively (HUEY 1982). In habitats with reduced basking opportunities, such as in rainforests, with species that do not thermoregulate actively, these species are called thermoconformers. The core temperatures of such species are often correlated with air temperatures. Between both ends of the spectrum, many intermediate forms exist (SHINE & MADSEN 1996). Thermoregulation is also influenced by intra- or interspecific behaviour, the availability of food and essential microhabitat structures, especially basking sites (POUGH et al. 2001). Beside these factors, phylogenetic origins also play a role (AVERY 1982, VAN BERKUM et al. 1986). Many thermoconformers have the ability to switch to active thermoregulation in case of need. This ability is, depending on the species, correlated with sex, age, seasonal

activity, and incubation requirements (CHARLAND 1995). Thus, the study of thermoregulative behaviour in tropical reptiles allows us to infer physiological flexibility and niche and habitat utilisation. In addition, the analysis of the thermoregulation of a reptile species also allows for evaluating the flexibility in response to short- and long-term climatic changes. This could be a crucial factor for predicting the impact of global climatic change in that critical limits and their relevance for tropical rainforest species become recognizable.

Space utilization and heat distribution in an environment are two key variables in reptile ecology. A potential habitat has to fit to the ecology of a species (HEATWOLE 1977, SMITH & BALLINGER 2001). This does not imply a simple ‘yes’ or ‘no’ to the aptitude of a habitat, though. Reptiles can utilise habitats selectively, which can be triggered by local changes to habitat quality. Many species are flexible with regard to habitat selection. Thus, habitat selection is influenced by physiological activities, population dynamics, and intraspecific behaviour (HOLT 1987, MORRIS 1988,

HUEY 1991, PULLIAM & DANIELSON 1991, ROSENZWEIG 1991). In the end, space utilization is a complex interaction between dynamics in a habitat and the utilizing of these dynamics by the species. This makes this aspect a key point for the survival of all reptile species.

Rhacodactylus leachianus (CUVIER, 1829) is one of the largest gecko species in the world with a maximum SVL of 30 cm (Fig. 1). It is endemic to New Caledonia where it inhabits a variety of primary forest areas. It has an omnivorous diet with a predilection for fruits (BAUER & SADLER 2000). The goal of this study was the simultaneous analysis of thermal ecology and space utilization of this gecko in the context of sex-dependent differences to detect trigger factors in thermal ecology and space utilization.

Materials and methods

The study was carried out on the Île de Bayonnaise (167°25'24.05" E, 22°40'15.09" S), New Caledonia. This island is a satellite island of the Île des Pins, located 1.2 km to the south of it. The island's area size is 23.78 ha, and it is of coralline origin. It is covered with two types of forest, lowland rainforest and maquis forest. The northeast is covered with scerophyl forest with the fruit trees *Cassine curtispindula*, *Acropogon bullata* and *Eugenia* sp.

We used internal transmitters (SOPT 2070, Wildlife Electronics) to record movements and core temperatures between 20 October and 5 November 2002. Five individuals were caught for this study; all were released 24 hours after the procedure. The transmitters were removed after the study was completed. Additionally, all individuals found (i.e., 23 in total, see Results) on the island were marked with internal Passive Integrated Transponders

(PITs) to enable long-distance individual identification. Transmitter-equipped specimens were tracked once every hour throughout the survey. All movements and core temperatures were mapped. All trees, which were used by specimens during the survey, were marked. Home ranges were measured by the minimum convex polygon (MCP) method.

Statistical analysis was performed with Statistica®. Analyses of differences between temperature profiles were examined via a WILCOXON test for abnormally distributed data. The equality of variances between the different samples was tested with the LEVENE test and BROWNE-FORSYTHE-test to obtain secure data on the homogeneity of variances between the sexes. To avoid autocorrelation, all tests were repeated with different sample sizes using the frequency of two days.

Additionally, the distribution of the species on the entire island was mapped. The mapping was repeated in 2005, 2007 and 2013 (see Results). We opportunistically searched the forest for the geckos from dusk until dawn. All captured specimens were marked with PIT transponders.

