REPRODUCTION AND REDUCED BODY SIZE OF REPTILES IN UNPRODUCTIVE INSULAR ENVIRONMENTS

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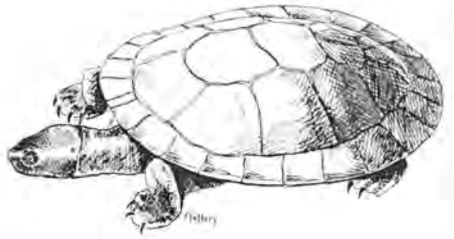

The life history traits of the freshwater turtle *Emydura krefftii* on Fraser Island, off the coast of Queensland, differ considerably from those of populations on the adjacent mainland. The island turtles mature at a smaller size, lay fewer smaller eggs per clutch, have a much lower reproductive potential, and reach smaller maximum sizes.

Following colonization of Fraser Island, the low productivity of the dune lakes may have placed energetic constraints on the clutch sizes of the island morph. Since clutch size and body size are correlated, growth to a size greater than that required to contain the maximum *attainable* clutch is probably disadvantageous, because the surplus would be better spent on reproduction. A low reproductive output caused by energetic constraints may have resulted in selection for smaller body sizes on the island. The proposal may explain reduced body size in other insular reptile populations.

Pages 311-18 *in* BIOLOGY OF AUSTRALASIAN FROGS AND REPTILES ed. by Gordon Grigg, Richard Shine and Harry Ehmann, Royal Zoological Society of New South Wales, 1985.

INTRODUCTION

SOME species of Australian reptile show marked differences in the body sizes attained by individuals from different populations. *Crocodylus johnstoni* from the McKinlay River in the Northern Territory achieve normal maximum sizes for the species of 2.1 m for females and 2.6 m for males, whereas in the Liverpool River to the east, females reach a maximum length of only 1.2 m and males a maximum of 1.5 m, which are below the sizes at onset of maturity in the McKinlay River (Webb 1984). The sizes of tiger snakes *(Notechis ater niger*) vary markedly between populations on islands off the coast of South Australia (Schwaner 1985). In particular, Roxby Island snakes are "dwarfed" (maximum weight < 200 g) compared to tiger snakes on other islands (maximum weight *c.* 630-1240 g). The freshwater turtle *Emydura krefftii* is abundant and widespread in Queensland where it inhabits large rivers and associated large waterholes and billabongs (Cogger 1975). The species is also abundant (*c.* 81 turtles/ha) in the many perched dune lakes of Fraser Island, off the coast of Queensland, where it matures at smaller sizes, lays fewer smaller eggs per clutch, has a much lower reproductive potential, and reaches smaller maximum sizes than on the mainland (Table 1).

Perched dune lakes are best described as dystrophic as they contain dilute acidic waters (pH 4.0-6.0) and high proportions of organic material of terrestrial origin (Bayly 1964; Bayly *et al.* 1975). The dominance of humic acids among this organic material and the relatively low pH values are not conducive to intensive bacterial degradation, so that particulate and dissolved humic compounds are metabolized only very slowly (Wetzel 1975). The brown colour of the water severely limits penetration of light (Bayly 1975) which, together with low concentrations of inorganic ions, restricts photosynthetic activity. Phytoplankton is poorly developed in lakes on Fraser Island (Bayly 1964) and chlorophyll-a concentrations (Miller 1975) fall within the range of concentrations reported for dystrophic and ultra-oligotrophic lakes (Wetzel 1975). Limited photosynthesis and slow bacterial degradation of humic materials presumably result in low secondary productivity.

Low productivity, virtual isolation from other water bodies, and possible direct effects of the organic acids and other secondary compounds on potential inhabitants (Janzen 1974), explain the low biotic diversity of perched dune lakes. Macrophytes are represented by only a few species and macro-invertebrates are low in both diversity and numbers, when compared with other freshwater lakes (Timms 1973). These lakes are generally inhabited by only one or two species of small fish (Arthington 1977) and waterbirds do not aggregate upon the lakes in large numbers (Kikkawa *et al.* 1979). Hence, compared with the more usual habitats of *E. krefftii* on the mainland, those on Fraser Island are deficient in nutrients, of low productivity and of low biotic diversity.

