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The natural regulation of giant tortoise populations on Aldabra Atoll: recruitment

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The reproductive ecology of the giant tortoise (*Geochelone gigantea* Schweigger) in three isolated populations was studied for 2 years on Aldabra Atoll.

Density-dependent recruitment was demonstrated. Nest destruction in the low density area was dependent on the density of mature females providing a mechanism for regulating population size. Increases in annual rainfall and the resultant increase in food availability induced an increase in mean egg mass in the low density area (and thereby total hatchling production), whereas in the high density population mean clutch size, mean egg mass, total number of nests and total hatchling production all increased significantly. Large eggs produced large hatchlings which survived better during the first year than hatchlings from small eggs.

Hatchling mortality was 94 and 81 % in the first year in the high and low density populations respectively. Recruitment into the 5 year age class (after which predation is considered negligible) had almost ceased in the high density population compared with 0.44 per 100 breeding females per year in the low density population.

INTRODUCTION

Aldabra Atoll (in the western Indian Ocean) has the largest population (150000) of giant land tortoises known. Because the Atoll is split by lagoon passes into a number of discrete land masses, the tortoise populations on three of these masses (Picard, Malabar and Grande Terre), which have different population densities, are isolated from one another.

The Aldabran giant tortoise (*Geochelone gigantea* Schweigger) is a tractable subject for ecological research because (i) it is long lived; (ii) it retains a record of growth and ageing by deposition of rings on the scutes; (iii) it is a seasonal breeder facilitating monitoring of the nests and hatchlings; (iv) it is the principal herbivore; and (v) the adults are not affected by predation, most deaths being caused by thermal stress. The uniqueness of this situation gives an unusual opportunity to make a comparative study of natural regulation in a terrestrial vertebrate population.

By using information on the Aldabran giant tortoise, an attempt has been made to answer four main questions: (i) what are the limiting factors determining the mean level of a population; (ii) is regulation taking place; (iii) if so, what is the mechanism; and (iv) is the primary or ultimate cause of regulation resource limitation, predation or disease? This paper on recruitment is the third of a number concerning the natural regulation of tortoise populations on Aldabra Atoll (Swingland 1977; Swingland & Coe 1978).

Several theories on the natural regulation of animal numbers (Chitty 1960; Christian 1961; Wynne-Edwards 1962) require that variations in reproductive success act as a negative feedback regulator within the population. To investigate this, measurements of the reproductive rate over a period of time within two isolated populations are needed. That variations occur

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between populations of reptiles is well known (Tinkle 1961; Gibbons & Tinkle 1969; Ernst 1971; Christiansen & Moll 1973) but none have been shown to be density-dependent.

A further problem concerns whether or not nutrition influences reproductive rate. The changes in recruitment are described in two isolated populations of the Aldabran giant tortoise over a period of 2 years (1975 and 1976). Some information on individual growth, mortality, nest destruction, predation and ovarian characteristics is also presented. These data are discussed in relation to variations in rainfall, population density and food supply.

The study areas

Two principal study areas were used in this work, southeast Grande Terre and eastern Malabar. The Grande Terre study area was 11 km^2 while that of Malabar was 2 km^2.

The highest tortoise densities occur in southeast Grande Terre where there is low vegetation or bare ground and where there is little, but at least some, shade (Bourn & Coe 1978). Tortoises, although browsers as well as grazers, are primarily grazers, feeding largely on grasses, herbs and sedges, e.g. 'tortoise turf' (Grubb 1971; Merton *et al.* 1976) and *Sporobolus virginicus* L. (Hnatiuk *et al.* 1976), which are the two major components of low vegetation. In areas composed mainly of bare ground there are large expanses of exposed rock, but there are also small soil pockets in which a variety of plant species commonly eaten by tortoises occur. High tortoise concentrations occur in habitats where favoured food plants are more plentiful. 'Tortoise turf' is a complex of at least 21 plant species whose growth form has been suggested by Grubb (1971) and Merton *et al.* (1976) to be the result of selection through intense tortoise grazing pressure. Moreover, the effects of heavy browsing are conspicuous with browse lines on most tree species, particularly on those woody plant species which are palatable (Grubb 1971; Frazier 1972; Merton *et al.* 1976). Tortoises, through their activities by shading, are responsible for considerable soil erosion and the death of many trees and shrubs with the resultant reduction in the amount of shade cover (Merton *et al.* 1976). Indeed a significant relation exists between tortoise density and the density of dead trees (I.R.S.).

