Diet and Reproductive Biology of the Australian Sand-swimming Lizards, *Eremiascincus* (Scincidae)

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Abstract

The diets, morphology and reproductive biology of two little-known sand-swimming skinks, *Eremiascincus fasciolatus* and *E. richardsoni*, were compared by using preserved museum specimens ($n = 458$). In addition, some ecological data are presented for *E. fasciolatus* from a mark–recapture study in spinifex grasslands in central Australia. The species are similar in morphology and body pattern, but reportedly differ in microhabitat preferences. Both species ate a range of invertebrate taxa, with beetles, grasshoppers and spiders making up most of the prey consumed. Vertebrate prey (lizards) were rare in the diets but were large and energetically important items when consumed. There were no significant differences in the taxonomic composition of the diets between species, between sexes of a species, or among age classes of a species. Females tended to be longer in body length (snout–vent length, SVL) than males, but adult males were heavier than females of the same body length. Testes of males were enlarged in spring (September–December), coinciding with the appearance of females with vitellogenic follicles. Both species are oviparous, and eggs were laid from October to February. Clutch sizes averaged around four eggs and were not significantly different between the species at the same SVL. Adult *E. fasciolatus* moved extensively during the field study; average displacement between recaptures was $63 \cdot 5 \pm 128$ m. Population estimates for *E. fasciolatus* varied seasonally between 14 and 108 individuals on the 60-ha study site. *E. fasciolatus* was most abundant in microhabitats on dune crests with a sparse cover of spinifex but frequently traversed large areas in swales with hard soil and denser spinifex cover.

Introduction

The scincid genus *Eremiascincus* was recently erected for two species of sand-swimming lizards found throughout the arid and semi-arid regions of Australia (Greer 1979). *Eremiascincus fasciolatus* and *Eremiascincus richardsoni* are characterised by a series of bands down the body and tail, three or four parallel rows of low rounded dorsal ridges, and a highly polished appearance (Greer 1979). The two species are similar in general body pattern, morphology and size, and the main diagnostic characteristics distinguishing them, the number and width of caudal bands, cannot be used if the tail has been regenerated; hence, there can be difficulty in distinguishing the species on morphological traits.

Although the two species of *Eremiascincus* are sympatric throughout most of their ranges (Cogger 1986), there are reported differences in the habitats they occupy. *E. fasciolatus* is commonly found in areas with sandy soils (usually sand dunes) and spinifex grass (*Triodia* spp.), whereas *E. richardsoni* is found mainly on harder soils and rocky ground. This habitat separation is not absolute, with both species being found in a range of habitats (Greer 1979).

For example, Henle (1989) found that *E. richardsoni* was most common in microhabitats with 'soft sandy substrates around large *Dodonaea*-bushes and avoided bare areas of heavily compressed very hard sand'. Both species are crepuscular and nocturnal, and little is known of their ecology in the natural environment (see Henle 1989).

In captivity, *Eremiascincus* have been reported to be voracious predators, frequently eating vertebrates (Greer (1979). The only study of the diet of *Eremiascincus* from animals collected in the field (Henle 1989) suggested that *Eremiascincus* are primarily insectivorous. We investigated the diets of both species to determine whether they have different diets, and whether they are unusually carnivorous compared with other scincid lizards of similar body mass.

A number of sources (Waite 1929; Worrell 1963; Bustard 1970; Rawlinson 1971) have reported that *Eremiascincus* are viviparous (bear live young), whereas a more recent study (Greer 1979) reported that *E. richardsoni* is oviparous (lays shelled eggs). We investigated the reproductive biology to determine the mode of reproduction and general life-history characteristics of the species.

In light of their morphological and ecological similarities, we examined diets, morphological relationships within and between species, and the reproductive biology of *Eremiascincus*. We primarily used preserved museum specimens of *Eremiascincus* for this study. We also present some limited ecological data from the first mark–recapture study of *E. fasciolatus* in the natural environment, and make suggestions for future studies of *Eremiascincus*.

Materials and Methods

A total of 458 specimens was examined from the following museums: Australian Museum (Sydney), Northern Territory Museum (Darwin), South Australian Museum (Adelaide), Queensland Museum (Brisbane), Australian National Wildlife Collection (CSIRO, Canberra) and Western Australian Museum (Perth). Stomach contents were removed, identified to Order and each intact prey item weighed (to $\pm 0 \cdot 1$ g). Specimens were blot-dried and weighed. For each prey type, the mean prey mass was calculated. The total mass for a given prey type was calculated by multiplying the mean mass of intact prey (prey from both species were combined for this calculation because no differences were apparent in prey size between species) by the total number of items of that prey type.

