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POPULATION INTERACTIONS BETWEEN THE TOADS *BUFO BUFO* (LINNAEUS) AND *BUFO CALAMITA* (LAURENTI): SOME THEORETICAL CONSIDERATIONS AND CONSEQUENCES

TREVOR J. C. BEEBEE

*School of Biology, University of Sussex, Falmer, Brighton BN*1 9*QG*

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SUMMARY

This paper investigates some possible effects of *Bufo bufo* on *B. calamita* using: 1. A very simple model incorporating age-specific mortality of *B. calamita*; 2. Logistic growth of *B. bufo*; and 3. Predation of tadpoles of *B. calamita* by those of *B. bufo*. The consequences of different rates of common toad population growth on natterjack populations with different steady-state parameters (which are believed to correspond to natural situations) are investigated.

INTRODUCTION

The natterjack toad *Bufo calamita* has recently undergone a severe decline in numbers in Britain, especially on the heathlands of southern and eastern England (Beebee, 1976, 1977). It has been postulated that this decline may have been caused at least in part by changes in habitat structure and the subsequent appearance of *Bufo bufo* as an effective predator species (Beebee, 1977). *B. calamita* and *B. bufo* are, under normal circumstances, allopatric in Britain; the former is essentially confined to sandy, open terrain (heaths and dunes) while the latter is much more widespread in a large variety of habitats (Smith, 1951). However, the recent and extensive encroachment of trees on heathland has been associated with the appearance of *B. bufo* in large numbers, and with the disappearance of *B. calamita*, well before forest conditions have been reached. *B. bufo* larvae, which are advanced in development by the time *B. calamita* spawn is laid, are known to predate newly hatched natterjack tadpoles (Beebee, 1977) and the following exercise is intended to examine the possible effects of this observation on *B. calamita* populations.

METHODS AND RESULTS

Various aspects of the population dynamics of the species are considered on a theoretical basis, using data from published observations to illustrate some of the possible implications.

STEADY-STATE DESCRIPTION

It is convenient to consider the anuran lifecycle as being divisible into three discrete stages: (i) larval, from egg to metamorphosis and including all tadpole stages; (ii) juvenile, the period between metamorphosis and attainment of sexual maturity; and (iii) adult. For the species in question these stages occupy about 6–14 weeks, the remainder of the year and two subsequent years, and an indefinite number of years, respectively, in the British Isles. Faster growth rates in more southerly latitudes are known to reduce the juvenile period by a complete year (Heusser & Meisterhans, 1969), but the occurrence of distinct size classes of animals in Britain confirms that the longer period of juvenile development is normally operative (personal observations).

If it is assumed that under steady-state conditions the ratio of juveniles:adults remains approximately constant, then since the population is undergoing no net change the relationship must hold that:

$$K(1-d)-\sigma a-\gamma=0 \qquad (1)$$

Here, K = the number of eggs produced per head of adult population per year; d = the proportional mortality during stage i; σ = the overall proportion of juvenile mortality per year (average of all age groups); a = the ratio of juveniles: adults; and γ = the proportion of adult mortality per year.

A practical use of this simple relationship can be envisaged because metamorphic success rates in amphibian populations are virtually impossible to measure directly. However, the other parameters in the equation can be more readily obtained and larval mortality calculated thus:

$$d=\frac{K-\sigma a-\gamma}{K} \qquad (2)$$

Of course measurements would need to be taken over several years to cancel out probable population oscillations which are likely to occur even in situations fundamentally stable, especially in a species like the natterjack in which steady-state considerations should be thought of as applying only over a long time scale.

PERTURBATION FROM STEADY-STATE

It follows from equation (1) that any change in individual components of recruitment or mortality will result in an overall change in the population. This can quite simply be defined as:

$$\Delta P=X_0(K[1-d]-\sigma a-\gamma) \qquad (3)$$

Here, ΔP = the change in numbers of the entire population (not just adults) and X_0 = the number of adults before the perturbation.