The Malabar population is restricted to the comparatively open mixed scrub of a relatively narrow coastal belt on the ocean side of the island. This vegetation type is coincident with and probably dependent on, the underlying rock structure of Aldabra Limestone (Braithwaite *et al.* 1973), which has some accumulations of soil in which various grasses, sedges and herbs commonly eaten by tortoises (Grubb 1971; Frazier 1972) are found. Very dense scrub, dominated by *Pemphis acidula* Forst., is further inland and grows on Takamaka Limestone. It is at a slightly lower elevation, much more deeply pitted and eroded, has very little soil and few forms of low vegetation. This scrub is not inhabited by tortoises.

Unlike southeast Grande Terre, Malabar has (i) no residual pools of freshwater during the dry season, (ii) abundant shade, (iii) no evidence of overbrowsing or overgrazing, (iv) few areas suitable for nesting, and (v) a much less dense population (7 per hectare compared with 27). Moreover, the tortoises on Malabar continue to grow almost throughout the year in contrast to Grande Terre (I.R.S.) and are larger for their age (Bourn & Coe 1978).

In order to collect comparative information on tortoise densities and clutch size, two additional study areas were investigated in 1976. The first area, Picard, has a tortoise density of 5 per hectare and in most other respects is similar to Malabar. The second lies just outside the main Malabar study area and consists of two adjacent nesting sites, both approximately 20 m^2.

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METHODS

Data on the location of nests, clutch size, egg mass, fertility, the number of eggs that successfully hatched and the number of hatchlings that left the nest were obtained from the 431 nests examined, 206 from southeast Grande Terre, 213 from Malabar, and 12 from Picard. In the first year (1975) intensive nest searches were carried out each month during the laying season beginning in June. Once a nest had been located and opened for examination it was closed and left undisturbed until November by which time those eggs which would hatch had done so. In the second year (1976) the same procedure was adopted, although special attention was paid to searching the same nest areas used in the previous year.

After the nest had been located and opened the eggs were removed, individually marked with a pencil, weighed, measured and replaced in the nest in the same order. Care was taken to ensure that the orientation of the egg remained the same at all times to avoid tearing or damaging the embryo inside. The nest was marked.

By examining the eggs and interfering with the nests it was possible that the successful development of the eggs may have been impeded or that the chance of a predator locating and destroying the eggs was increased. To test this, several nests were left unopened in each nest site and their success compared with neighbouring opened nests. No significant differences were found between opened and unopened nests in terms of the proportion of successfully hatched eggs ($t = 1.6$, $n = 40$, $p > 0.10$) or in increasing the incidence of predation ($t = 2.3$, $n = 40$, $p > 0.01$).

For the purposes of this paper, recruitment is defined as the number of hatchlings per 100 adult females. Once they have left the nest they lead a secretive existence for up to 2–3 years. Hatchlings were marked and intensive searches carried out up to 1 year after emergence (from the nest) in an attempt to estimate mortality.

The method of determining age was the same as in Bourn & Coe (1978) or by counting annual rings on the scutes. Rainfall data were collected using standardized plastic rain gauges (Hnatiuk 1979, this volume).

The variables in the following analyses were normally distributed, and Student two-tailed t and z-score tests were used to compare mean values.