Interspecific and sexual differences in morphology were examined by measuring the following variables on museum specimens: snout–vent length (SVL; to ± 1 mm), jaw length (JL; to $\pm 0 \cdot 1$ mm) from the tip of the snout to the anterior edge of the ear opening, jaw width (JW; to $\pm 0 \cdot 1$ mm) across the quadrates measured ventrally, and tail length (TL; to ± 1 mm). All individuals with broken or regenerated tails were excluded from comparisons of tail length. Analyses of covariance (ANCOVA) were used on ln-transformed data to examine intersexual and interspecific differences in body size and jaw morphology.

The reproductive data recorded from museum specimens were sex, state of maturity (immature or mature), stage of reproductive cycle (reproductive or non-reproductive), level of development of gonads in reproductive females (yolking ovarian follicles or oviductal eggs), the dimensions of the gonads (length and breadth, to $\pm 0 \cdot 1$ mm), and the clutch size from females with enlarged vitellogenic follicles greater than 2 mm in diameter, oviductal eggs or macroscopically visible corpora lutea. Stage of maturity for males was judged by the appearance of the testes and epididymides, which were small and without obvious convolutions in immature specimens. Immature females had small follicles ($< 0 \cdot 5$-mm diameter) and thin, strap-like oviducts. Males were judged to be reproductive if their testes and epididymides were turgid and white; reproductive females were those with either vitellogenic ovarian follicles or oviductal eggs. Hatchling size was estimated from the SVL of the smallest museum specimen that had an obvious umbilical scar. Size at sexual maturity was estimated to be at the overlap in SVL of the largest immature specimen and the smallest reproductive specimen.

Length and breadth measurements of the testes, vitellogenic follicles and oviductal eggs were used to calculate their volumes with the formula for a prolate spheroid: $4/3\pi ab^2$, where a is the radius of the longest axis and b is the radius of the shortest axis (James 1991a). Testis volume was used to infer spermatogenic activity (Taylor 1985).

The field study site was located at Ewaninga, 40 km south of Alice Springs in central Australia (24°00′S.,133°54′E.). The site consisted of 60 ha of spinifex grassland habitat (*Triodia* sp.) on a sand dune system. Lizards were captured in pit traps, measured, weighed, toe-clipped and released. There were 204 pit traps divided into 12 subsites of 17 pits each, and the subsites were 100–150 m apart. Further details of the field methods, vegetation and climate of the Ewaninga area can be found in James (1991*a*). A total of 71 *E. fasciolatus* was captured from October 1985 to April 1988. Capture data were used to examine movements, growth rates, population size and structure, and microhabitat preferences. Movements on two scales were recorded: within each subsite (<50 m) and between subsites (100–1500 m). Population size was estimated for the whole study site (60 ha) during each spring and autumn by Jackknife statistics on the frequency of capture of individuals (Burnham and Overton 1979; Chao 1987). The subsites covered a range of differences in spinifex and shrub covers, and topographic features (dune crests and swales). Vegetational and topographic features for each subsite were quantified (James 1989) and the distribution and abundance of *E. fasciolatus* in relation to microhabitat features was examined with correlation analysis.

Results

Diet

The diets of the two species were similar (Tables 1 and 2). Numerically, coleopterans, orthopterans and ants (Hymenoptera : Formicidae) were the predominant prey types (isopterans accounted for 20% of *E. fasciolatus* prey because one individual contained 31 termites). No other prey type constituted more than 7% of prey items of either species. More than half the individuals of both species contained coleopterans in their stomachs; ants and orthopterans were each taken by more than 19% of individuals of both species. No other prey type was eaten by more than 10% of *E. fasciolatus*, and only isopterans (18%) and blattids (11%) were eaten by more than 10% of *E. richardsoni*. Contingency-table tests indicated that the species did not differ in the proportion of individuals eating coleopterans, orthopterans or ants (x^2, $P>0\cdot05$ in all cases). The proportional biomass of each prey type indicated quite different patterns. Coleoptera were still the most important prey, constituting more than 40% of total prey mass for both species. However, orthopterans contributed less than 7% of total prey mass, and ants contributed even less. Because of their relatively large size, vertebrate prey (primarily lizards) constituted a major proportion of prey mass despite the relatively few instances of carnivory. Similarly, relatively large insect larvae also were a substantial proportion of prey mass.

There was no evidence of sexual differences in diet in either species. For both sexes of both species, coleopterans, ants and orthopterans were the predominant prey, with the exceptions that male *E. richardsoni* ate more blattids than orthopterans and male *E. fasciolatus* ate more spiders than ants. Within each species, contingency-table tests (x^2 and Fisher's exact test) revealed no significant differences ($P>0\cdot05$) in the proportion of each sex eating any prey type. Among males (but not females) of both species, smaller individuals were more likely to eat coleopterans; however, Kolomogorov–Smirnov Two-Sample tests did not indicate an ontogenetic shift in diet with increasing SVL ($P>0\cdot05$). There were no indications of ontogenetic shifts in other prey types. In neither species was there a relationship between body size and prey size (*E. fasciolatus*: $r^2=0\cdot09$, $F_{1,15}=2\cdot54$, $P>0\cdot15$; *E. richardsoni*: $r^2=0\cdot08$, $F_{1,6}=0\cdot25$, $P>0\cdot25$; for lizards with more than one prey item, the largest item was used). The species did not differ with respect to mean prey size ($t=0\cdot50$, d.f. $=23$, $P>0\cdot65$).