The aim of this paper is to construct a hypothesis that explains the smaller body sizes of *E. krefftii* on Fraser Island. It is an evolutionary hypothesis and supporting evidence is drawn from available data on the population structure,

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Table 1. A comparison of selected life history parameters for mainland and Fraser Island populations of *Emydura krefftii*. Reproductive potential is used as defined by Legler and Cann (1980) and was calculated for the Fraser Island population from an October sample.

	FRASER ISLAND	MAINLAND
EGG WEIGHT	7.44 ± 0.14 g (n = 42)	9.75 ± 0.37 g* (n = 82)
CLUTCH SIZE	Max. 10 eggs	Mean 16.4 eggs*
MINIMUM REPRODUCTIVE POTENTIAL PER ANNUM	10-23 (n = 3)	29-66* (n = 5)
MAXIMUM REPRODUCTIVE POTENTIAL PER ANNUM	12-26 (n = 3)	35-75* (n = 5)
CARAPACE LENGTH AT MATURITY		
MALES	110-117 mm	180-190 mm†
FEMALES	150-155 mm	—
MAXIMUM CARAPACE LENGTH		
MALES	197 mm	277 mm†
FEMALES	246 mm (n = 728)	281 mm† (n = 111)

* Legler and Cann (1980)
† Georges and Hamley, unpubl. data

reproduction, and growth of the species. The hypothesis may explain reduction in body size in isolated populations of other reptiles.

MATERIALS AND METHODS

E. krefftii was trapped at Lake Coomboo on Fraser Island at approximately six-week intervals from March 1977 until September 1979, and then annually in the winters of 1980 to 1983. A final trip was undertaken in January 1984. On each occasion, turtles were caught using 12 hoop traps (Legler 1960) set at locations (117 in all) on a 25 m square grid spanning the entire lake. The traps were cleared of turtles and rebaited at 75 minute intervals. A bait of white sliced bread was used and trapping yielded up to 14 turtles in a single trap setting and 180 turtles per day.

Adult and sub-adult turtles were sexed using tail length and the position of the anterior margin of the cloacal aperture relative to the margin of the carapace (Georges 1982a). Small juveniles could not be sexed. Maximum carapace length and plastron length, from the most anterior point on the intergular scute to the most anterior point of the anal notch, were measured. Individuals caught for the first time were marked uniquely by filing or cutting notches in the marginal scutes and underlying bone, and were checked for irregularities in scutellation, for deformities of the head and limbs, and for scars of past injury.

Growth ceases in winter (May to August) (Georges 1982a), so incremental growth in plastron length from winter to winter was chosen as the index of growth. Error in the determination of growth increments was $\pm$ 0.5 mm.

Samples of *E. krefftii* were collected for studies of reproduction, from various dune lakes on Fraser Island between March 1977 and April 1980 (Georges 1983). Four of the male specimens of mainland *E. krefftii* collected from the Burnett River (two just upstream from the Mundubbera weir, two from Grey's Waterhole, Gayndah) were dissected and histological examination of their testes and epididymides was used to determine the size of males at the onset of maturity. Females were not examined. Additional data on the reproductive characteristics of *E. krefftii* on the mainland came from Legler and Cann (1980, Fitzroy River, Qld).

Means are presented with standard errors throughout this paper.

RESULTS

Size Distribution:

In all known populations of *Emydura* from the mainland, adults either predominate or are present in equal numbers with juveniles (Fig. 1). The trend is most striking for *E. krefftii* from the Burnett River where adults outnumber juveniles 92 to 19. The modal size for the Burnett population is 245 mm. In contrast, juveniles outnumber adults on Fraser Island by 378 to 283 with a distinct mode in size at only 85 mm.

