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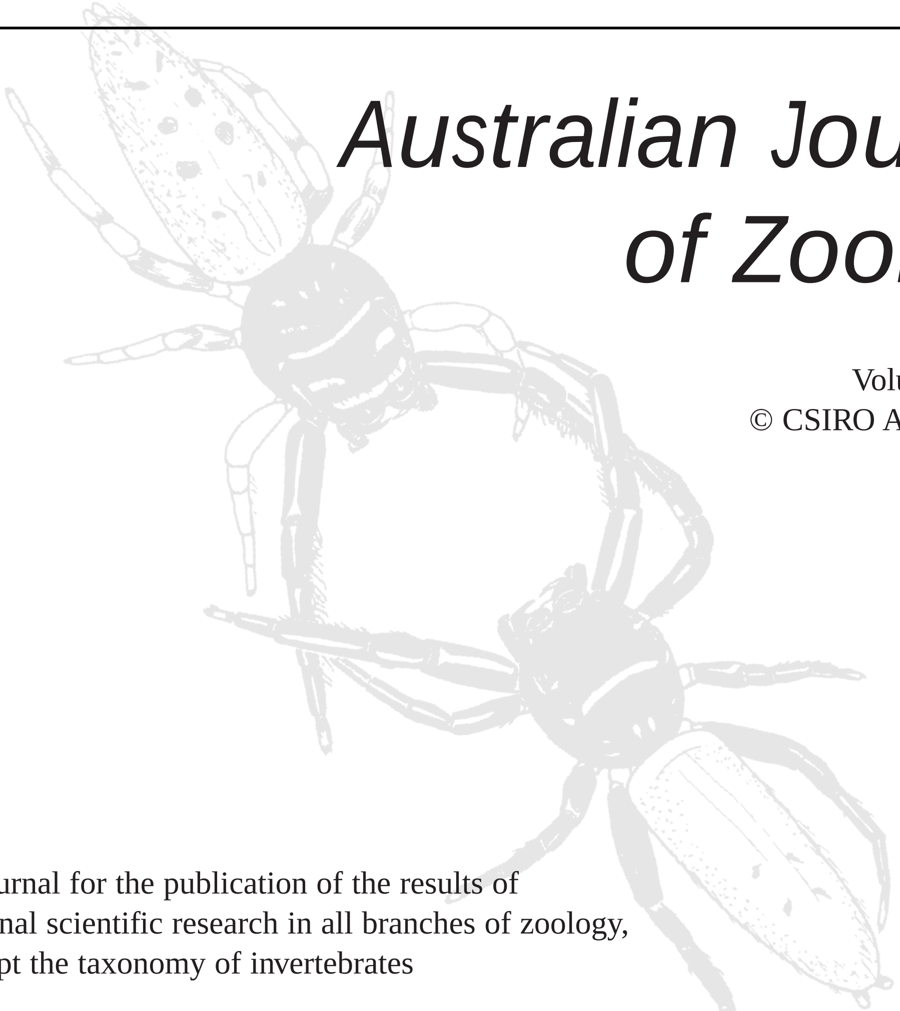

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Longevity, reproductive effort and movements of three sympatric Australian arid-zone geckos

John L. Read

Environmental Department, WMC (Olympic Dam Corporation),
PO Box 150, Roxby Downs, SA 5725, Australia.

Abstract

Three sympatric diplodactyline geckos were studied in chenopod shrubland over a six-year period in northern South Australia. Females of each species were significantly larger than males. *Rhynchoedura ornata* and *Diplodactylus conspicillatus,* both termite specialists, consistently produced multiple clutches of two eggs in a long breeding season each year, whereas the reproductive output of *D. stenodactylus*, a dietary generalist, was more erratic. Females of the two *Diplodactylus* species bred in three consecutive years, whilst *R. ornata* seldom lived for more than two years. Mean relocation distances ranged from 26 to 35 m, which suggests that some individuals of all species maintained home ranges. However, many individuals of each species, especially *R. ornata*, were apparently transitory over areas greater than the 1-ha study site.