Morphology

Sexual dimorphism

Females grew to a larger SVL than males in both species (Table 3). In neither case was the difference in mean SVL between males and females statistically significant (*E. fasciolatus*: $F_{1,123}=3\cdot26$, $P=0\cdot07$; *E. richardsoni*: $F_{1,208}=3\cdot07$, $P=0\cdot08$), but both analyses were close to the critical level. Adult male *E. fasciolatus* were heavier at a given SVL than

Table 1. Prey in the stomachs of 52 *Eremiascincus fasciolatus*

No. of prey is the total number of items of a given prey type in all lizards.
No. of lizards is the number of lizards eating each prey type. Numbers in
parentheses are the proportion of all prey constituted by each prey type
and the proportion of all lizards that ate each prey type. % Prey mass is
the proportion of the total mass of all prey constituted by each prey type.
See Methods for the description of the calculation of prey mass

Prey taxa	No. of prey	No. of lizards	% Prey mass
Arthropoda			
Arachnida			
Araneae	3 (0·02)	3 (0·06)	—
Scorpiones	1 (0·01)	1 (0·02)	0·7
Isopoda	1 (0·01)	1 (0·02)	0·06
Insecta			
Blattoidea	4 (0·02)	4 (0·08)	3·0
Coleoptera	51 (0·30)	35 (0·65)	48·1
Hemiptera	2 (0·01)	2 (0·04)	—
Hymenoptera	42 (0·25)	10 (0·19)	5·1
Isoptera	33 (0·20)	2 (0·04)	0·2
Lepidoptera			
Larvae	1 (0·01)	1 (0·02)	0·4
Orthoptera	16 (0·10)	13 (0·25)	6·6
Unidentified			
Adult	3 (0·02)	3 (0·06)	—
Larvae	5 (0·03)	3 (0·06)	12·2
Other	2 (0·01)	2 (0·04)	—
Vertebrata			
Reptilia			
Scincidae[A]			
Ctenotus	4 (0·02)	4 (0·08)	
Eremiascincus	1 (0·01)	1 (0·02)	
Total	169	52	
Mean number of items per lizard ± s.e.	3·25 ± 0·65		

[A] The *Eremiascincus* and three of the four *Ctenotus* sp. were tails.

adult female *E. fasciolatus* (ANCOVA: slopes $F_{1,69} = 4·78$, $P < 0·05$) but the same was not
true for *E. richardsoni* (ANCOVA: slopes $F_{1,53} = 0·02$, $P > 0·85$; intercepts $F_{1,54} = 0·39$,
$P > 0·54$). Analysis of size structure of the specimens in museum collections (Fig. 1) showed
that females were usually the largest individuals in the populations. There was significant
sexual dimorphism in JL (Fig. 2) but not in JW (Fig. 3). Jaw lengths were significantly
longer in adult males than in adult females (*E. fasciolatus*: slopes $F_{1,84} = 5·71$, $P < 0·02$;
E. richardsoni: slopes $F_{1,62} = 0·69$, $P > 0·4$, intercepts $F_{1,63} = 8·26$, $P < 0·01$). There was no
sexual dimorphism in tail length for either species.

Interspecific comparisons

Eremiascincus richardsoni had a larger mean adult SVL than did *E. fasciolatus* (Table 3)
($F_{1,334} = 26·0$, $P < 0·0001$) but there was no significant difference between the species in
body mass at a given SVL. Interspecific comparisons between males (slopes $F_{1,61} = 0·81$,
$P > 0·35$; intercepts $F_{1,62} = 1·0$, $P > 0·3$) and between females (slopes $F_{1,61} = 0·34$, $P > 0·55$;
intercepts $F_{1,62} = 0·03$, $P > 0·85$) showed no differnces in body mass relative to SVL. There

Table 2. Prey in the stomachs of 45 *Eremiascincus richardsoni*

Data are presented as for Table 1. See Methods for the description of the calculation of prey mass