Indirect evidence for lower mortality rates on the island than on the mainland is provided by comparison of the frequencies of injuries. Of 56 specimens of *E. krefftii* captured in Grey's Waterhole (Gayndah), eighteen bore the scars of past injury. Some had lost limbs or parts of limbs and many had shell damage (as opposed to genetic abnormalities). Of the 670 specimens examined for injuries on Fraser Island, only twenty bore the scars of past injury and none had damaged shells. These data must be interpreted with caution, however, as not all of the injuries observed in the Grey's Waterhole specimens

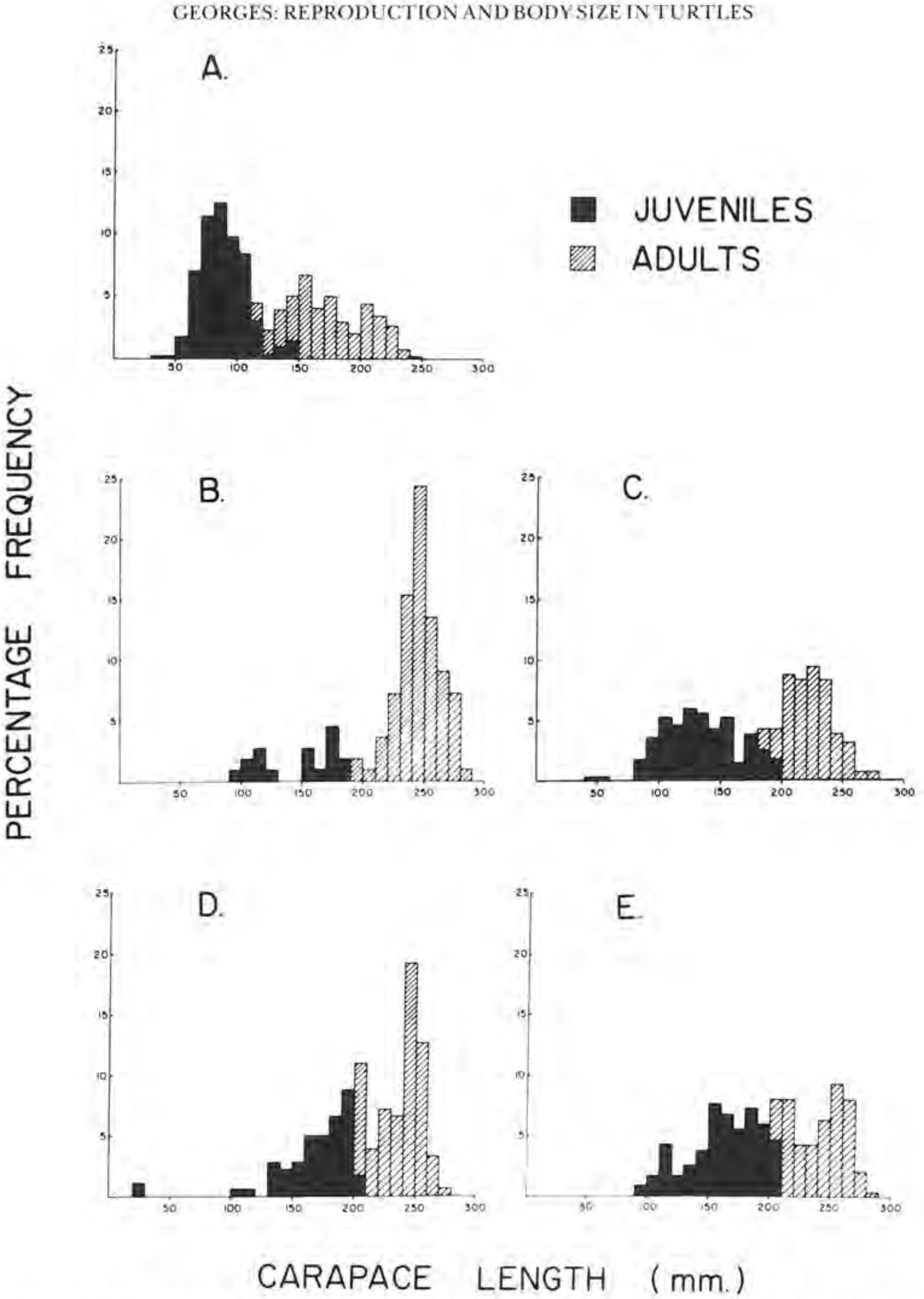

Fig. 1. Size distributions of populations of the genus *Emydura*. Filled columns represent counts of juveniles and shaded columns represent counts of adults.
A. *E. krefftii*, Fraser Island, n = 661
B. *E. krefftii*, Burnett River, Qld, n = 111 (Georges and Hamley, unpubl. data)
C. *E. signata*, Brisbane region, n = 288 (Georges, Hamley and Terley, unpubl. data)
D. *E. macquarii*, Murray River, n = 181 (Thompson, 1983)
E. *Emydura* sp., Cooper Creek, n = 234 (Thompson 1983)
Turtles in the latter two populations are assumed to mature at the sizes determined for *E. macquarii* by Chessman (1978).

could be attributed to predation, but rather could have resulted from encounters with power boats or from severe batterings during floods.

Reproduction:

There is a strong relationship between clutch size and maternal body size for *E. krefftii* (n = 8, circles of Fig. 2). This relationship was reinforced by indirect estimates of clutch size determined from counts of pre-ovulatory follicles and corpora lutea on the ovaries of further specimens dissected before or after the oviductal period. The Pearson correlation between clutch size and maternal body size was 0.86 ($n = 24$, $p << 0.001$). There was also a general tendency for mean egg weight (calculated for each individual) to increase with female body weight ($r_s = 0.78$, $n = 7$, $p < 0.05$).

