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NOTES ON THE ECOLOGY AND NATURAL HISTORY OF TWO UNCOMMON ARBOREAL AGAMID LIZARDS *DIPORIPHORA PARACONVERGENS* AND *LOPHOGNATHUS LONGIROSTRIS* IN THE GREAT VICTORIA DESERT OF WESTERN AUSTRALIA

By ERIC R. PIANKA
Integrative Biology
University of Texas at Austin
Austin, Texas 78712 USA
Email: erp@austin.utexas.edu

ABSTRACT

Ecological data on *Diporiphora paraconvergens* and *Lophognathus longirostris* are presented. Both species are arboreal, with long tails used as counterbalances during climbing. Both species are associated with sandridges. *Diporiphora* and juvenile *Lophognathus* live in large shrubs, whereas adult *Lophognathus* are often found higher up in Marble Gum trees well above ground. Both species frequently forage on the ground. Both are active thermoregulators. Ambient air temperatures average about 25°C and active body temperatures average 33–34°C in both species, and average time of activity is during midday around noon. These lizards are generalized predators that consume a wide range of insects, especially wasps, hemiptera, beetles, ants, mantids and phasmids as well as larvae of various insects. *Diporiphora* is partially herbivorous and eats both leaves and flowers. *Lophognathus* consumes katydids and grasshoppers. Both dietary and microhabitat niche breadths are greater than those of many other sympatric lizard species. Mating occurs and eggs are laid during the Austral Spring. Average clutch size is 3 eggs in *Diporiphora* and 4.4 in *Lophognathus*. Relative clutch mass of 4 gravid female *Lophognathus* with eggs in their oviducts is 0.151.

INTRODUCTION

The agamid genus *Diporiphora* has undergone recent revision (Doughty *et al.* 2012) with description of a new species *Diporiphora paraconvergens*. During the Austral Springs and Summers of 1966–68, I encountered *Diporiphora paraconvergens* and *Lophognathus longirostris* on two sandridge study sites, the D-area (34 km W. Lorna Glen HS, 26° 14' S. x 121° 13' E.) and the E-area (8 km NE Dunges Table Hill, 28° 08' S. x 123° 55' E.), both in the Great Victoria Desert. In many years of subsequent field work at other sites, I never found any more *Diporiphora* but did collect some *Lophognathus* at my long-term Redsands study site (10 km WSW Yamarna, 28° 12' S. x 123° 35' E.), although they were never very abundant. Two juvenile *Lophognathus*, probably not residents but rather dispersers, were pit-trapped 4 km south of Redsands on my B-area (28° 13.5' S. x 123° 35' E.). I consider these propagules evidence of metapopulation structure. Similarly, *Diporiphora* were locally extinct at the Redsands study site where suitable habitat and microhabitats occur.

The Great Victoria Desert of Australia is predominantly sandy with red sands, and supports a vegetation consisting mainly of so-called "spinifex" or "porcupine" grasses (genus *Triodia*) plus various species of gum trees (*Eucalyptus*), especially Marble Gums (*Eucalyptus gonglyocarpa*). Marble Gum trees are the favored habitat of adult *Lophognathus*. Shrubs including *Eremophila*,

Figure 1. *Diporiphora paraconvergens* in typical alert posture in a shrub.

Figure 2. *Lophognathus longirostris* poised in a small desert tree (note its very long tail).

Grevillea, *Hakea*, and *Thryptomene* also occur and are used by juvenile lizards of both species. Stabilized long red sandridges, parallel to prevailing winds are scattered throughout the Great Victoria Desert, particularly in the eastern interior. Extensive areas of flat sandplain occur as well. The region is very heterogeneous with mixed ecotonal habitats of shrubs, *Triodia*, *Acacia*, and *Eucalyptus* on desert loams. Beard (1974) and Shephard (1995) describe and illustrate the vegetation of the region. The climate is an arid continental regime, with cool usually dry winters and warm springs and autumns but quite hot summers. Most precipitation falls during summer thunderstorms. Wildfires are frequently set by lightning and vegetation biomass and cover vary through time as plants undergo secondary sucession following fire (Pianka 1996; Pianka and Goodyear 2012).