Dataloggers were placed on treetops and 2 m above the ground to record temperatures and humidity (Tinytag Plus, Gemini Data Loggers®).

Results

Thermoregulation

The five specimens studied included two females and three males (Table 1). Average core temperatures during the survey were 23.5°C (♀) and 24.1°C (♂). There were no significant differences between the sexes, however. The com-



Figure 1. Female *R. leachianus* on *Aruacaria* sp. during the survey.

Table 1. Descriptive statistics of mean core temperatures of male (T°C M), female (T°C F), air (air T°C), treetops (T°C Treetop), and relative humidity (%).

	Number of samples	Mean	Minimum	Maximum	Variance
T°C M	109	23.04	19.44	30.33	8.08
T°C F	301	23.27	19.03	30.33	6.92
T°C air	456	23.77	18.48	31.41	5.11
T°C treetop	453	23.55	19.03	31.15	5.51
Rel. humidity (%)	409	56.00	21.80	84.50	172.82

Table 2. Wilcoxon-test for pairwise samples, comparison of average core temperatures of male (T°C M) and female (T°C F) with air temperatures (T°C air) and air temperatures in treetops (T°C treetop) (significant values are in bold).

	N	T	Z	p-value
T°C M & T°C air	109	1953.00	3,15	< 0.05
T°C M & T°C treetop	109	1384.00	4,87	< 0.001
T°C F & T°C air	301	20257.00	1,63	> 0.05
T°C F & T°C treetop	301	22033.00	0,45	> 0.05

parison of core temperatures with air temperatures in the forest (T°C Air) and the air temperatures in the treetops (T°C treetop) showed clearly different results for both sexes. The core temperatures of the males (T°C M) differed significantly from the that of the air and the treetops (T°C M and T°C air, $z = 3.15$, $p < 0.05$; T°C M and T°C treetop, $z = 4.87$, $p < 0.001$) whereas the core temperatures of the females (T°C F) were not significantly different from these (T°C F and T°C air, $z = 1.63$, $p > 0.05$; T°C F & T°C treetop, $z = 0.45$, $p > 0.05$) (Table 2). Samples differed by up to 3°C between the sexes. The analysis of the variances of the core temperatures of both sexes in comparison with the air temperatures revealed that they significantly differed from the variances of the environmental temperatures (T°C M and T°C air, LEVENE = 17.7965, $p < 0.001$, BROWNE-FORSYTHE = 13.704, $p < 0.001$; T°C M and T°C treetop, LEVENE = 12.792, $p < 0.001$, BROWNE-FORSYTHE = 9.5193, $p < 0.01$; T°C F and T°C air, LEVENE = 14.209, $p < 0.001$, BROWNE-FORSYTHE = 11.062, $p < 0.001$; T°C F and T°C treetop, LEVENE = 8.6013, $p < 0.01$, BROWNE-FORSYTHE = 6.4282, $p = 0.05$) (Table 3).

Space utilisation

In total, 22 adult individuals were caught (13 ♀, 9 ♂) in 2002. No juveniles could be traced and only one subadult was found throughout the years of survey. The mapping results during all surveys showed that the focal species was spatially concentrated in the northeastern portion of the

Table 3. The equality of variances (LEVENE, BROWN-FORSYTHE) for pairwise samples; comparison between average core temperatures of male (T°C M), female (T°C F) and air (T°C air) and tree top temperatures (T°C tree top) (significant values are in bold).

	Levene	DF	p-value	Brn-Fors	DF	p-value
T°C M & T°C air	17.7965	563	0.001	13.704	563	< 0.001
T°C M & T°C tree top	12.792	560	0.001	9.5193	560	< 0.01
T°C F & T°C air	14.209	755	0.001	11.062	755	< 0.001
T°C F & T°C tree top	8.6013	752	0.01	6.4282	752	< 0.05

island. This is also where fruit trees were mostly found. Records on other parts of the islands were only made on occasion. There was no obvious structure in the spatial patterns of males versus females.