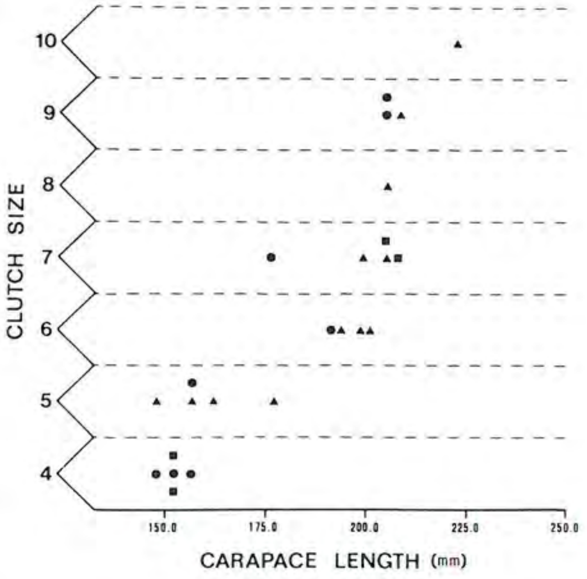

Fig. 2. Clutch size as a function of body length for *Emydura krefftii* from Fraser Island. Clutch size was estimated from counts of oviducal eggs (●), corpora lutea (■), and pre-ovulatory follicles (▲).

Growth Rates and Maximum Size:

The growth rates of turtles with plastron lengths greater than 120 mm were much lower than those of turtles less than 100 mm long (Fig. 3). This range, 100-120 mm, includes the plastron lengths at which both males and females mature.

Juveniles of the same size often grew at markedly different rates. Some juveniles did not grow in a year, while others initially the same size may grow over 1 cm per year on average. This high variability explains the low value of the coefficient of determination ($r^2 = 0.25$) for a semi-logarithmic regression of growth rate on plastron length (Georges 1982a). Juvenile turtles were grouped into fast growers (growth > 8.5 mm/yr) and those that remained. Variability in growth rates was not related to the habitat types (Georges 1982a) in which the turtles were first captured ($G = 1.01$, $df = 3$, $n = 164$), nor were the fast growers caught more frequently on average than the slower growers ($t = 0.80$, $df = 97$). The latter comparison was perhaps important as the turtles were often able to eat much of the bait. Although small juveniles are impossible to sex from external features, data on growth are available for juveniles that were caught later when they had grown to a size at which they could be sexed. There was no significant difference between the growth rates of juvenile males and females ($t = 0.22$, $df = 72$).