METHODS

My assistants and I observed and collected 37 *Diporiphora paraconvergens* at 2 study areas and 93 *Lophognathus longirostris* at 4 study sites. These data were augmented with limited observations on a few other lizards that were not collected. We recorded air and body temperatures, times of activity, microhabitat, fresh

snout-vent length (SVL), tail length, and weight for as many lizards as possible. Stomach contents were identified and prey volumes estimated for all lizards collected. Reproductive condition was also recorded: for males, lengths of testes were measured; for females, egg sizes were measured and numbers were counted, and whether eggs were ovarian or oviductal was noted [some of these data were summarized in appendices in Pianka (1986)]. Niche breadths were calculated using the inverse of Simpson's (1949) index of diversity [$D = 1/ \Sigma p_i^2$] where p_i is the proportion of resource state *i*.

RESULTS

Habitat

Both species are habitat specialists, and seem to prefer slopes and crests of sandridges, although *Lophognathus* has a broader habitat niche breadth and is more frequently found at the base of sandridges or out on flat sandplains away from sandridges (Table 1).

Table 1. Numbers and percentages of lizards found in different sandridge habitat zones. Sample sizes (N) and habitat niche breadths (HNB) are given at bottom of the table. Lizards at an interface between habitats split in half.

Habitat	*Diporiphora*		*Lophognathus*	
	N	%	N	%
Flat	0.5	1.3	11	11.8
Base	1.5	3.9	12	12.9
Slope	8	21.1	13	13.9
Crest	28	73.7	57	61.3
Sample (N)	38		93	
HNB.	1.698		2.348	

Anatomy

Diporiphora is smaller (mean SVL = 45.6 mm, adults = 50.4 mm) than *Lophognathus* (mean SVL = 67 mm, adults = 100.3 mm). Female *Lophognathus* reach sexual maturity at about 94 mm SVL. No sexual size dimorphism is evident in *Lophognathus*, but adult female *Diporiphora* are larger than adult males (56.5 mm versus 47.9 mm).

Diporiphora and *Lophognathus* are arboreal, with very long tails used as counterbalances during climbing. They may climb to increase their visual field as well as to avoid high surface temperatures during the heat of the day in summer.

Microhabitat

Both species are usually associated with large bushes (Table 2). In both species, over 30% of lizards were above ground when first sighted. *Lophognathus* also frequents trees and they are more often found higher up than *Diporiphora*.

Thermoregulation

Both species are active thermoregulators. Body temperatures of 32 active *Diporiphora* ranged from 26.3 to 41°C averaging 33.7°C with a standard deviation of 3.31 (average air temperature was 25.1°C with a standard deviation

Table 2. Percentages of lizards encountered in 14 different microhabitats. Microhabitat niche breadths (MHNB) is given at the bottom of the table.

Micro-habitat	*Diporiphora*	*Lophognathus*
Open Sun	5.7	6.96
Grass Sun	10	3.91
Bush Sun	38.6	31.30
Tree Sun		2.17
Other Sun	1.4	0.87
Open Shade		2.61
Grass Shade	1.4	2.17
Bush Shade	10	7.83
Tree Shade		5.65
Other Shade	1.4	0.87
Low Sun	17.1	10.87
Low Shade	8.6	6.52
High Sun	5.7	9.13
High Shade		9.13
Sample (N)	35	115
MHNB	4.7	6.75

of 6.12). Body temperatures of 76 active *Lophognathus* ranged from 24.8 to 45.4°C, averaging 34.3°C with a standard deviation of 3.84 (average air temperature was 25.6°C with a standard deviation of 6.26). Body temperature is correlated with air temperature (Fig. 3 and Fig.4).