Introduction

Geckos are one of the most diverse and abundant families of Australian reptiles, yet the biology of many arid-zone species is poorly known (Heatwole and Taylor 1987). Although detailed biological information on a few species has been collected (Bustard 1968*a*, 1968*b*; How *et al.* 1986), the validity of extrapolations from these studies to other species is limited by possible intrageneric variation in lizard life-history strategies on geographical and temporal scales (Ballinger 1979; Tinkle and Dunham 1986; Adolph and Porter 1993). An understanding of longevity, reproductive effort, and movements is a necessary precursor to the interpretation of studies into the impacts of anthropocentric changes to gecko populations, which are potentially valuable bioindicators of environmental health (Read 1998*a*). Therefore, studies on the life-history characteristics of closely related species (Henle 1989; James 1991*b*; Adolph and Porter 1993), as well as long-term examination of the dynamics of lizard communities (Whitford and Creusere 1977), are necessary.

Three of the most common terrestrial gecko species throughout the *Triodia,* mulga and chenopod deserts of Australia are *Diplodactylus stenodactylus, D. conspicillatus* and *Rhynchoedura ornata* (Reid *et al.* 1993; James 1994; Read 1995*a*). These three species occupy a broad range of substrates (Pianka and Pianka 1976; Storr *et al.* 1990) and often coexist in high numbers. *Diplodactylus stenodactylus* is a generalist insectivore whereas the other two species feed almost exclusively upon termites (Pianka and Pianka 1976; Pianka 1986).

I studied the biology of *Diplodactylus stenodactylus, D. conspicillatus* and *Rhynchoedura ornata* at Olympic Dam in northern South Australia, where they were sympatric with five other terrestrial geckos, namely *Diplodactylus tessellatus, D. damaeus, Heteronotia binoei, Nephrurus levis* and *N. milii*, and two arboreal species, *Strophurus cilliaris* and *Gehyra* sp. (Read 1994). In particular, this study aimed to determine whether these species were restricted to home ranges and to investigate interspecific differences in longevity and breeding success.

Methods

Because of their small size, monitoring of gecko movements was dependent upon multiple captures of individuals because tracking devices were not viable alternatives. Although pitfall trapping is an efficient method of capturing terrestrial geckos, calculation of home ranges from pitfall studies is rarely possible since at least 16, and typically over 30, independent locations are required for robust calculations (Rose

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1982; Christian and Waldschmidt 1984; Vernes *et al.* 1995; Comport *et al*. 1996). However, mean recapture or relocation distances are a powerful estimator of relative movements (Tinkle and Woodward 1967; Worton 1987) and have provided useful insights into the movements of other Australian arid-zone lizards surveyed by pitfall traps (James 1991*b*, 1996; Read 1998*b*).

Study site

Geckos were trapped in a 1-ha, 5-m grid of 401 unfenced pitfall traps, in chenopod shrubland near Olympic Dam (30°29′S, 136°55′E) in northern South Australia. The long-term average annual rainfall at Olympic Dam is 168 mm (Read 1995*b*) and the climate is characterised by hot summers and mild winters with unpredictable rain equally likely during any month. Full details of the habitats and trap design of the pitfall-grid study site are presented by Read (1995*a*). Uniquely numbered pits were opened for a total of 68 170 trap-nights in 17 sessions from January 1991 until February 1996. Each trapping session consisted of 10 trap-nights, separated by at least one night when the traps were closed. Trapping occurred once each season for the first three years and in November and February (summer) in subsequent years. Only the summer months were sampled in the later years since geckos and most other reptiles are largely inactive over the cool winter period at Olympic Dam (Read 1992).

Traps were checked and closed early in the mornings. Geckos were sexed, weighed (to ±0.1 g), measured (to ±1 mm), and inspected for eggs, which could be seen through the belly wall of gravid females. Enlarged vitellogenic follicles may have been occasionally obscured by distended stomachs and hence the number of females in reproductive condition was possibly slightly underestimated. All new individuals were marked with a unique toe-clip combination. All trapped animals were released at their pit of capture within 12 h of capture. Geckos were released in the evening on hot days to avoid heat stress but were still allowed at least one night of unimpeded movement and foraging before traps were reopened. Therefore, each of the 170 trap-nights was treated as being independent with respect to the localities where individuals were captured. This assumption was tested by plotting the time interval to the first recapture against the distance moved by individuals of each species.