Of all turtles caught over a period of four or more years, only adults failed to grow (Fig. 4), which is in keeping with a previous observation of a reduction in growth rate with onset of maturity. The turtles that failed to grow were spread over a wide range of sizes; for males the range was 110-155 mm in plastron length, for females it was 130-185 mm. Although conceivably many of these turtles may commence growing once more, these data probably reflect considerable variability in maximum sizes attained by these animals This is consistent with the high variability in growth rates already noted.

The largest male captured on Fraser Island had a carapace length of 196.9 mm (plastron length 126.4 mm), compared to 246.3 mm (plastron length 198.3 mm) for the largest female.

DISCUSSION

Although the frequency distributions shown in Fig. 1 are size and not age distributions, low levels of predation may explain the unusual predominance of immature individuals in Fraser Island populations of *E. krefftii*. The absence of large predatory fish and of large aggregations of waterbirds have probably resulted in much less predation (excluding eggs) on the island than on the mainland, a conclusion supported by the comparison of the frequencies of injuries for the two populations. Despite differences in the diets of small and large turtles, there is substantial dietary overlap (Georges 1982b), and the relatively large sub-population of juveniles (Fig. 1A) may exert considerable competitive pressures on adults, for resources that are already in short supply.

That resources are limiting for these animals on Fraser Island is indicated by the dramatic drop in growth rate at the onset of maturity (Fig. 3) The slower growth of larger turtles probably results from a redirection of available energy to reproduction at the expense of growth rate. Future reproductive potential is therefore delayed (given that clutch size and body size are related) in order to maximize immediate reproductive output.

Low *per capita* food resources can be expected to result in slower growth of adult specimens and a lower reproductive output compared to turtles of the same species in more productive environments. A lower overall reproductive output in response to food in short supply, may take on several forms — the turtles may lay smaller eggs, fewer eggs per clutch, fewer clutches per season or a combination of two or more of these strategies. They might also skip seasons, requiring more than one year's accumulation of nutrients to produce a clutch of eggs. However, ovarian follicles are not carried over by *E. krefftii* from one season to the next (Georges 1983), and only five in thirty females showed no indication of breeding during the season in which they were examined. One of these females lacked functional oviducts. Both the largest and smallest