Prey taxa	No. of prey	No. of lizards	% Prey mass
Arthropoda			
Arachnida			
Araneae	7 (0·05)	6 (0·13)	—
Insecta			
Blattoidea	5 (0·03)	5 (0·11)	3·6
Coleoptera	46 (0·31)	23 (0·51)	41·2
Diptera	6 (0·04)	3 (0·07)	5·8
Hemiptera	10 (0·07)	1 (0·02)	—
Hymenoptera	30 (0·20)	12 (0·27)	3·4
Isoptera	11 (0·07)	8 (0·18)	0·05
Orthoptera	16 (0·11)	13 (0·29)	6·2
Unidentified			
Adult	3 (0·02)	3 (0·07)	—
Eggs	3 (0·02)	2 (0·04)	—
Larvae	4 (0·03)	2 (0·04)	9·4
Other	4 (0·03)	4 (0·09)	—
Vertebrata			
Reptilia			
Gekkonidae			
Diplodactylus	1 (0·01)	1 (0·02)	0·5
Scincidae			
Ctenotus	1 (0·01)	1 (0·02)	19·5
Typhlopidae			
Ramphotyphlops			
cf. *guentheri*	1 (0·01)	1 (0·02)	10·3
Total	148	45	
Mean number of items per lizard ± s.e.	3·29 ± 0·55		

Table 3. Snout–vent lengths (mm) of adult *Eremiascincus* in museum collections

Numbers are mean ± two standard errors, with the sample size in parentheses

	Males	Females	All adults
E. fasciolatus	75·1 ± 18·0 (70)	78·0 ± 19·4 (55)	76·4 ± 14·4 (125)
E. richardsoni	80·8 ± 13·8 (103)	83·3 ± 26·4 (107)	82·0 ± 14·4 (210)

were also no interspecific differences in body mass relative to SVL for males and females combined (slopes $F_{1,158} = 0·06$, $P > 0·8$; intercepts $F_{1,159} = 0·17$, $P > 0·65$).

Eremiascincus richardsoni had relatively longer tails than *E. fasciolatus* when the allometric effect of body size was removed (Fig. 4: slopes $F_{1,65} = 0·08$, $P > 0·75$; intercepts $F_{1,66} = 17·98$, $P < 0·001$).

An interspecific comparison of jaw dimensions suggested that JL and JW increased more rapidly with increasing SVL in *E. richardsoni* than in *E. fasciolatus* (JL, Fig. 2: slopes $F_{1,192} = 62·94$, $P < 0·001$) (JW, Fig. 3: slopes $F_{1,190} = 4·58$, $P < 0·05$). Therefore, adult *E. richardsoni* have longer and wider jaws at a given SVL than do *E. fasciolatus*.
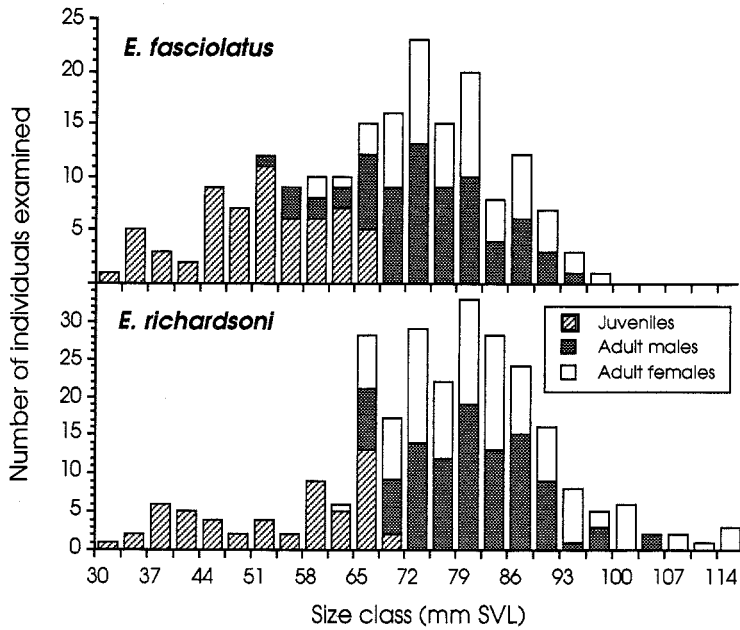
Fig. 1. Population size-structure of *Eremiascincus* in museum collections. The criteria used to distinguish between juvenile and adult lizards are explained in the Methods.
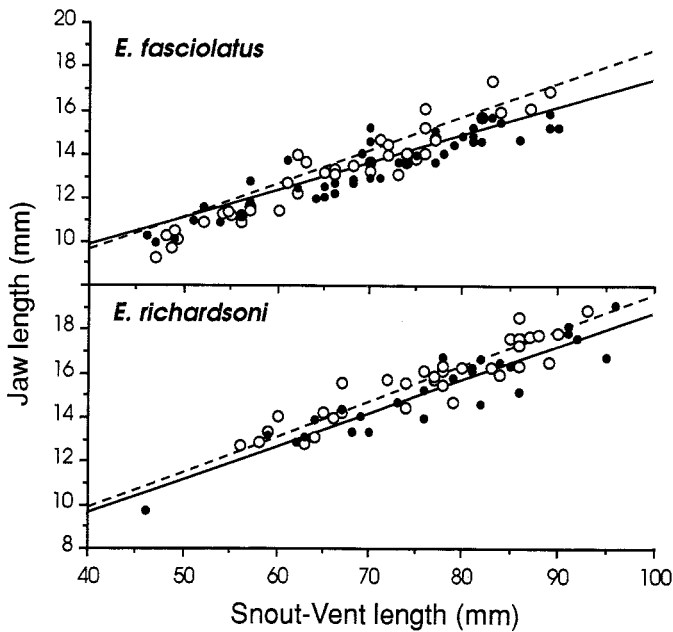

Fig. 2. Scatter plot of SVL against jaw length (from the tip of the snout to the anterior edge of the ear opening) in male and female *Eremiascincus*. Adult males have longer jaws than adult females at the same SVL. The slopes of the lines are significantly different between the two species. ---○, male; ——●, female.