These lizards bask when it is cold, and seek shade when it is warm. During the heat of mid-day, they sometimes climb up above ground and face directly into the sun, thereby positioning themselves in cooler air and reducing heat load. Climbing also increases the area of their visual field and may help them avoid contact with potential predators.

Diets

Diporiphora and *Lophognathus* are sit-and-wait ambush predators with fairly broad diets. They are omnivorous, eating both plant and animal foods (Table 3). The most important insect prey item eaten by both species is wasps (29% and 20.7%). Both species also prey on hemipterans (11.2% and 13.3% of diets by volume), beetles (9.8% and 7.2% of diets by volume), as well as larvae of various insects (8.7% and 9.6% of diets by volume). Other less important prey items include ants, mantids and phasmids. *Diporiphora* are omnivorous con-

Table 3. Percentages of various dietary items by volume along with total volume and dietary niche breadths.

Prey Category	*Diporiphora*	*Lophognathus*
Centipedes	0	0.634
Spiders	3.1873	0.9863
Ants	7.1713	7.2913
Wasps	20.7171	29.13
Locustids	2.3904	10.391
Roaches	0	0.7045
Mantids/ Phasmids	5.1793	5.3892
Beetles	7.1713	9.7922
Termites	0	2.1134
Hemiptera	11.1554	13.3145
Diptera	1.1952	2.6418
Larvae	9.5618	8.7355
Other Insects	3.1873	5.7062
Vegetation	29.0837	1.6555
Other	0	0.0704
UnID	0	1.4442
Total Volume	2.51	28.39
Dietary Niche Breadth	**6.07**	**6.95**