RESULTS

Seasonality of breeding

On both Malabar and Grande Terre the first nests were found in late June (slightly earlier on Grande Terre in 1976) and nesting continued until late September, the peak being in July and August. Moreover, hatching occurred from early October and mid-December. The data show that incubation periods varied from 98 to 148 days and that the earlier a nest is laid during the nesting season, the longer the incubation period. Additionally once the yolk sac is absorbed the hatchling emerges from the nest from mid-October to December. This is before and at the start of the single rainy season.

Maturity and age-specific fertility

Information from post-mortem examinations (Swingland & Coe 1978) indicates that female tortoises reach sexual maturity on Grande Terre at 23 ± 1.7 years and 17 ± 0.8 years on Malabar

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(age determination from a modification of the method used by Bourn & Coe (1978)), the criterion of sexual maturity in females being the presence of pre-ovulatory follicles or corpora lutea. Maturity in males was somewhat less clearly defined and was determined by a seasonal increase in size of the testes during the copulation season (January–June). Males on Malabar reach sexual maturity at 20 ± 2.3 years and on Grande Terre at 26 ± 5.8 years. The mean age of copulating males was 29 ± 2.8 years on Grande Terre but 21 ± 4.3 years on Malabar. Grande Terre males appear to mature before they are of sufficient size to mount females successfully.

No cases of reproductive senescence were observed and there was no detectable relation between age and the numbers of non-atretic pre-ovulatory follicles at the beginning of the nesting season (i.e. potential clutch size) in either study area (Swingland & Coe 1978). The information from examinations *post mortem* indicates that most sexually mature females in both study areas had follicles of pre-ovulatory size ($>$ 3.5 cm) during March and April, a month or two before nesting (Swingland & Coe 1978).

The incidence of infertility in eggs is difficult to determine. Where an egg had been cracked or broken during laying the whole clutch would generally become infected regardless of fertility. Moreover, as infertility could only be determined by the absence of embryonic development, eggs which had become infected at an early stage, although perhaps fertile, would appear infertile. Nevertheless, a crude estimate of infertility from nests which did not contain mechanically damaged eggs nor any evidence of having produced live young varied between 10 and 20% with no difference between Malabar and Grande Terre.

TABLE 1. POPULATION DENSITY, CLUTCH SIZE, EGG MASS AND REPRODUCTIVE SUCCESS IN TWO ISOLATED POPULATIONS (1975–6)

	Grande Terre	Malabar
mean tortoise density per hectare (± s.e.)	27.0 ± 1.8 (n = 168)	7.0 ± 0.7 (n = 32)
mean clutch size (± s.e.)	4.9 ± 0.1 (n = 206)	13.7 ± 0.5 (n = 213)
mean egg mass (± s.e.)	78.5 ± 0.6 g (n = 1008)	87.1 ± 0.9 g (n = 2913)
mean live hatchlings per clutch (± s.e.)	3.8 ± 0.5 (n = 206)	8.1 ± 0.3 (n = 213)

All figures within rows are significantly different at $p < 0.01$.

MEAN POPULATION REPRODUCTIVE SUCCESS

The mean population density in southeast Grande Terre was nearly four times higher than on Malabar (Bourn & Coe 1978). Moreover, the mean clutch size on Grande Terre was almost three times smaller than on Malabar, the eggs were smaller, and fewer hatchlings emerged successfully from a nest (table 1). Nevertheless, nearly 80% of Grande Terre eggs produced hatchlings whereas only 60% of Malabar eggs were successful.

As has already been mentioned, Malabar, in contrast to Grande Terre, has few nesting areas, which resulted in high levels of nest destruction by nesting females. No records of nest destruction were recorded from Grande Terre. The mean annual density of mature females is correlated to the proportion of nests destroyed (figure 1).

The trend of increasing clutch size with decreasing population density is corroborated when the figures from Picard are included (table 2). Nevertheless, this trend is not followed by mean egg mass which, although larger at Malabar than Grande Terre, is actually smaller on Picard.