Fig. 3. Scatter plot of SVL against jaw width (JW) (across the quadrates measured ventrally) in male and female *Eremiascincus*. There is no sexual dimorphism in JW, but the slopes of the lines are significantly different between the two species. ---○, male; ——●, female.
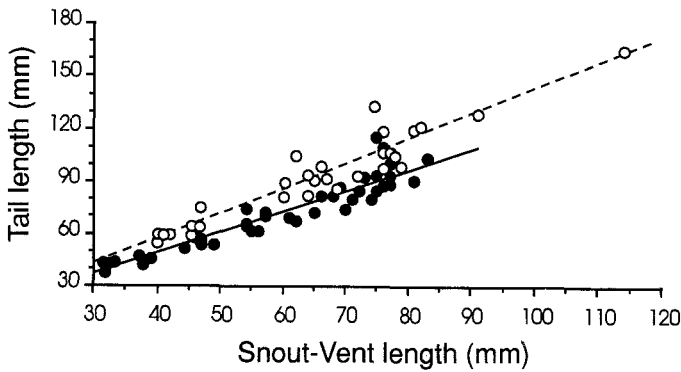

Fig. 4. Scatter plot of SVL against tail length for *Eremiascincus*. *Eremiascincus richardsoni* (---○) has a significantly longer tail at the same SVL compared with *E. fasciolatus* (——●).

Table 4. Percentage of individuals in museum collections with broken or regenerated tails

Sample sizes are shown in parentheses (number with broken tails/total number examined)

	Males	Females	All adults
E. fasciolatus	45·5 (20/44)	26·7 (12/45)	37·7 (40/106)
E. richardsoni	20·0 (7/35)	37·5 (12/32)	31·5 (29/92)

Tail loss

Approximately 35% of adult *Eremiascincus* in museum collections had regenerated tails (Table 4). Intersexual comparisons within a species were not significantly different (*E. fasciolatus*: $\chi^2 = 3 \cdot 44$, $P > 0 \cdot 07$; *E. richardsoni*: $\chi^2 = 2 \cdot 48$, $P > 0 \cdot 1$). The frequencies of tail break were also not significantly different in comparisons between species ($\chi^2 = 0 \cdot 86$, $P > 0 \cdot 25$).
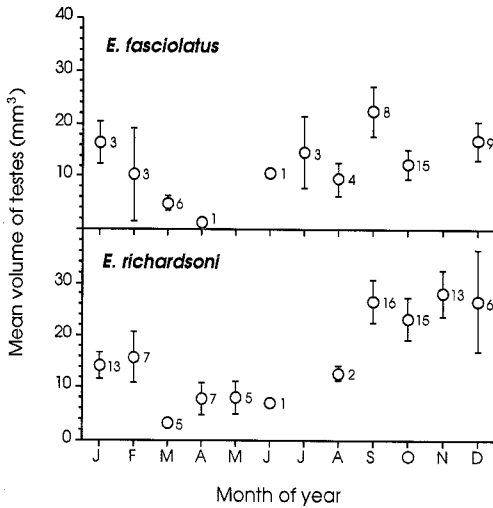

Fig. 5.   Mean volume of testes (± 2 s.e.) of adult *Eremiascincus* in each month of the year. Sample sizes for each month are shown.
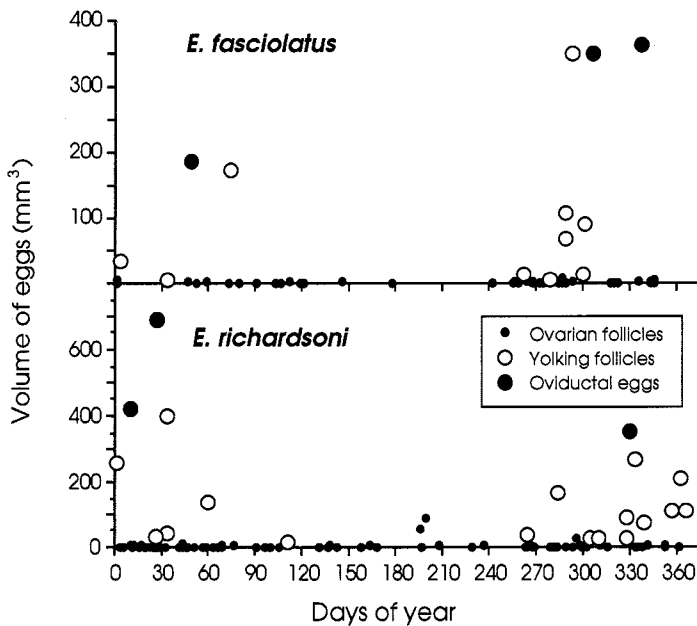