The species showed active behaviour between dusk and dawn indicating an activity period of about 11 hours. Moving patterns were observed regularly every hour. All females mapped during the survey were gravid. Males were observed marking territories vocally without structural differentiation in rooming behaviour. Individuals of both sexes were observed on fructiferous trees and occasionally also seen feeding.

The home ranges of males and females overlapped. No sex-dependent differences were found (Fig. 2). The three radio-tracked males inhabited home ranges of 630, 843 and 3,646 m², respectively, while the radio-tracked females had activity areas of 551 and 1,653 m² (MCPs). The greatest areas used for activity in both sexes were recorded from single movement events (Fig. 3). One male migrated for 200 m within 2 h. One radio-tracked female and four additional

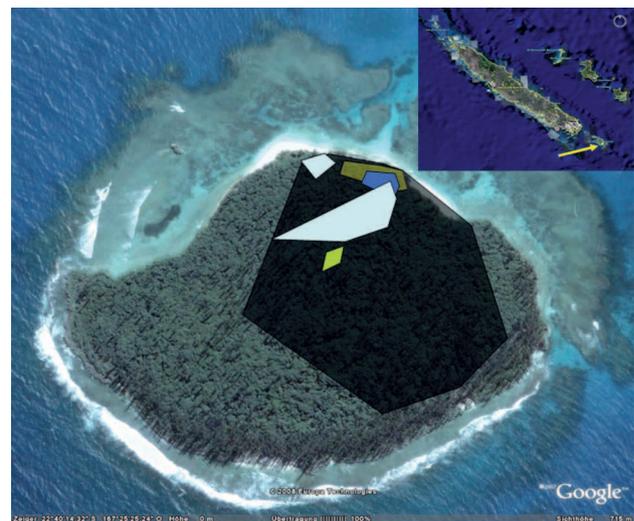


Figure 2. Mapped distribution of *Rhacodactylus leachianus* on the Île de Bayonnaise (black: minimum convex polygon), in relation to the five radio-tracked specimens. Picture by Google Earth, modified by the authors.

ones were observed during oviposition on a coastal dune ca. 5 m from the seashore (Fig. 4). After depositing their eggs, females immediately returned into the forest.

Discussion

The results of this study have to be viewed before the background of the survey periods and the particular conditions on the Île de Bayonnaise. That is, they probably cannot be generalized for the target species as a whole, but for its examined population on the studied island only, where

Rhacodactylus leachianus is not homogenously distributed. During four surveys, all mapped specimens were concentrated in the climatically advantageous northeastern part of the island where the only fructiferous trees were mapped. For this mainly frugivorous gecko species (SEIPP & HENKEL 2000, BAUER & SADLIER 2001, de VOSJOLI et al. 2003), this could be an explanation for the dense mapping results on this part of the island. These findings correspond also with distribution patterns observed in other frugivorous species like *Phelsuma madagascariensis* (CRUZE et al. 2009). It is possible that the majority of the *R. leachianus* population is concentrated in this portion of the island