It is therefore possible, on a hypothetical basis, to investigate the kinds of alterations which will most affect the population size by substituting some relevant values into the equation. In a steady-state situation, X_0 may be arbitrarily set at 10 000; K at 1000 on the basis of a sex ratio of male : female = 1.67 : 1 and an average of 2600 eggs per female (Heusser & Meisterhans, 1969; Smith, 1951). This value of K is nevertheless somwhat uncertain because the average numbers of eggs laid per female may actually be lower (Davies & Halliday, 1977); male : female ratios may be higher (Mathias, 1971), although the figure used is derived from the most thorough investigation of this variable yet published, and it is conceivable that every female does not spawn every year though there is no evidence to support this possibility. K may therefore have to be revised downwards when more data accumulate. From the work of Flindt & Hemmer (1968a; 1968b), it is possible to state that setting $d = 0.9909$ and $\gamma = 0.1$ will be within the normal range. Juvenile numbers and mortality rates are much more difficult to assess. In a Swiss population with the shorter juvenile growth period, a ratio of juveniles : adults of 1.25 : 1 was observed (Heusser & Meisterhans, 1969). This computation did not, however, include the numbers of first-year juveniles, i.e. the large numbers of very small animals which appear after metamorphosis and which suffer rapid and high mortality rates. Because of this and the longer period of juvenile life in Britain, overall values of $a = 10$ and $\sigma = 0.9$ were chosen in the absence of definitive information. Although individually somewhat arbitrary, it is clear from equation (1) that a steady-state population with the other components as previously defined must have an overall value of $\sigma a = 9.0$.

Table I shows the results of altering σ, γ or d individually on such a population over a single year. Clearly, as might be expected, variation of d has by far the most dramatic consequences in the short term. Interestingly, this is reflected even two years later if a single perturbation followed by a return to the previous steady-state conditions is monitored by subsequent changes in adult numbers. Thus, decreasing σ by 0.05 results in an increase of 50 adults the following year and a further 45 the year after (net gain = 95 adults). Decreasing γ by 0.05 leads to a net increase of 500 adults over the same year; whereas decreasing d by 0.05 would lead to 5000 extra adults in the third year thereafter. Of course it should be stressed that these numbers have a very arbitrary basis, and (for example) in practice it is certain that juvenile mortality will not be a constant proportion for each year of juvenile life, and this together with density-dependent factors would very much reduce the overall effects; but the important point is that in populations with this kind of structure the proportion of larval development that is successful is at least theoretically capable of exerting the most profound effects on adult numbers.

TABLE I. Results of steady-state perturbation on population numbers

σ	ΔP	γ	ΔP	d	ΔP
0.85	+5 000	0.05	+500	0.9409	+500 000
0.87	+3 000	0.10	0	0.9500	+409 000
0.89	+1 000	0.15	−500	0.9750	+159 000
0.90	0	0.20	−1 000	0.9900	+9 000
0.91	−1 000	0.25	−1 500	0.9909	0
0.93	−3 000	0.50	−4 000	0.9950	−41 000
0.95	−5 000	0.95	−8 500	0.9990	−81 000

GROWTH OF AN INTRODUCED POPULATION

In considering possible interactions between *B. calamita* and *B. bufo* it is necessary to discuss not only steady-state conditions such as may normally exist for the indigenous *B. calamita* population but also the growth rate of the insurgent species *B. bufo*. Perhaps the most suitable expression of growth in this instance may be given by:

$$\frac{dN}{dt} = rN\left(\frac{Z-N}{Z}\right) \qquad (4)$$

In this instance, dN/dt represents the change in number of animals (N) with time (t), and includes a growth-rate factor r and an environmental constraint factor Z. Z equals the maximum possible size of the population in the habitat and under the conditions pertaining, *i.e.* N when $dN/dt = 0$ (Boughey, 1968).