Fig. 6.   Ovarian condition for all sexually mature female *Eremiascincus* examined in the study.
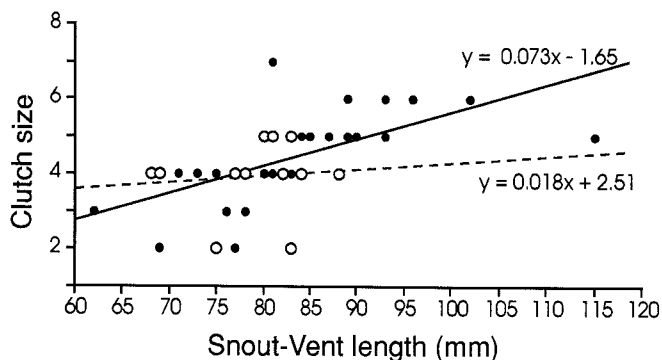
Fig. 7. Regressions of clutch size with maternal SVL for *Eremiascincus*. ——●, *E. richardsoni*; ---○, *E. fasciolatus*. Clutch size is significantly correlated with maternal SVL in *E. richardsoni* ($r^2 = 0.417$, $P = 0.0009$) but not in *E. fasciolatus* ($r^2 = 0.011$, $P = 0.74$).

Table 5. Clutch sizes and egg volumes for museum specimens of *Eremiascincus*

Numbers are means ± two standard errors (range and sample size in parentheses)

	Clutch size	Egg volume (mm³)
E. fasciolatus	3·9 ± 0·58 (2–5, 12)	300·4 ± 113·1 (187·6–362·9, 3)
E. richardsoni	4·5 ± 0·54 (2–7, 23)	487·0 ± 208·6 (350·4–691·9, 3)

Reproduction

Adult male *E. richardsoni* with enlarged testes were collected from September to December (spring). Although adult male *E. fasciolatus* also had enlarged testes during the same period, the pattern is not as clear as it is for *E. richardsoni* (Fig. 5). Reproductive females of both species were collected in spring and summer (Fig. 6). Females with vitellogenic follicles were collected as early as September and females with oviductal eggs were collected until mid-February. Both species had well developed shells on oviductal eggs, suggesting that eggs would have been laid.

The approximate SVL at sexual maturity was similar for males and females although it appears that females may mature at slightly larger SVLs than males: estimated size at maturity for *E. fasciolatus* was 63 mm for males and 66 mm for females, and for *E. richardsoni* was 67 mm for males and 69 mm for females. The size at maturity for *E. fasciolatus* from the Ewaninga site, determined from ten individuals collected and preserved during the field study, was estimated to be 63 mm SVL for males and females.

The sex ratio of adult *Eremiascincus* in museum collections was not significantly different from unity for either species (*E. fasciolatus*: ♂ : ♀ 70 : 55 = 1·27, $\chi^2 = 1·80$, $P = 0·18$; *E. richardsoni*: 103 : 107 = 0·963, $\chi^2 = 0·076$, $P = 0·78$).

Clutch size was correlated with maternal body size in *E. richardsoni* but not in *E. fasciolatus* (Fig. 7). An extra egg was added for every 14-mm increase in SVL of *E. richardsoni*, whereas the clutch size of *E. fasciolatus* was usually four eggs (7 of 12 reproductive females). Mean clutch size of *E. richardsoni* was larger than that of *E. fasciolatus* (Table 5), but the difference was not significant when the effect of maternal body size was removed (ANCOVA on ln-transformed data: slopes $F_{1,31} = 1·31$, $P = 0·26$; intercepts $F_{1,32} = 0·22$, $P = 0·65$). There were too few females of either species for analysis of differences in the sizes of eggs (Table 5).