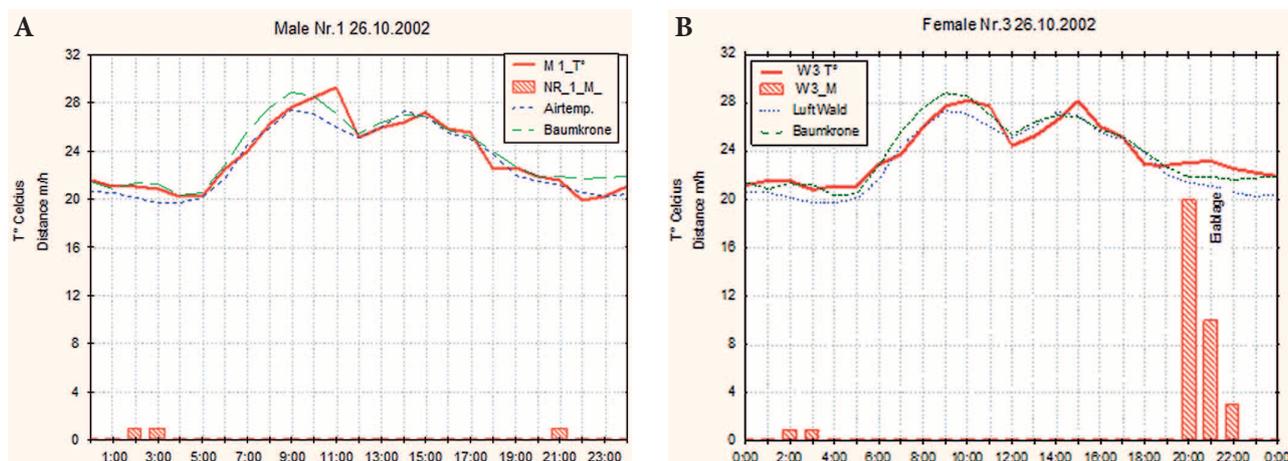


Figure 3. A) Example of changes in core body temperatures of A) male No. 1 and B) male No. 3 (red lines), air temperature (blue lines), tree top temperatures (red dotted lines), and movements within 24 h (histograms).

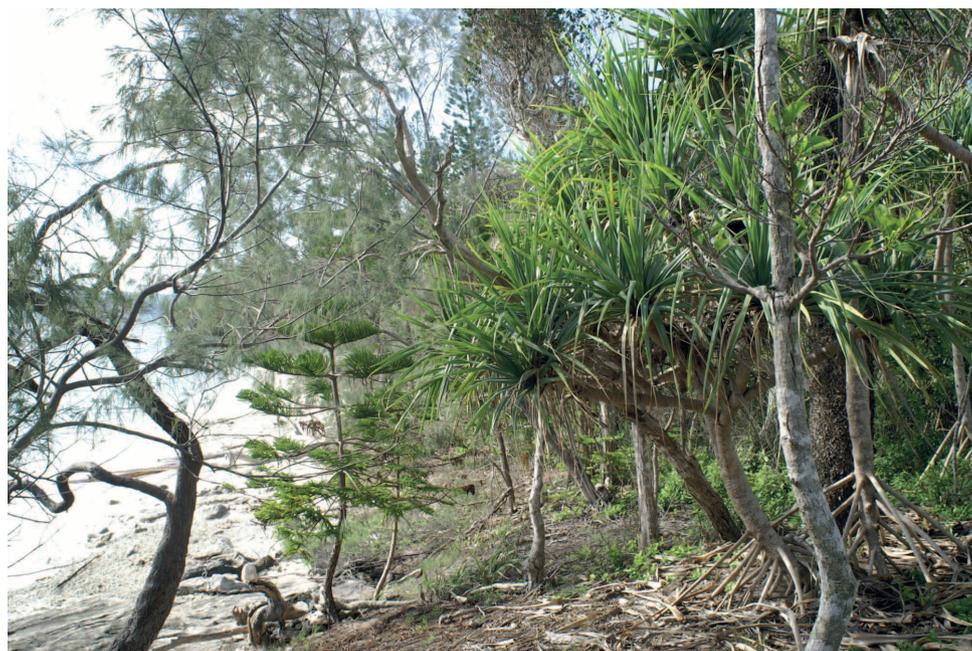


Figure 4. Communal oviposition site on the coastal dune ca. 5 m from the seashore.

throughout the year, which might emphasize the importance of this part of the habitat for the future survival of this population.

The fact that gravid females were observed during oviposition on the coastal dune could be of additional importance, as special microhabitat qualities have also been reported for other species (IKEUSHI et al. 2005).

This is the first report of clear habitat selection in *R. leachianus*. Even though the Île de Bayonnaise is relatively small in size, the studied gecko species is fastidious in its habitat selection. Thus, it could also explain its presence and absence in other rainforest relicts (BAUER & SADLIER 2001). This factor could also play a major role in the heterogeneous distribution of this species on the satellite islands of the Île des Pins.