Longevity and dispersal estimates

Although the precision of recapture data was maximised by not fencing pit traps and by closing traps between each sampling night, this method yields low capture rates. Therefore, the probability of achieving multiple captures of the same individuals was decreased. Since a maximum of 11 locations were recorded for any individual, the sizes of home ranges were not calculated. However, the movements of each species were compared by measuring the average distance between successive recaptures and the maximum distance between localities of individuals retrapped more than once. The average relocation distance for a surrogate individual moving at random within the confines of the monitoring site was modelled using 10 000 000 pairs of random locations. This figure was then compared with the relocation distances of males and females of each species using Wilcoxon Signed Rank tests to determine whether the activities of individuals were confined to areas less than the 1-ha study site.

Morphological and ecological data

Additional information on the morphometrics, length of the breeding season and age at maturity of each species was extracted from over 35 000 nights of drift-fence-enhanced pitfall trapping and other studies in similar habitats within 20 km of the principal trapping site from 1986 until 1996 (Read and Badman 1990; Read 1992; author's unpublished data). Attainment of sexual maturity in females was assessed by the minimum size of individuals with eggs.

Results

Size distribution and age at female maturity

In total, 851 *D. conspicillatus*, 871 *D. stenodactylus* and 1235 *R. ornata* were measured in this study. All species were sexually dimorphic, with females larger (*D. conspicillatus*: t = 19.16, d.f. = 849, $P < 0.001$; *D. stenodactylus*: t = 10.7, d.f. = 869, $P < 0.001$; *R. ornata*: t = 26.36, d.f. = 1233, $P < 0.001$) and heavier (*D. conspicillatus*: t = 11.86, d.f. = 847, $P < 0.001$; *D. stenodactylus*: t = 4.38, d.f. = 859, $P < 0.001$; *R. ornata*: t = 19.9, d.f. = 1227, $P < 0.001$) than males (Table 1).

Table 1. Size for adult males and females, and size and weight data for hatchling *D. conspicillatus*, *D. stenodactylus* and *R. ornata* at Olympic Dam

Maximum and mode measurements are more relevant than means for species that grow throughout their life. The percentage of females that were gravid in two different size classes is presented to justify demarcation of adult size. SVL, snout–vent length

	D. conspicillatus		*D. stenodactylus*		*R. ornata*	
	Male	Female	Male	Female	Male	Female
Maximum SVL (mm)	57	61	57	59	55	57
Mode SVL (mm)	48	53	47	52	45	48
Hatchling SVL (mm)	24–26 (*n* = 3)		22–27 (*n* = 6)		22–27 (*n* = 8)	
Hatchling weight (g)	0.3–0.4 (*n* = 3)		0.2–0.4 (*n* = 6)		0.2–0.3 (*n* = 8)	
Gravid females <46 mm	0% (*n* = 8)		1.4% (*n* = 42)		2.5% (*n* = 61)	
Gravid females <50 mm	1% (*n* = 19)		26.2% (*n* = 125)		31.4% (*n* = 185)	

Females of *D. stenodactylus* and *R. ornata* matured at a considerably smaller body size than did those of *D. conspicillatus*. The demarcation of adult size in these smaller species was adopted as 46 mm whereas the cut-off for adult *D. conspicillatus* was adopted as 50 mm due to the small percentage of females less than these lengths that were gravid (Table 1). Mark–recapture data showed that females of all three species matured in less than one year, with mid-summer hatchlings recorded as gravid early the following summer. Females hatching from later clutches were probably unable to breed immediately after their winter dormancy but an overwintering immature *D. stenodactylus* trapped in November was gravid two months later in January.

Breeding season and evidence of multiple clutches

Gravid females of each species were recorded throughout all trapping periods from October until February (Fig. 1). Limited trapping before and after this period restricted determination of the full breeding season. However, enlarged vitellogenic follicles were evident in all species as late as mid-February, and hence the breeding season probably extended until at least March. Mating of *D. stenodactylus* was observed in January and egg-laying recorded in November, December and February. Hatchling *D. conspicillatus* and *D. stenodactylus* were trapped in December, January and February. One recaptured *R. ornata* female laid between 15 January 1991 and 13 February 1991 and hatchlings were recorded from December until March.