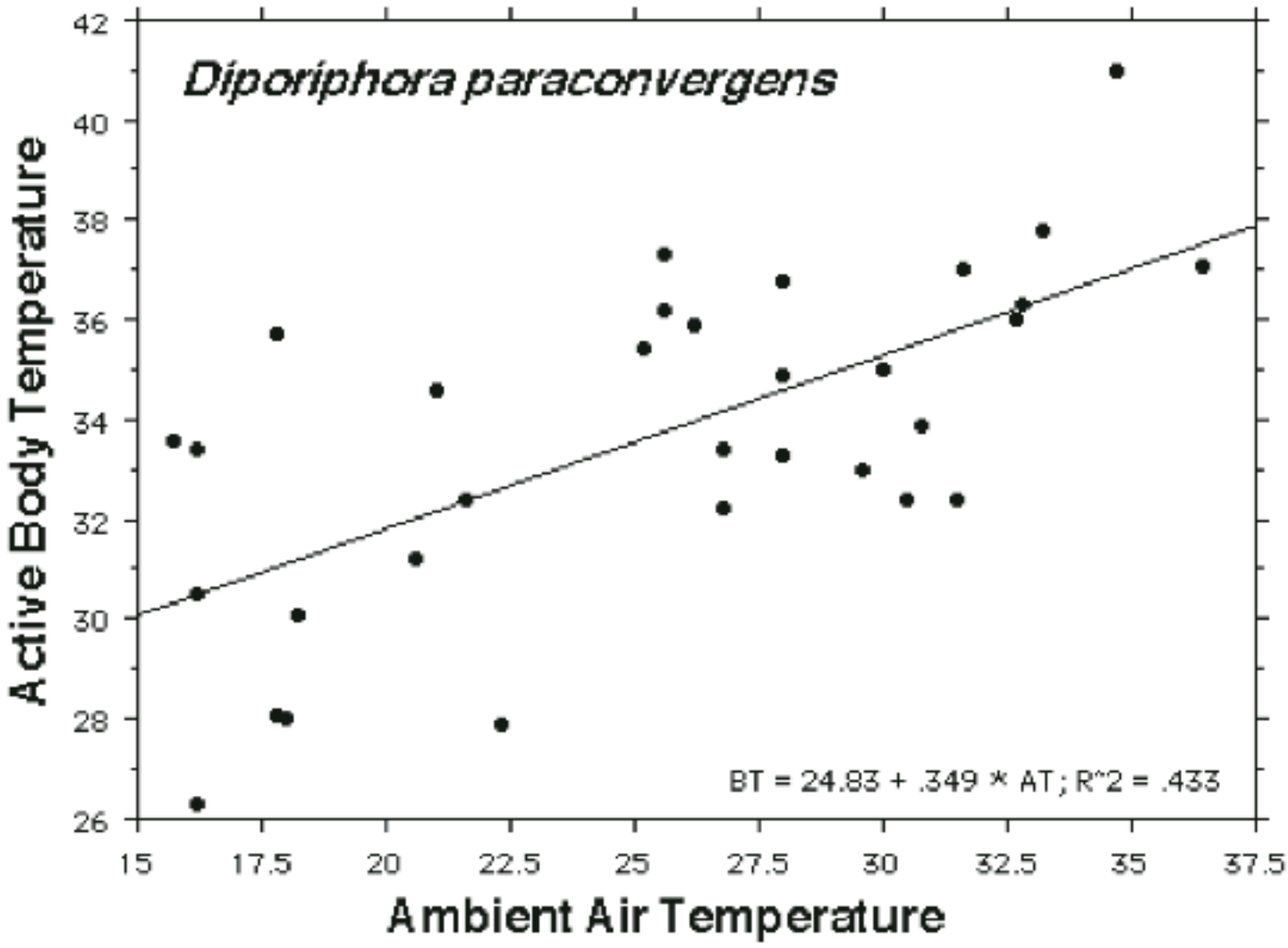

Figure 3. Body temperatures plotted against ambient air temperature for 32 active *Diporiphora*.