In the particular case under consideration, the rate of increase (r) of *B. bufo* is thought to have been determined by the rate at which the habitat became suitable for the species rather than by any intrinsic reproductive capacity and mortality rates of the organism. This is probably true because the encroachment of scrub conditions on healthland has occurred over rather long periods, perhaps 20–30 years depending on the total size of the heath, whereas the rate of increase of other anurans with similar K values introduced into immediately suitable habitat can occur much faster than this. Thus *Rana ridibunda* (Pallas) increased from a few individuals to many thousands (probably to limit densities) within ten years of its introduction to Kent marsh habitats (Smith, 1951; Menzies, 1962). If r is calculated on the basis of habitat change rate, a value of 0.33 produces growth curves which span the observed time periods (Fig. 1), assuming a start from a single pair of animals. This r value requires that each animal should breed three times in order to replace itself, *i.e.* an average lifespan of at least 6 years would be needed and life beyond this would increase the total population. Such values are well within those observed in the wild. There are, of course, very many variables which could affect this growth description, but it is invoked only as a general indication of the way in which an insurgent species is likely to increase in a newly available habitat. One major assumption, discussed later, is that the increase is in no way hindered by the presence of the indigenous *B. calamita* population. It should be noted that the computed curves probably underestimate the rate of increase rather than the converse; the start point may often involve more than a single pair of animals, and the encroachment may be in the vanguard of prolific scrub growth (the exact temporal relationship is not known).

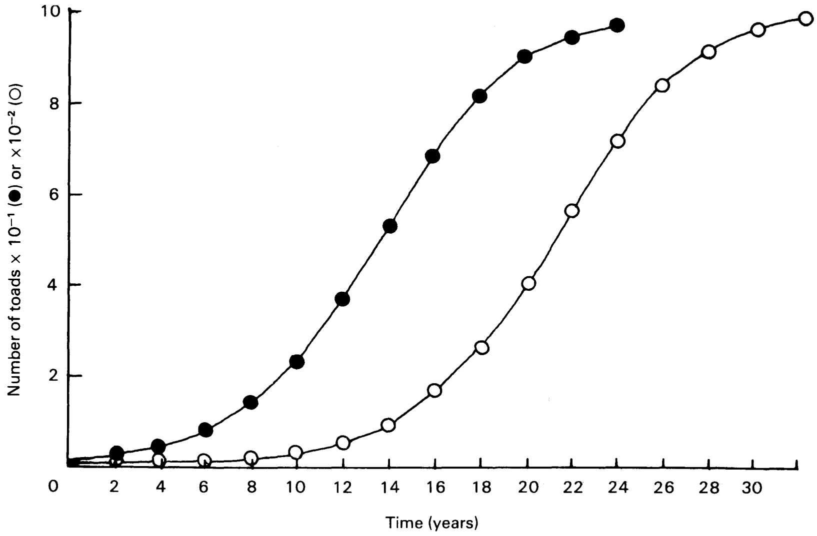

FIG. 1. Growth plan for *Bufo bufo* incursion. Numbers were calculated as starting from a single pair using equation (4) with $Z = 100$ (●——●) or $Z = 1000$ (O——O).

INTERACTION OF BUFONID POPULATIONS

The postulate to be considered here is that direct predation of *B. calamita* larvae by those of *B. bufo* could lead to the extinction of the former species (Beebee, 1977). Observation suggests that natterjack larvae are vulnerable only over a short period during their development. Neither spawn itself nor free-swimming tadpoles were significantly predated, but heavy casualties were suffered during the period of about five days while the newly emerged larvae clung immobile and exposed on the spawn string. Extensive studies by Mathias (1971) failed to show competition between the two species at any other point during the life cycles, and larval predation is thought to be the major point of interaction.