The high percentage of gravid females throughout the long breeding season suggests that most individuals of all species were capable of producing multiple clutches within the same season. This breeding pattern could also have been generated if first-year individuals attained sexual maturity at different times during the activity season. However, multiple clutches within a season were confirmed for three recaptured *D. conspicillatus* and three *R. ornata* females. In total, 12 female *D. conspicillatus* were recorded breeding in more than one season, 10 in consecutive years and two in three different breeding seasons. Likewise, seven *D. stenodactylus* individuals were gravid in consecutive years and two gravid females were also gravid when recaptured after 24 months. In contrast, breeding was not recorded in any female *R. ornata* in three successive years, although eight females were gravid in two consecutive years. Despite 77% of the 421 adult female *R. ornata* captured being gravid, an apparently anomalous individual was not gravid on any of the six occasions she was caught between December 1991 and February 1993.

One marked female *R. ornata* was recorded with oviducal eggs on 10 November 1993, and with yolked ovarian follicles 22 days later on 2 December 1993, which indicates that vitellogenesis may occur rapidly after oviposition.

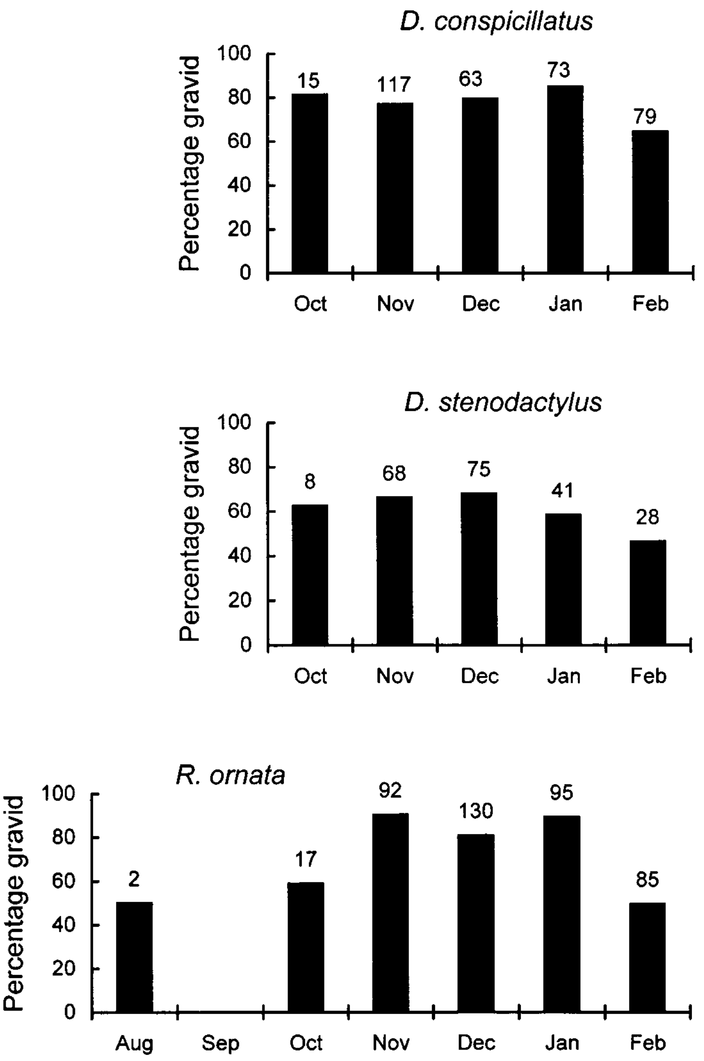

Fig. 1. Percentage of gravid adult female *D. conspicillatus, D. stenodactylus* and *R. ornata* throughout the breeding season. Sample sizes are shown for each month.

Reproductive statistics

Gravid females of all species had two eggs with the exception of three *D. conspicillatus* and one *R. ornata*, which had a sole oviducal egg. The annual percentage of gravid adult females from November to February was 65–89% in *D. conspicillatus* and 55–86% in *R. ornata* (Fig. 2). However, the percentage of gravid adult female *D. stenodactylus* varied more than in the other species, from a low of 23% in 1990/91 to a peak of 83% in 1992/93 (Fig. 2).