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However, if one considers the individual reproductive output ((mean egg mass) × (mean clutch size)) the effect of increasing density on suppressing reproduction can be seen (1450:1260:432 for Picard:Malabar:Grande Terre).

The study areas are considered to be representative of the two populations and their habitats. On Grande Terre, the study area covered most of the southeastern portion; moreover, three nests found at Dune Blanc, where the population density is 20 ± 2.3 tortoises per hectare, had four, five and six eggs, the mean of which is similar to the study area mean clutch size of five. Likewise the study areas on Malabar and Picard did not circumscribe the whole of the two islands. The figures of clutch size and egg mass from Picard were collected on two successive occasions in 1976 and no significant differences were found between samples ($t = 1.4$–1.7, $p > 0.05$). Those figures from the Malabar study area (table 3), when compared with those from another neighbouring area, also show no significant differences.

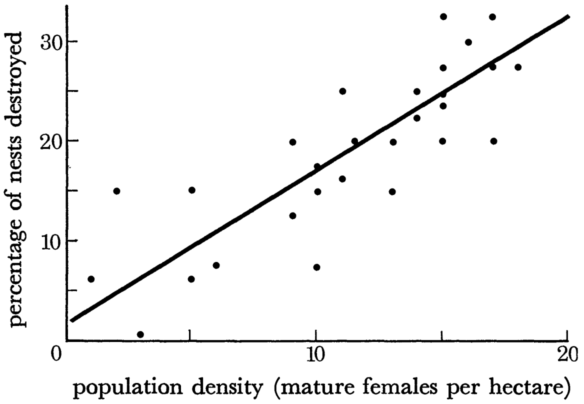

FIGURE 1. The relation between the proportion of nests destroyed and the density of mature females on Malabar. Regression coefficient = 0.78; probability < 0.01.

TABLE 2 COMPARISON OF CLUTCH SIZE, EGG MASS, POPULATION DENSITY AND 'REPRODUCTIVE OUTPUT' IN THREE ISOLATED POPULATIONS (1976)

	Grande Terre	Malabar	Picard
mean tortoise density per hectare (± s.e.)	27.0 ± 1.8 (n = 168)	7.0 ± 0.7 (n = 32)	5.0†
mean clutch size (± s.e.)	5.3 ± 0.2 (n = 129)	14.0 ± 1.1 (n = 84)	19.2 ± 0.7 (n = 12)
mean egg mass (± s.e.)	81.6 ± 0.7 g (n = 684)	90.0 ± 1.3 g (n = 1176)	75.5 ± 0.4 g (n = 230)
individual reproductive output‡	432	1260	1450

All figures within rows are significantly different at $p < 0.01$.
† Extensive search estimate.
‡ (Mean egg mass) × (mean clutch size).

The production of more than one set of eggs in a single breeding season is common in reptiles, particularly chelonians, but is often undetected. It is practically impossible to observe the same female tortoise in successive natural layings. Most of our evidence for multiple clutches is inferential and based on examination of the ovaries of 115 females. The ovaries of mature females from Grande Terre showed no evidence of both old and fresh sets of corpora lutea and since these structures regress and disappear within a few weeks of ovulation there is little chance that a set from one breeding season would persist to the next. However, on Malabar all mature ovaries showed evidence of different sets of corpora lutea during the nesting season

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indicating they would have laid from two to four clutches (mean 2.2 ± 0.9 clutches per year). The presence of sets of corpora lutea of differing sizes together with non-atretic pre-ovulatory follicles were commonly found in females from Malabar but not in females from Grande Terre.

Although the importance of follicular atresia or regression in chelonian ovarian cycles is not clearly understood, an experiment carried out during 1976 (Swingland & Coe 1978) suggests that a reduced (or an inadequate) diet induces atresia in pre-ovulatory follicles. The contention that food may be limiting on Grande Terre is also supported by the retarded/suppressed growth, and the delay in maturity, of individuals in this high density population compared with Malabar.