Difficulties arise in computing the quantitative effects of an insurgent *B. bufo* population because of the need to know the numbers of natterjack larvae consumed on average by each common toad tadpole. Values of up to six were observed under captive conditions (Beebee, 1977) using a single sample of natterjack spawn (*i.e.* over one hatch period). However, *Bufo calamita* has a protracted breeding season and spawn may be deposited any time over six to eight weeks during most of which period *B. bufo* larvae are likely to be available as predators. Thus the figure could rise to more than six, but on the other hand by the time *B. calamita* spawn appears *B. bufo* larvae are several weeks old and likely to have suffered extensive mortality rates themselves. In the ensuing calculations a figure of 1.3 natterjack larvae consumed per *B. bufo* egg laid is used on the basis of $>75\%$ mortality of common toad tadpoles prior to natterjack spawn arrival and only one natterjack spawn string being encountered on average by each *B. bufo* tadpole at the appropriate time of vulnerability. These figures are largely arbitrary but should tend to underestimate the effects of the insurgent on the incumbent species.

Combining the data from previous sections, Fig. 2 shows the putative effects of *B. bufo* encroachment under three different sets of circumstances. (1) Where the natterjack population has a high value of d and a relatively low γ. This kind of situation may be envisaged on sand-dune type habitats where the breeding pools are ephemeral and larval mortality known to be very high. Similar values to those used here are implicit in observations of European populations of *B. calamita* under similar circumstances, where d may actually have been as high as 0.9975 (Flindt & Hemmer, 1968b). (2) A natterjack population with lower d and higher γ, where more permanent pools occur and less concentration of mortality at the larval stage seems likely. No data are available to confirm whether this is a realistic model for *Bufo calamita* on heath, but similar values for d have been measured for other anurans under circumstances where freshwater is not so strictly limiting as on dunes. γ is set perhaps unrealistically high to demonstrate an extreme case, though it is clear that in a population with reduced values of d compensation must come from increases in γ or σ or both. These could arise ultimately as a result of a greater overall Z value of the habitat when the freshwater limitation is reduced associated with higher densities of predators. For both of the above models it has been assumed that the species are sufficiently similar such that Z will be the same for both (*i.e.* the habitat will be able to support a particular number of toads made up from either or both species). However, during the postulated transitions the total numbers of adult animals rise above Z quite substantially (up to about $1.4 \times Z$ at 24 years) in the dune population, though only slightly above under "heath" type conditions where adult natterjack numbers decline more rapidly. This could itself act to repress the rate of *B. bufo* increase, although small differences in food preference and behaviour may mean that the two Z values are not totally inclusive and an increase in toad numbers permissible due to slight differences in niches (Mathias, 1971). (3) A natterjack population under "dune" type conditions subject to encroachment of *B. bufo* in a habitat where Z for the latter species remains much lower than that for *B. calamita*.