Longevity

Considerable numbers of both *D. conspicillatus* and *D. stenodactylus* were retrapped at intervals greater than two years, with some retrapped after more than four years (Fig. 3). The maximum interval between captures of individual *D. conspicillatus* and *D. stenodactylus* was

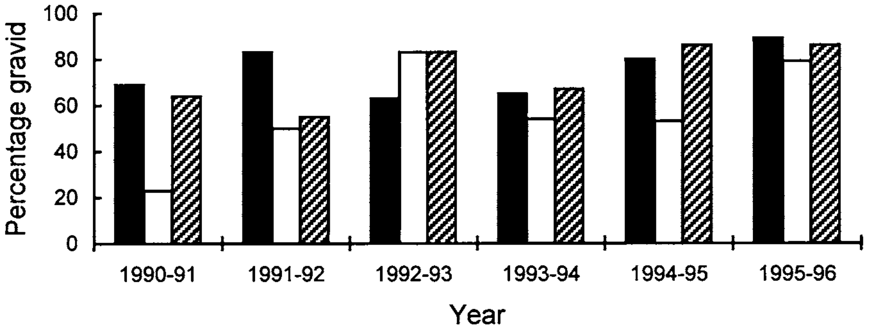

Fig. 2. Annual percentage of gravid adult female geckos of each species each summer from 1990/91 to 1995/96. Sample sizes for each species exceeded 20 in all years, with the exception of 13 *D. stenodactylus* in 1990/91 and 19 *D. conspicillatus* in 1991/92. Black bars, *D. conspicillatus*; white bars, *D. stenodactylus*; hatched bars, *R. ornata*.

1152 days and 1488 days respectively. In contrast to the *Diplodactylus* geckos, fewer than 1% of the marked *R. ornata* were recaptured more than two years after their initial capture (Fig. 3) and the maximum time between recaptures was 1016 days. Maximum recapture times for male and female *R. ornata* were significantly less than that of male *D. stenodactylus* ($P < 0.001$); the differences between other species and sexes were all nonsignificant ($P > 0.05$). Average maximum recapture times also reflected the apparently shorter lifespan of *R. ornata*, with individuals typically sampled for just over half the period (174–197 days) usually recorded for the other two species (308–402 days: Table 2).

One adult male *D. stenodactylus* was regularly recaptured without growing from January 1991 until February 1995, which indicates that males can live for at least five years. Only one of the nine *D. stenodactylus* recaptured more than three times was a female and this same individual was the only female recaptured more than two years after her initial capture (Fig. 4). Such sexual dichotomy in longevity or site fidelity was not evident in *D. conspicillatus* (Fig. 4).

Relocation distances

Low regression correlation coefficients (*D. conspicillatus*: $r^2 = 0$, $F = 0.011$, d.f. = 31, $P = 0.918$; *D. stenodactylus:* $r^2 = 0$, $F = 0.774$, d.f. = 19, $P = 0.39$; *R. ornata:* $r^2 = 0.045$, $F = 3.318$, d.f. = 70, $P = 0.073$) indicate that there was no clear relationship between the time elapsed and distance moved of singly retrapped individuals of each species. Therefore, as with the analogous

Table 2. Recapture success and movement data for three gecko species at the Pitgrid monitoring site 1991–96

Sample sizes are shown in parentheses

Species	% retrapped	Mean distance between retrappings (m) ± 1 s.e.		Mean maximum relocation for individuals (m)	Mean maximum days between retrappings ± 1 s.e.	
		Male	Female		Male	Female
D. conspicillatus	34.3 (166)	27 ± 3.5	35.1 ± 4.4	35.8	320 ± 44 (35)	337 ± 83 (20)
D. stenodactylus	44.4 (108)	26 ± 2.2	29 ± 5.3	39.2	402 ± 62 (31)	308 ± 42 (16)
R. ornata	32.5 (351)	30 ± 3.3	33 ± 2.2	38.3	197 ± 36 (52)	174 ± 24 (59)

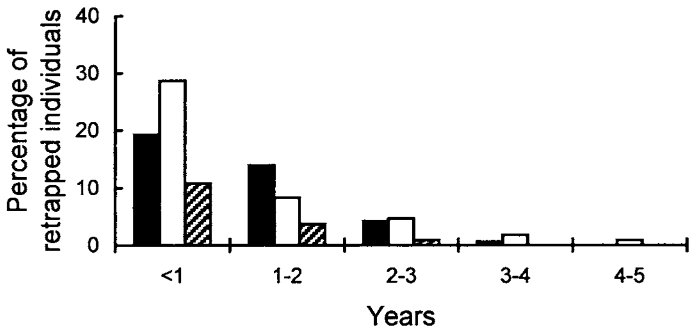

Fig. 3. Percentage of individuals trapped in successive years. Black bars, *D. conspicillatus*; white bars, *D. stenodactylus*; hatched bars, *R. ornata*.