TABLE 3. COMPARISON OF CLUTCH SIZE, EGG MASS, AND REPRODUCTIVE SUCCESS IN TWO AREAS ON MALABAR (1976)

	main study area	comparative study area
mean clutch size (± s.e.)	14.0 ± 1.1 (n = 84)	14.7 ± 0.9 (n = 45)
mean egg mass (± s.e.)	90.0 ± 1.3 g (n = 1176)	90.8 ± 1.4 g (n = 662)
mean live hatchlings per clutch (± s.e.)	9.2 ± 0.7 (n = 84)	8.8 ± 1.4 (n = 45)

Figures within rows are not significantly different ($p > 0.50$).

Translocation of tortoises from the high density area of Grande Terre to the very low density area of Picard clearly demonstrated, by the increase in the rate of growth (over 80 %), the food limitations under which the population exists.

VARIATION IN ANNUAL RECRUITMENT

In 1976 the amount of rainfall increased over that for 1975 by approximately 40 % by raining significantly more in January and March and by continuing to rain longer (through June, July and August) into the dry season (i.e. nesting season). Because of this unusually extended wet season, tortoises continued to feed actively, particularly on Grande Terre where various shrubs atypically flowered and fruited (also R. P. Prŷs-Jones 1976, personal communication). Additionally the white growth rings around scute margins, indicative of growth, persisted for longer than usual in Grande Terre animals.

On Malabar this increase in rainfall did not affect the numbers of nests present nor did it significantly increase the clutch size (see table 4). However, egg mass did increase by 10 % and total hatchling production increased by 35 %. In contrast on Grande Terre there was no significant change in the number of hatchlings produced from each nest; therefore the principal reason for the increase in total hatchling production (55 %) was due to the increase in the number of nests (67 %) (table 5). This increase in nests was caused either by breeding females' producing multiple clutches or a greater proportion of the mature females' breeding. Nevertheless, no evidence of multiple clutches was seen during post-mortem examination.

SEX RATIO OF HATCHLINGS

The sex ratio of the hatchlings was determined by dissection. On Grande Terre, of 43 hatchlings examined, 21 were males and 22 females; from Malabar, of 37 hatchlings, 18 were males and 19 were females. Combining the figures, a total of 39 males and 41 females have been recorded, indicating an equal sex ratio at birth.

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Table 4. Rainfall-induced modifications of reproductive rate and success on Malabar (1975–6)

	1975	1976	percentage change
corrected total rainfall, October–September	878 mm	1205 mm	+37†
mean clutch size (± s.e.)	12.8 ± 0.7 ($n = 84$)	14.0 ± 1.1 ($n = 84$)	+9
mean egg mass (± s.e.)	81.8 ± 0.7 g ($n = 1075$)	90.0 ± 1.3 g ($n = 1176$)	+10†
mean egg mass per clutch	1047 g ($n = 84$)	1260 g ($n = 84$)	+20†
total number of nests	84	84	—
mean live hatchlings per clutch (± s.e.)	6.8 ± 0.6 ($n = 84$)	9.2 ± 0.7 ($n = 84$)	+35†
total live hatchling production	571	773	+35†

† Significant at $p < 0.01$.

Table 5. Rainfall-induced modifications of reproductive rate and success on Grande Terre (1975–6)

	1975	1976	percentage change
corrected total rainfall, October–September	923 mm	1315 mm	+43†
mean clutch size (± s.e.)	4.3 ± 0.2 ($n = 77$)	5.3 ± 0.2 ($n = 129$)	+23†
mean egg mass (± s.e.)	70.5 ± 1.4 g ($n = 332$)	81.6 ± 0.7 g ($n = 685$)	+16†
mean egg mass per clutch	303 g ($n = 77$)	432 g ($n = 129$)	+42†
total number of nests	77	129	+67†
mean live hatchlings per clutch (± s.e.)	4.0 ± 0.7 ($n = 77$)	3.7 ± 0.2 ($n = 129$)	−8
total live hatchling production	308	477	+55†

† Significant at $p < 0.01$.