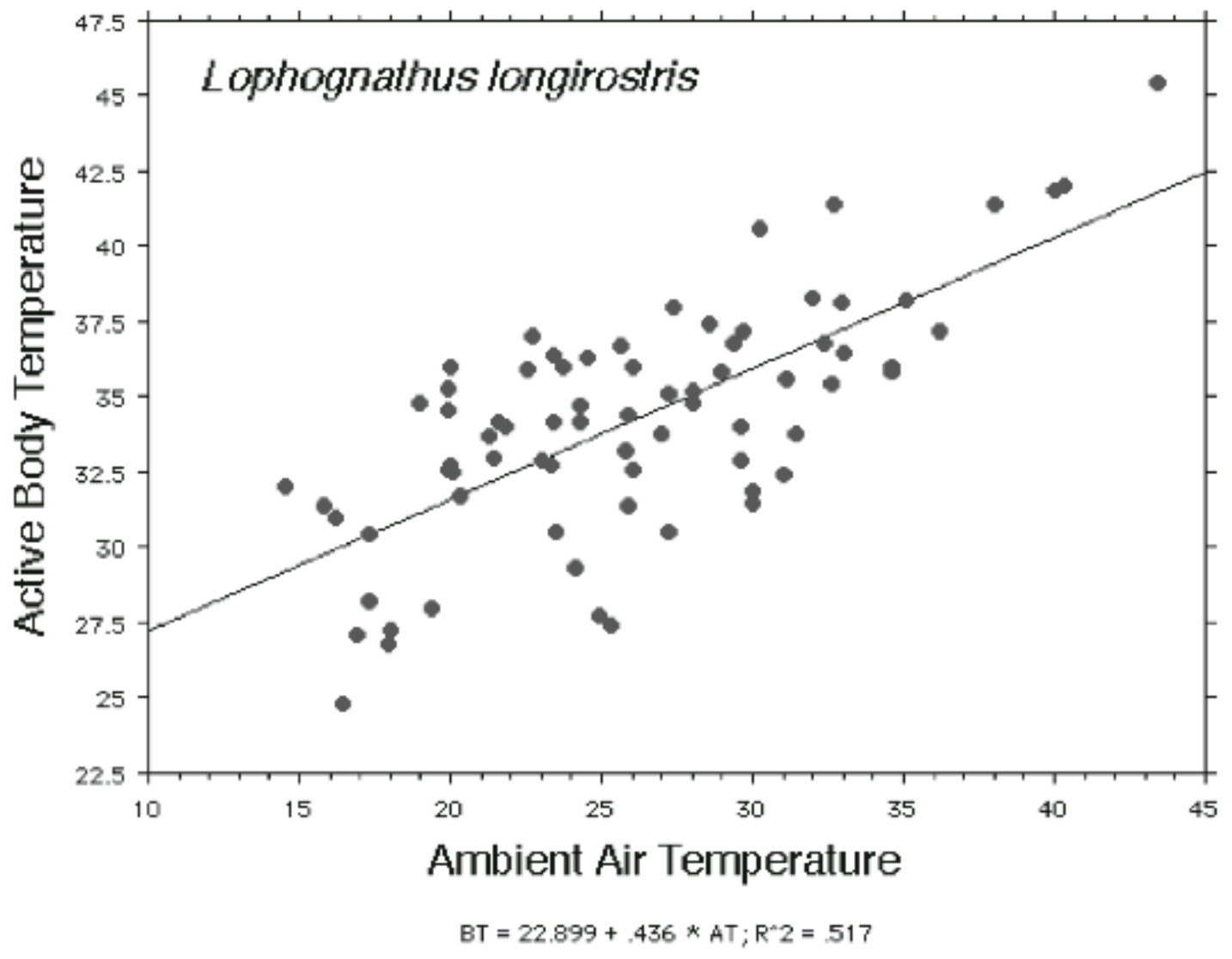

Figure 4. Body temperatures plotted against ambient air temperature for 76 active *Lophognathus longirostris*.

suming many plant materials, both leaves and flower heads, which constitute about 29% of their diet by volume. Katydids and grasshoppers constitute 10.4% of the *Lophognathus* diet by volume.

Both dietary and microhabitat niche breadths are greater than those of many other sympatric lizard species (Pianka 2014).

Reproduction

15 adult male *Diporiphora* averaged 47.9 mm in SVL and 9 adult male *Lophognathus* with enlarged testes found in November and December averaged 101.6 mm in SVL. Average adult female SVL is 56.5 mm in *Diporiphora* and 99 mm in *Lophognathus*. Clutch sizes of 6 female *Diporiphora* averaged 3. Gravid female *Diporiphora* were found in September, November and early December. One gravid female *Diporiphora* was found in January, suggesting that some females could lay a second clutch. Gravid female *Lophognathus* contained from 3 to 6 eggs (mean 4.44) and were found in October, November and December. Relative clutch mass in *Lophognathus* is 0.151. Hatchlings are small (SVL 30–33 mm in *Diporiphora* and 40–44 mm in *Lophognathus*). Juveniles appear to grow fast and undoubtedly suffer fairly heavy mortality. These lizards are not social and I have never observed courtship or mating.

Predation

Predators on *Diporiphora* and *Lophognathus* would include various species of birds of prey especially Brown Falcons and Australian Kestrels, bustards, large snakes, and monitor lizards *Varanus eremius*, *V. tristis* and *V. gouldii* as well as introduced cats and foxes. Both *Diporiphora* and *Lophognathus* rely heavily on camouflage to avoid predators, typically freezing and holding very still until the threat goes away. However, if pursued, of course they run rapidly away from an attacker. *Lophognathus* can run bipedally on their hind legs with tails held high as counterbalances.

DISCUSSION

Dietary and microhabitat niche breadths are greater in both *Diporiphora paraconvergens* and *Lophognathus longirostris* than in many other sympatric lizard species. However, because both species are habitat specialists being restricted to sites with sandridges and are never very abundant, these two arboreal species were categorized as rare by Pianka (2014). Both species exhibit features suggestive of metapopulation structure, such as dispersal propagules, local extinctions, and/or being absent from sites with suitable habitats and microhabitats (see Table 4 in subsequent paper.

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