Growth Rates

The growth rates of six *E. fasciolatus* recaptured on the Ewaninga site were examined (Fig. 8). All growth records were for adult lizards and averaged $0·0413 ± 0·0304$ mm day^{-1} (mean ± s.d.) over recapture intervals of 22–230 days. None of the juvenile *E. fasciolatus*
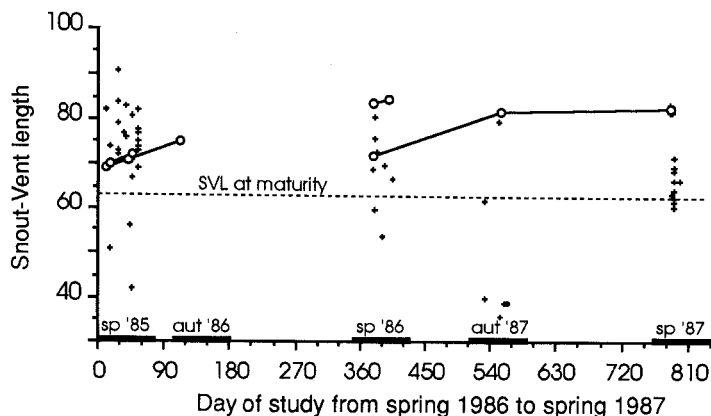
Fig. 8. Scatter plot of the SVLs of all *E. fasciolatus* captured on the Ewaninga study site over three years. Recaptures of individuals are joined by a line to show growth increments. Black bars along the *x*-axis indicate sampling times.

Table 6.   Mean Jackknife population estimates for active *E. fasciolatus*

Each estimate is calculated from recaptures on 12 subsites on the Ewaninga study site (60 ha). No *E. fasciolatus* were captured in autumn 1986

Season	Jackknife estimate ± s.e.	95% Confidence interval
Spring 1985	108 ± 21	66–150
Autumn 1986	—	—
Spring 1986	54 ± 14	26–82
Autumn 1987	14 ± 9	0–31
Spring 1987	104 ± 18	68–139

that were marked were recaptured, so it is not known how long they would have taken to reach maturity. However, the size structure for the population suggests that lizards hatching in autumn 1987 (about day 540 in Fig. 8) grew to around 65 mm SVL by their first spring (10 months of age). Thus, some individuals may become sexually mature and reproduce in their first spring or summer after hatching.

Movements and Population Estimates

Adult *E. fasciolatus* moved extensively across the study site. The mean displacement between successive recaptures was $63 \cdot 5 \pm 127 \cdot 9$ m ($n = 23$). There was no correlation between displacement and the time interval between recaptures. One individual moved 525 m in 22 days between the first and second captures, then moved 215 m in 24 h between the second and third captures. Another individual was captured only 12 m from its first location after 230 days. As a result of the extensive movements, it is not surprising that recapture rates were low, and, with the small sample size, it was not possible to distinguish between those population changes due to mortality and those due to dispersal. Estimates of the active population size from Jackknife models varied from 14 to 108 individuals on the study site (Table 6). It was not possible to estimate the density of *E. fasciolatus* on the Ewaninga site because the variability in the movements of adults prevented us from reliably estimating the area over which lizards were trapped.

Eremiascincus fasciolatus were more commonly trapped on subsites situated on dune crests that had a relatively sparse cover of spinifex (multiple correlation of the variables

for relative elevation and spinifex cover, $r^2 = 0 \cdot 38$, $P = 0 \cdot 072$). This result supports the suggestion that *E. fasciolatus* inhabits areas with loose sand.

Discussion

Diet

The diets of the two *Eremiascincus* species differ little. Coleopterans are the most important prey for both species, and ants and orthopterans are also important. Our results differ from Henle's (1989) analysis of the diet of *E. richardsoni*, in which he found that orthopterans constituted a third of the total prey volume, followed by spiders ($16 \cdot 3\%$), ants ($12 \cdot 3\%$) and coleopterans ($7 \cdot 4\%$).

Neither in their active foraging (Henle 1989) nor diet, are *Eremiascincus* exceptional relative to other skinks. The prey types recorded for *Eremiascincus* are important dietary taxa for many species of skink (e.g. Hamilton and Pollack 1958; Hamilton 1961; Minton 1966; Pianka 1969; Huey and Pianka 1977; Andrews *et al.* 1987; Bauer and DeVaney 1987; Daniels 1987; Porter 1987; Auffenberg and Auffenberg 1988). For example, termites are frequently eaten by *Eremiascincus* and are a major prey item of many species of scincid lizards in the arid zone in Australia (Pianka 1986; James 1991*b*), and for skinks in other parts of the world [8 of 10 species of Philippine skinks (Auffenberg and Auffenberg 1988); 84–97% of the diet of *Typhlosaurus* in Africa (Huey *et al.* 1974)]. In captivity, *Eremiascincus* will voraciously attack and consume mice and lizards, rotating rapidly around their long axis to subdue the prey (Greer 1979). Occasional predation on vertebrates is common among skinks [8 of 11 species of Philippine skinks (Auffenberg and Auffenberg 1988); 3 of 4 species of *Mabuya* (Burt and Hoyle 1934; Fitch 1955; Huey and Pianka 1977; Gressitt and Nadkarni 1982; Arena 1986; Taylor 1986; James 1991*b*)] and other families of similar sized lizards (Greene 1982). Henle (1989) found that 2 of 42 *E. richardsoni* examined had eaten mammals. Our data confirm that vertebrates (primarily lizards) constitute an occasional prey item in the diet of *Eremiascincus*. Although numerically insignificant, such relatively large prey may constitute a substantial proportion of the energy intake of a lizard.