Nest and hatchling predation

The incidence of predation is higher on eggs and hatchlings than any other stage in the life cycle. On Malabar the major nest predator is the coconut crab (*Birgus latro* L.). Moreover, the density of *Birgus* increases as the density of nests increases (figure 2), which is not so on Grande Terre where the principal nest predator is the land crab (*Cardisoma carnifex* Latr.). The incidence of nest predation here is lower (7 compared with 17%) and occurs at any time throughout the period of incubation whereas on Malabar nest predation is highest during the period when the hatchlings are erupting from the nest (October and November). *Birgus*, *Cardisoma*, the white-throated rail (*Dryolimnas cuvieri* Pucheran) and the rat (*Rattus rattus* L.) are the main predators of hatchlings. The rail is not found on Grande Terre.

Immediate post-emergence recruitment figures, where Grande Terre females are taken to lay one clutch per year (an overestimate, as not all adult females will breed annually) and Malabar females an average of 2.2 clutches per year, is 3–5 times higher per 100 mature females on Malabar than on Grande Terre (Malabar 924 in 1975, 1251 in 1976; Grande Terre 379 in 1975, 370 in 1976). However, in reviewing these figures it must be borne in mind that, although hatchling recruitment per 100 adult females did not increase on Grande Terre because of the greater proportion of adult females that laid in 1976, the total hatchling production did increase (table 5).

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Recruitment and hatchling mortality

Of 100 marked hatchlings released by hand from nests on Malabar (once their yolk sacs were absorbed) in 1975, 19 were found after an exhaustive search 1 year later. An equal number of marked hatchlings were released on Grande Terre and a year later only 6 could be found.

Assuming all those alive were found this represents a maximum mortality rate during the first year of 94% on Grande Terre and 81% on Malabar. The denser vegetation and heavily dissected champignon (rock substrate type) of Malabar compared with the more open habitat of SE Grande Terre and the predominance of the flat pavé and platin substrates made it more difficult to find young tortoises on Malabar than on Grande Terre.

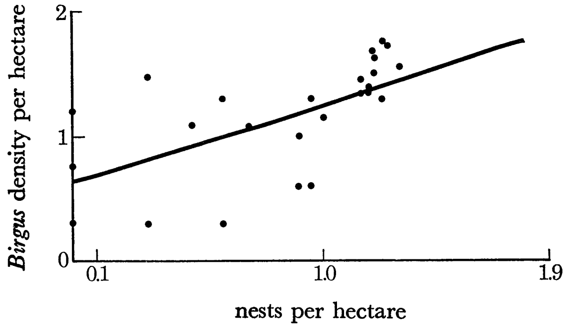

Figure 2. The relation between the density of the coconut crab (*Birgus latro* L.), the principal nest predator, and the density of nests on Malabar. Regression coefficient = 0.62; probability < 0.01.

Table 6. Comparison of egg mass, hatchling mass and relative survival of 100 hatchlings released in 1975 in each study area

	mean egg mass (± s.e.) g	mean hatching mass (± s.e.) g	minimum number surviving to one year
Malabar			
heaviest 50 eggs	86.7 ± 3.1	60 ± 4	13
lightest 50 eggs	78.3 ± 1.9	48 ± 5	6
Grande Terre			
heaviest 50 eggs	76.0 ± 2.3	42 ± 4	6
lightest 50 eggs	63.2 ± 5.6	32 ± 3	0

Figures within columns for each separate study area are significantly different at $p < 0.01$.