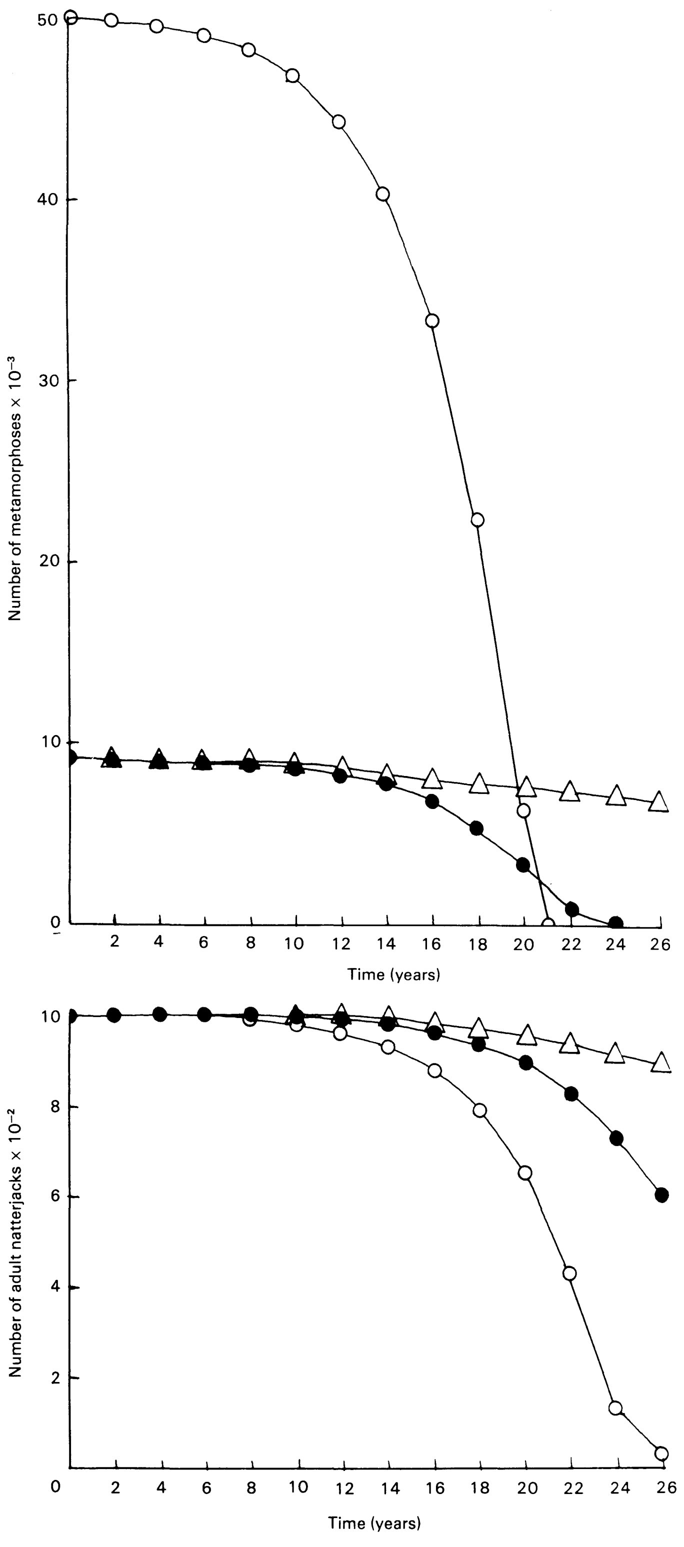

FIG. 2. Effects of *B. bufo* encroachment on *B. calamita* metamorphosis and adult numbers. The results of Fig. 1 were used to compute the numbers of *B. bufo* eggs laid each year during incursion, using *K* (*B. bufo*) = 1000. The effects of predation on *B. calamita* metamorphosis were computed on the basis that the proportion consumed of those which would otherwise have metamorphosed would be the same as the overall proportion of hatching larvae vulnerable to attack. Adult numbers were computed allowing for two years of juvenile mortality rates after a particular metamorphic success rate. ●——● = "dune" population; $\gamma = 0.1$, $\sigma = 0.9$, $a = 10$, $d = 0.9909$, $Z = 1000$ for *B. calamita* or *B. bufo*. ○——○ = "heath" population; $\gamma = 0.5$, $\sigma = 0.90$, $a = 55$, $d = 0.9500$, $Z = 1000$ for *B. calamita* or *B. bufo*. △——△ = "dune" population with parameters as above except that Z for *B. bufo* = 100. A: Numbers of metamorphoses. B: Numbers of adults.

These computations demonstrate some interesting features. Under "heath" type conditions, both metamorphic success rates and adult numbers of *B. calamita* drop over similar time periods and the extinction of the species would occur, under the conditions of this particular hypothetical model, some 24–25 years after encroachment commenced. With "dune" conditions, both metamorphic success rates and especially adult numbers decline much more slowly with the result that although d has risen to 1.0 after 24 years adult numbers are still up at around 60% of the original level. Again it should be stressed that these figures are derived from arbitrary situations and should not be interpreted in any specific way. Also it should be noted that the actuality of extinction as depicted in Fig. 2 is an inevitable outcome of the premises upon which the model is based, and therefore of less value than the kinetic aspects of decline considered here. With lower Z value for *B. bufo* the decline of *B. calamita* is of course much less dramatic and random annual fluctuations of breeding success, etc. likely to become more important. *B. calamita* would probably not spiral down to extinction under these circumstances but stabilise at some lower level, though the simple model is insufficiently comprehensive to cope with these later aspects.