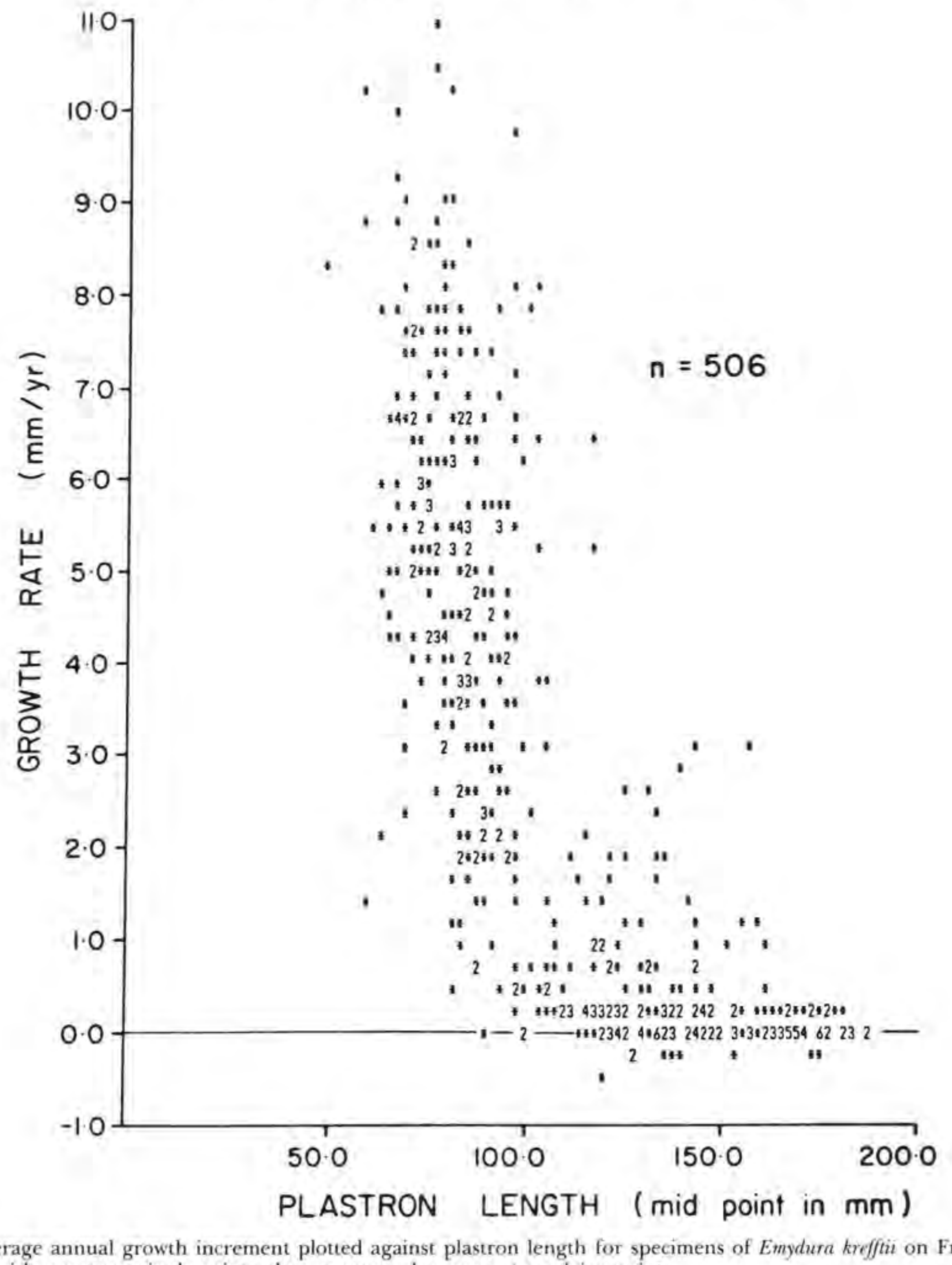

Fig. 3. Average annual growth increment plotted against plastron length for specimens of *Emydura krefftii* on Fraser Island. Asterisks represent single points whereas numerals represent overlying points.

mature individuals lay up to three clutches annually on Fraser Island (Georges 1983), suggesting that the number of clutches laid per year has not been reduced in response to a shortage of food. Hence, reproductive output has been reduced in Fraser Island populations primarily by reduction in clutch size, and to a lesser extent, in egg size.

Current explanations for variation in maternal body size and reproductive output among populations of reptiles fall into two broad and overlapping categories. In the first category such variation is chiefly attributed to direct environmental influences. Larger body sizes of *Chrysemys scripta* in a reservoir receiving heated effluent from nuclear reactors, compared to those of turtles of the same species from nearby populations, were attributed to the increased productivity at lower trophic levels resulting from the heated effluent (Gibbons 1970). Elevated water temperatures were also directly involved (Gibbons *et al.* 1979). Larger body sizes of *Chrysemys scripta* in freshwater lakes on barrier islands off the coast of South Carolina, compared to those of inland populations, are thought to result from better food quality, greater food availability, and higher water temperatures on the islands (Gibbons *et al.* 1979). Variation in maximum body size and size at maturity among isolated populations of *Crocodylus johnstoni* have been attributed to availability of food (Webb 1984). Differences in