The results of the thermoregulation analysis suggest that *R. leachianus* is generally a thermoconformer, which is a common mode for species in the tropics (COLLI et al. 2003, FITZGERALD et al. 2003, PEARSON et al. 2003). Clear sex-dependent differences were recorded, with females clearly showing thermoconforming behaviour. This in connection with the oviposition period indicates that there is a dependency on ambient temperatures, as has also been reported from other species (ANDREWS et al. 1997). Male core temperatures differed significantly from the ambient temperatures, indicating active thermoregulation. These sex-dependent differences in thermoregulative behaviour are also known from other reptile species regardless of their occurrence in a climatic zone (CHRISTIAN & BEDFORD 1995, SHINE & MADSON 1996, PEARSON et al. 2003, SOUND 2006). It is notable that females exhibited a strict correlation to ambient temperatures despite possibly higher core temperature needs during the oviposition season. The fact that no such requirements could be demonstrated for other species (WERNER 1990, SOUND 2006) suggests that this factor might be of minor importance.

The analysis of variances revealed that both sexes are basically able to actively thermoregulate. This implies that females are at least facultatively able to perform thermoregulation as is also known from other taxa (CHRISTIAN et al. 1983, 1995). However, it remains unclear whether the females are also able to switch between modes. Reaching higher and stable core temperatures through thermoregulation could be connected to activity patterns in the males during the mating season. Males could regularly be heard staking territories vocally (cf. BAUER et al. 1992). Thus, higher degrees of activity could potentially be a reason for active thermoregulation.

The results for space utilization indicate no sex-specific differences; male and female home ranges overlapped. The majority of radio-tracked specimens of both sexes had home ranges smaller than 1000 m². Only two specimens occupied more than 1000 m² but these ranges were used in short single movement events. Thus, *R. leachianus* shows a space utilization similar to that of other frugivorous arboreal gecko species (cf. IKEUSHI et al. 2005). Although this is one of the largest gecko species currently known, its home ranges are only moderately larger than those of oth-

er species. There is no correlation between body size and home range. A possible explanation for that could be the lower degree of activity of nocturnal geckos (AUTUMN et al. 1994, 1997, 1999). On the other hand, the extraordinarily high diversity of gecko species on the relatively small island of New Caledonia (BAUER et al. 2012) could provide an explanation for the extreme body size of this gecko, hypothetically forcing at least *R. leachianus* to evolve into the ecological niche of a keystone species.

Females were observed depositing their eggs in communal oviposition sites on the coastal dune. These were recorded in 2002 and 2013, indicating that these sites are used on a regular basis and that these females followed a regular behavioural pattern, as is also known in other reptile species (cf. CASSIANO et al. 2011). This is the first record of *R. leachianus* depositing its eggs on a coastal dune and indicates that habitat structure may be an important ecological factor for the studied island populations. One explanation could be the exploitation of a more balanced microclimate for egg development. Also, it may be considered that juveniles will emerge into a habitat not regularly used by adults and in this manner escape intraspecific predation, which is known to occur in the studied gecko (HENKEL 1993, SEIPP & HENKEL 2000, BAUER & SADLIER 2001). Adult individuals normally inhabit the deeper parts of the forest on this island, and their absence in the dunes could therefore improve survival success in juveniles. Actively using this microhabitat could also indicate an advantage in female reproductive success, as has also been suggested to be the case in other species (cf. DANIEL & SHINE 2008).

No juveniles were recorded during any of the surveys even though gravid females and oviposition were recorded. As has been mentioned, it is possible that juveniles have different ecological and spatial preferences than adults (cf. WARNER & SHINE 2008). Differentiated habitat utilization by juveniles may also be advantageous with regard to thermal factors, similar to that of smaller species (ANGUILLETTA et al. 1999).

In summary, our results indicate that *R. leachianus* on the satellite islands of the Île des Pins utilizes its habitat in a complex manner and thermoregulates actively. This in turn also demonstrates that such populations are vulnerable to changes in microhabitat structures and microclimatic conditions. The increasing human impact through tourism, agricultural utilization, and invasive alien species in conjunction with the impacts of climatic change, like the currently observed rising sea level, renders these populations very vulnerable to extinction processes. Only the complete protection of these small populations can help to conserve them.

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