If one also assumes a steady mortality rate (although mortality rate would probably decrease) with increasing age until 5 years old, after which mortality by predation is assumed to be low and relatively constant, then the proportion in the population was an index of the minimum proportion that would reach sexual maturity. By 5 years old only 0.00008 of the original 100 would be alive on Grande Terre and 0.025 on Malabar; this represents 0.00030 five year olds per 100 breeding females per year on Grande Terre and 0.44 five year olds per 100 breeding females per year on Malabar. As there were 40% fewer nests (table 5) on Grande Terre in 1975 than 1976, and assuming that this reflects a difference in the proportion of adult females breeding, then only 0.0002 five year olds per 100 breeding females per year would be recruited.

From the release of the 200 marked hatchlings it is suggested that larger eggs produce larger hatchlings which survive better than hatchlings from small eggs (table 6). The heaviest 50

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eggs in each study area produced heavier hatchlings which survived better than hatchlings from the lightest 50 eggs.

Moreover, the change in mass over 1 year was greater in Grande Terre hatchlings (141 ± 22 g) than in Malabar hatchlings (106 ± 10 g).

Discussion

The major density-dependent effects discussed in this paper are on age at sexual maturity, clutch size, egg mass, hatchling production and growth rate. The study of three isolated populations (Malabar, Grande Terre and Picard) of different densities from 5 to 27 per hectare emphasizes the extent of the reproductive adjustments and suggests that in the study areas these regulatory processes begin to operate at densities as low as 7 tortoises per hectare. On Picard (5 tortoises per hectare) clutch size was larger than on Malabar (7 tortoises per hectare). However, the Picard population was able to produce higher clutch sizes only at the expense of a reduction in egg masses. It has been suggested that large eggs produce large hatchlings which survive better than those from small eggs (also seen in birds; Skogland *et al.* 1952; Parsons 1970; Schifferli 1973). The high egg masses of the Malabar clutches (table 2) may be interpreted in terms of natural selection, implying that hatchlings in this area have greater problems in obtaining adequate food for the critical first few months than in either of the other two areas (Picard and Grande Terre). However, although few data exist on the differential growth rates of hatchlings in the three areas to support this suggestion, casual observations of the abundance of plants on Malabar, which are favoured by hatchlings, tend to confirm that there are far fewer than on Grande Terre or Picard. Additionally, Malabar hatchlings do not appear to increase in mass during the first year to the same extent as Grande Terre hatchlings.

The wide range of these reproductive adjustments (sexual maturity, clutch size, egg mass and hatchling production) implies a very considerable regulatory effect on recruitment; from the data it is evident that recruitment is influenced by population density and modified by rainfall. Such regulatory effects have been noticed in the African elephant (*Loxodonta africana* Blumenbach) by Laws (1969) and Hanks & McIntosh (1973).

Moreover, the changes in clutch size, egg mass and hatchling production clearly illustrate a very rapid response to climate changes for such a long-lived animal. The changes were most marked in the high-density population of Grande Terre where there is strong evidence to indicate that a large proportion of the mature females do not breed every year (Swingland & Coe 1978). The increase in rainfall during the second year was coincident with changes in reproductive rate not only on Grande Terre but to a lesser degree on Malabar. The fact that total hatchling production (tables 4 and 5) increased in parallel in the two populations suggests that the same external factor (rainfall) was the cause. Pianka (1970) noted latitudinal intraspecific differences in lizard populations where both clutch size and population density appeared to be positively correlated with rainfall.

The Malabar giant tortoise population is multiple-brooded with large clutches and early maturity while the Grande Terre population is single-brooded with small clutches and late sexual maturity. Thus although the Malabar reproductive characteristics agree with one of the categories of Tinkle *et al.* (1970), the Grande Terre population does not, having small clutches rather than large clutches; moreover, the early-maturing Malabar individuals produce larger eggs (not smaller eggs) than the late-maturing Grande Terre tortoises. Andrews

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& Rand (1974) also rejected the suggestion that clutch size in tropical species is adjusted differently from that in temperate species because high intraspecific competition in the tropics would result in selection for large eggs with enhanced survivorship rather than for large clutch size. We also contest this suggestion in that the Grande Terre females produced small eggs under conditions of high intraspecific 'competition' and not large eggs. Malabar females did produce large eggs (and large clutches) which would enhance survivorship although little intraspecific 'competition' occurs among adults, with most resources being superabundant.