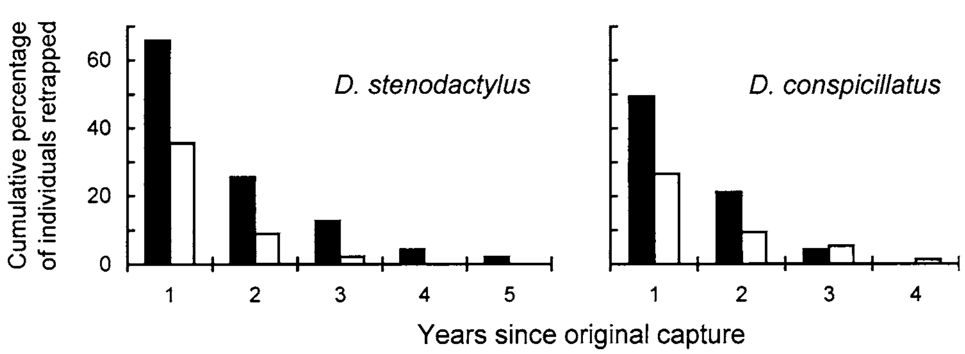

Fig. 4. Maximum recapture time for male and female *D. conspicillatus* and *D. stenodactylus*. Black bars, males; white bars, females.

study of *Ctenotus* skinks at the same site (Read 1998*b*), each trapping day can be considered to be independent with respect to the distance moved by individuals.

Individuals of all species apparently occupied home ranges within the monitoring site. The average maximum distance moved by recaptured males and females of each species (Table 2) was significantly less ($P < 0.001$) than the distance of 54.9 m, which was calculated as the average relocation distance on the basis of random movement within the grid. There were no significant differences in relocation distances between either sexes or species ($F = 1.09$, d.f. = 5,205, $P = 0.369$).

A limitation of this study was that less than half of the marked individuals from any species were subsequently recaptured. Although it was impossible to distinguish between the effects of mortality, home ranges only slightly impinging on the study site or nomadic movements for these individuals, it is likely that at least some individuals of each species moved considerably greater distances than suggested by the typical relocation distance of recaptured individuals. Frequent sampling of unmarked adult individuals, particularly *R. ornata*, at pits near the centre of the grid towards the end of most sampling sessions, provides further circumstantial evidence that some adults were transitory at the scale surveyed by this trapping array.

Discussion

Some *D. conspicillatus, D. stenodactylus* and *R. ornata* produce multiple clutches within a breeding season and breed in successive years. Multiple clutching has been reported for other Australian geckos (Bustard 1968*b*; How *et al.* 1986), although proof of more than two successive clutches is limited (Greer 1989). Captive geckos with laying periods separated by as little as 1–3 weeks (Girard 1993; Leptien 1996) and up to 7 clutches per year (Meshaka *et al.* 1994) have been reported. The sexual dimorphism in *D. conspicillatus, D. stenodactylus* and *R. ornata* is consistent with the larger body size of females than of males in some other gekkonid genera such as *Oedura*, *Strophurus* and *Nephrurus* (Bustard 1971; How *et al.* 1986; Read 1998*c*), although this trend is not uniform through all geckos (Greer 1989). Large size in females probably facilitates production of larger eggs, resulting in higher survivorship of juveniles compared with the smaller eggs laid by smaller females. No evidence of male combat, which typically leads to selection of large size in male reptiles (Fitch 1981), was evident in these geckos.