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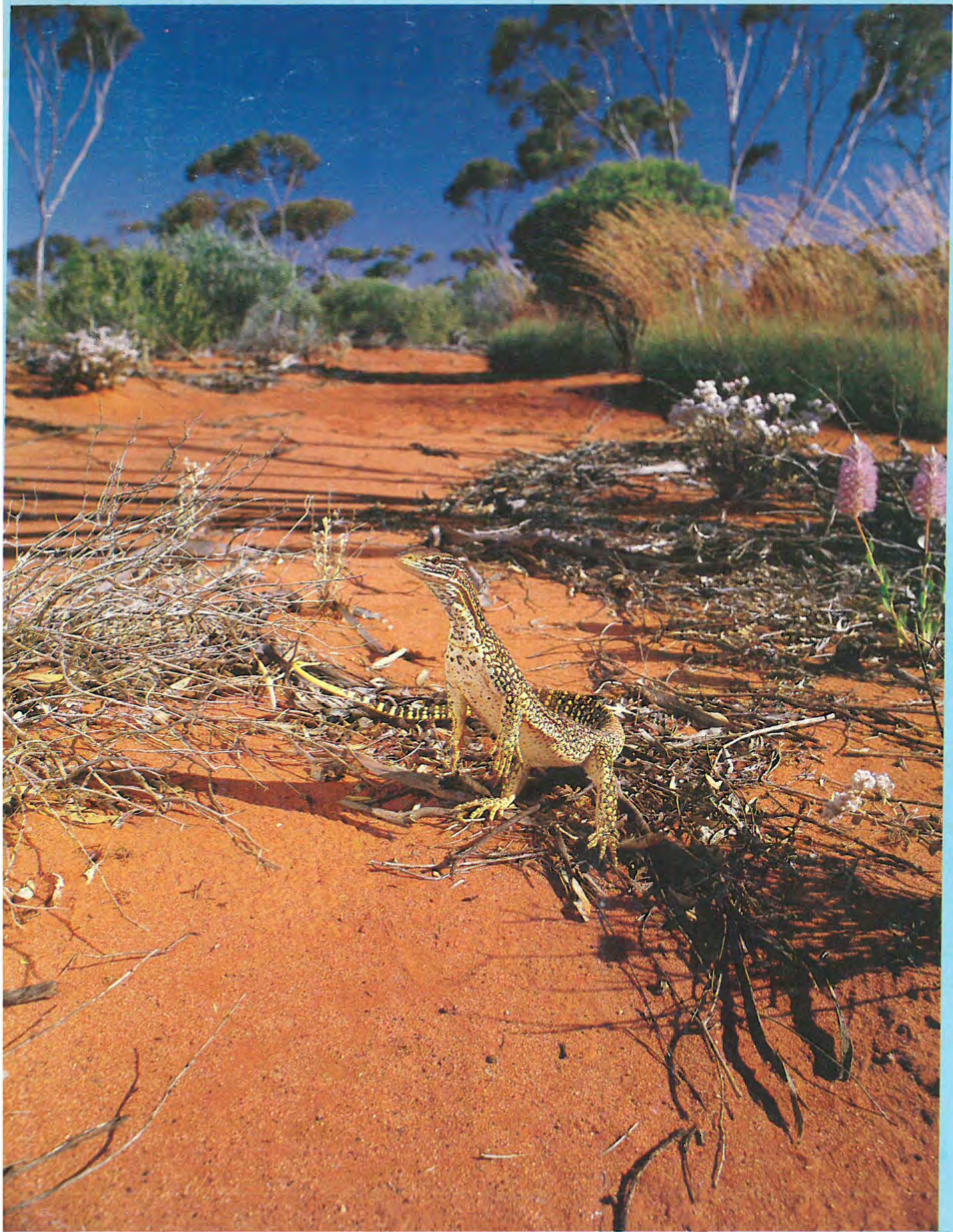

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The BIOLOGY of AUSTRALASIAN FROGS and REPTILES

G. GRIGG, R. SHINE & H. EHMANN, ED.

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