Morphology

Inter- and intraspecific differences in body size and the dimensions of trophic apparatus are often associated with differences in the size or type of prey (e.g. Hutchinson 1959; Schoener and Gorman 1968; DeMarco *et al.* 1985; Pianka 1986). However, although *E. richardsoni* is larger than *E. fasciolatus*, and has relatively longer and wider jaws, no differences in the diet of the two species are apparent. Further, neither species of *Eremiascincus* exhibits an ontogenetic increase in prey size. Further work is necessary to determine how, if at all, these morphological differences are adaptive.

Head dimensions are commonly sexually dimorphic in lizards (Carothers 1984; Vitt and Cooper 1985). Sexual dimorphism has been explained both as an adaptation for eating different-sized prey, perhaps to minimise competition, and as a result of sexual selection. In many lizards, jaw length is correlated with body size, and with the size of prey eaten (Schoener and Gorman 1968; Pianka 1969), but mouth and throat dimensions probably set the physical limits on the size of prey that can be ingested (DeMarco *et al.* 1985). Both species of *Eremiascincus* are sexually dimorphic in jaw length, but not in jaw width. Because the sexes do not differ in jaw width, the lack of intersexual differences in diet is not surprising. Sexual dimorphism in head width appears to be related to sexual selection in several lizards (Carothers 1984; Vitt and Cooper 1985). The proximate mechanism appears to be male–male competition: males with larger heads and greater jaw musculature (which contributes to head width) probably are more successful in intrasexual combat. *Eremiascincus*, however, is dimorphic in head length rather than head width. How and why sexual selection might favour this dimorphism is unclear. The causes of intersexual and interspecific morphological differences in *Eremiascincus* remain to be determined.

Reproduction

This study confirmed that *Eremiascincus* lay shelled oviductal eggs, supporting Greer's (1979) findings for *E. richardsoni* and providing new data on the mode of reproduction in *E. fasciolatus*. The timing of reproduction in these arid-zone skinks appears to be similar to that recorded for other species in arid Australia, and for species in more mesic areas of the temperate zone in Australia (James and Shine 1985; Henle 1989; James 1991a). Testes are enlarged during spring, presumably in association with copulatory activities. Eggs are laid from late spring to late summer and appear to hatch in early to mid-autumn.

Clutch sizes were not significantly different in the species, but, surprisingly, clutch size was correlated with maternal snout–vent length in *E. richardsoni* but not in *E. fasciolatus*. In two closely-related species such as these, one might expect clutch size to be adjusted in similar ways by natural selection. This puzzling difference may be an artifact of the smaller sample size for *E. fasciolatus*, or may result from combining specimens from a number of different geographic localities (Tinkle and Dunham 1986). Further comparative studies of the reproductive biology and life history of these species are required in areas where they occur sympatrically.

Field Studies

Data from the mark–recapture study indicated that *E. fasciolatus* are relatively mobile and capable of moving large distances in a short time. Henle (1989) also noted that *E. richardsoni* was an active forager, moving more than 20 m in 1 min. *E. fasciolatus* move much larger distances than similar-sized scincid lizards of other genera in the same habitat: five syntopic species of *Ctenotus* on the Ewaninga site rarely moved more than 100 m and had average movements of around 10–20 m (James 1991c). The large movements by *E. fasciolatus* resulted in low numbers of recaptures between seasons (i.e. individuals marked one spring were unlikely to be recaptured the following autumn, and were never recaptured after 12 months or more). Hence, at the spatial scale of our field study, mortality and home range estimates were not possible. The results suggest that home ranges may be large, or that *Eremiascincus* are sensitive to being handled and respond by moving away from the point of capture.

Eremiascincus fasciolatus have usually been collected on loose sandy soils, often associated with spinifex grass. The Ewaninga site was a system of dunes and swales with a covering of spinifex grasses and scattered shrubs (James 1991a). Most *E. fasciolatus* were trapped on subsites located on the crests of longitudinal dunes that rose up to 10 m above the swales. However, *E. fasciolatus* also seemed to be more abundant on dune crests that had a sparse covering of spinifex (30% projected ground cover) than on dune crests with a denser cover of spinifex (50% projected ground cover). These results support Greer's (1979) suggestion, based on museum records, that *E. fasciolatus* tends to be found on sandy soils. Henle (1989) reported that *E. richardsoni* preferred soft sandy substrates, a result that is contrary to the suggestion made by Greer (1979). The extensive movements of *E. fasciolatus* in this study, and of *E. richardsoni* in Henle's (1989) study, suggest that *Eremiascincus* are capable of traversing large areas, and they may be collected in a range of habitats as a result of these large movements. Alternatively, the two taxa of *Eremiascincus* may have distinct habitat preferences, but distinguishing between the taxa on the basis of morphological criteria is proving difficult.

Acknowledgments

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