Generation of yolked ovarian follicles while oviducal eggs were present was not confirmed for any of the gecko species studied, although this trait is widespread among related *Strophurus* geckos (How *et al.* 1986). However, the high percentage of gravid females throughout summer, the evidence of rapid vitellogenesis following egg-laying and the long breeding season recorded in this study, suggest that females of each species may lay three or more clutches each summer. Support for this conclusion comes from evidence that *Morethia boulengeri* also produced three clutches per year in the Australian arid zone (Henle 1989) even though oviducal eggs and enlarged vitellogenic follicles were never observed simultaneously. Similarly, although the proportion of reproductively active *Ctenotus* females was low at any one time, James (1991*a*) concluded that some females probably produced clutches in both November and January. The recorded mating of *D. stenodactylus* in January when the female exhibited enlarged vitellogenic follicles may indicate that clutches are fertilised by independent mating events, although this observation does not rule out the possibility of sperm storage, which occurs in some geckos (Girard 1993).

While some individuals of *D. stenodactylus* and *D. conspicillatus* bred in three consecutive years, females of *R. ornata* were apparently restricted to two breeding seasons. Few individuals of *R. ornata* lived for more than two years, which is also considerably less than the *Diplodactylus* species, which regularly lived for three or more years. The longer activity season of *R. ornata* compared with that of the two *Diplodactylus* species conforms with the model for a fast-growing lizard species that matures at a young age (Pianka 1970; James and Shine 1988).

Seasonal variation in the percentage of females gravid was more marked in *D. stenodactylus* than in the two termite specialists and accounted for the lower average fecundity of this species throughout the study period. A likely explanation for this variation in fecundity is variability in the availability of food, which, together with seasonal conditions, influences the annual reproductive output (James 1991*a*, 1996) and reproductive success (Whitford and Creusere 1977; James 1991*a*) of some arid-zone lizards. Primary productivity in the arid zone increases with annual precipitation (Whittaker 1970) and hence the abundance of many arid-zone insects is closely tied to rainfall (Morton 1978). Both plant biomass and recruitment of the skinks *Ctenotus regius* and *C. leonhardii*, which have generalist diets, peaked in 1993 and were also high in 1995 (Read 1998*b*). Therefore, high numbers of herbivorous insects after favorable rains in 1992, and to a lesser extent in 1994, may explain the high reproductive output of *D. stenodactylus* in 1992/93 and 1995/96. Likewise, low reproductive output of *D. stenodactylus* in the 1990/91 summer coincided with negligible recruitment of *C. regius* and *C. leonhardii* in that summer (Read 1998*b*).

By contrast, the consistently high fecundity of termite-specialist geckos, and *Ctenotus schomburgkii* which feeds predominantly upon termites (Read 1998*b*), suggests that termites are a reliable and abundant food source in both wet and dry years. Pianka and Pianka (1976) also found that reproductive effort was greater among termite-specialist geckos, in particular *D. conspicillatus* and *R. ornata*, than in geckos with less specialised diets. While the extreme climatic variability of the Australian arid zone is widely recognised as being a major force structuring and limiting reptiles and other faunal communities (Stafford-Smith and Morton 1990), evidence from this study and from research on *Ctenotus* skinks (James 1991*b*; Read 1998*b*) suggests that food resources are both rich and relatively consistently available for termite-specialist lizards.

Individuals of all three gecko species were regularly recaptured at the same site over several years, which suggests the maintenance of a territory, or confined activity range. Territoriality *per se* could not be confirmed since intraspecific aggression has not been reported for any of these species and recapture rates were too low to plot home ranges to determine the degree of overlap of conspecifics. The mean recapture distances of these geckos, which was typically 25–35 m, was more than the average recapture distance of small skinks at the same sites (15–25 m: Read 1998*b*). Males of all three species moved shorter distances in the same or longer recapture times than did females, suggesting that males exhibit higher site fidelity or have smaller home ranges than females, which may in part account for the apparently greater longevity of male *D. stenodactylus* than females in this study.

Although individuals of each gecko species maintained home ranges within the study site, some specimens of each species apparently either changed their home ranges, occupied a much larger home range than typical, or were nomadic. Population structures of these species may therefore accommodate a continuum of land-use strategies from truly nomadic individuals to residents with small, well-defined home ranges. This variability in residency status would account for the greater average movements of the geckos compared with those of the three common *Ctenotus* at the same site. Flexibility in site fidelity, as well as reproductive effort, may be an important attribute for gecko populations occupying unpredictable environments.

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