On Malabar, because of the limited nesting areas, nest destruction is dependent on population density and this provides a mechanism for regulating population size. Bustard & Tognetti (1969) produced a similar model for the green turtle (*Chelonia mydas* L.). Moreover, probably as a reflexion of the density of nests on Malabar, nest predator density (i.e. coconut crab, *Birgus*) is correlated with nest density.

A number of features support the view that food is the principal limiting factor:

(1) Mean body size is bigger (> 30%) on Malabar than on Grande Terre for mature animals of the same age and sex. (Food quality has been shown to be influential in causing large body size in populations of chelonians (Gibbons 1967; Jackson *et al.* 1976).)

(2) Growth is suppressed or severely seasonal on Grande Terre but almost continuous on Malabar.

(3) There is overbrowsing and overgrazing on Grande Terre.

(4) There is a significant increase in follicular atresia, especially preovulatory follicles, under conditions of sub-optimal diet (cf. Hahn & Tinkle 1965; Inger & Greenberg 1966; Swingland & Coe 1978); and the presence of follicular atresia in females on Grande Terre but not on Malabar.

The population density on Grande Terre is extremely high and although a large proportion of mature females did not breed in 1975, reduced but successful reproduction still occurred. It is argued that the reproductive rate is near its lowest level and that any reduction in population numbers must be brought about by mortality. The density of tortoises has been rising rapidly since the beginning of this century when numbers had probably been reduced by human activity (Stoddart 1971). It is also probable that the population on Grande Terre is currently reaching a maximum density and as young tortoises can and do feed in places inaccessible to adult tortoises they will not be so susceptible to the effects of this density asymptote. Moreover, as shade is important in influencing mortality it is interesting to note that trees and large bushes are reported as having been almost absent in SE Grande Terre at the beginning of the century. Thus the increase in available shade coincided with the increase in the population, which, together with the correlation between dead trees and tortoise density, implies (i) a very considerable regulatory effect on tortoise density by shade and (ii) that as tortoise density rises, shade is increasingly destroyed (cf. Merton *et al.* 1976). It also suggests that increases and decreases in tortoise density and shade may be correlated. Young tortoises which shade under rock or in clumps of sedges, but infrequently under bushes or trees, are isolated from such perturbations. This suggestion regarding the nature of the relation between tortoise density and shade is similar to that suggested for elephants by Caughley (1976). At present, regeneration of woody species on Grande Terre is prevented by the browsing pressure of the high tortoise density, in contrast to Malabar where shrubs and trees freely increase.

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CONCLUSION

If the reproductive rate were to regulate the total population of tortoises on Aldabra one would expect it to decrease as the population increased. Although this study lasted only 2 years, the differences in reproduction between the isolated populations of Grande Terre, Malabar and Picard suggest that density-dependent population regulation is occurring.

There is evidence that food quality and quantity remains high in dry tropical environments throughout the rainy season (Coe *et al.* 1976). Since the female presumably has higher food requirements during the latter stages of follicular development there are obvious advantages to ovulating just after the optimum nutritional time of year. The high incidence of follicular atresia in the high-density population compared with its absence in the low density population clearly supports the suggestion that nutrition is affecting population regulation. Various other parameters such as growth rate and age at sexual maturity differ between the study areas.

Hatchling recruitment varies from year to year on Malabar and on Grande Terre. This recruitment is related to rainfall and hence to nutrition during late follicular development. There is evidence to suggest that undernutrition in short or dry wet seasons caused a reduction in fecundity through poor food supply.

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