DISCUSSION

Although the calculations in the above account are based as far as possible on actual data, there is a paucity of detailed investigations into amphibian populations which needs to be remedied before more definitive statements can be made. Part of the purpose of this report is to highlight the areas in which information is required for further analysis. The parameters defined in equation (1) are clearly fundamental to such studies, but even these represent a conveniently simplistic approach to a complex situation. The practical use of both σ and a needs special attention, because σ will vary, probably greatly, during the juvenile growth period and a will vary during each year. Mortality rates during the second and third years of life should be directly measurable, but that between metamorphosis (which in the case of *B. calamita* itself spans eight weeks or more, Beebee & Beebee, 1978) and the end of the first year poses considerable practical difficulties. One simplification would be to use d as a measure of overall mortality during the first year of life, without separating pre- and post-metamorphic periods. The use of equation (2) would then become considerably easier, and this simplification would apply also to consideration of a values. For calculation of a only second- and third-year animals would be included, and averages taken from numbers present in spring and autumn without having to consider the enormous midsummer changes that metamorphosis would create if first-year toads were registered.

A major interest in the interactions considered above stems from the fact that *Bufo calamita* is an endangered species in Britain, and there is some urgency in obtaining adequate information to conserve the remaining populations. It seems clear that, in light of the facts so far known, *B. bufo* is indeed likely to exert a destructive effect on *B. calamita* that could lead to extinction when habitat changes permit the appearance of the former in large numbers. The nature of the declines postulated is also of interest. Natterjacks are already virtually extinct on heathland where calculation suggests that the response might be most rapid, but still occur in large numbers on some dune systems where *B. bufo* has become abundant. The important prediction of Fig. 2 is that under such circumstances metamorphic success rates may decline well in advance of adult numbers, and this seems worthy of critical examination in the field. It is clear that only if Z is controlled (i.e. the habitat maintained unsuitable for common toads) will it be possible to perpetuate *B. calamita* if these ideas are correct. Quite large differences in the population dynamics of the incumbent species will affect the pattern but not the eventual outcome of *B. bufo* incursion.

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A NOTE ON HOME RANGE IN THE COMMON TOAD IN MID-WALES AND A METHOD FOR TRACKING TOADS FOR BEHAVIOURAL OBSERVATION

A. G. Parker and S. P. Gittins

Department of Applied Biology, U.W.I.S.T., Llysdinam Field Centre, Llandrindod Wells, Powys, Wales

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Studies of home range and behaviour in the toad have been hampered by the problem of locating and marking toads. Identification of recaptures has usually been achieved by toe clipping, but there is some evidence to suggest that the marks may be lost over an extended period (Mathias, 1971), and in one study the method was discontinued because it led to a high incidence of swollen digits (Collier, 1970). Other methods of marking, including using bird rings, sewing on glass beads and spools of thread, have proved unsatisfactory as they are either unreliable or cause too much damage to the toads. In our study a coded system of toe clips was found satisfactory for individually marking toads. It did not appear to cause them any stress, and marks remained easily recognisable for the period of the summer.

All of the above systems have the disadvantage for behavioural work that identification requires handling the toads, or at least observing them at close range. A system was devised, therefore, for locating and identifying toads from a distance at night, using Beta-lights. The Beta-light is carried on a waist band made of soft rubber insulation sleeving, with the ends of the insulation caught under a small staple. The circumference of the band needs to be about 10% less than the snout vent length of the toad. The Beta-light is bound onto the band with thick cotton, and secured with impact adhesive. The type of Beta-light used was a TO3/G/190, made by Saunders-Roe Developments Ltd. A certain amount of coding is available by changing the pattern of binding, and by using different coloured Beta-lights up to twenty combinations are possible. The lights are visible at 5–7 m at night, and the colour and binding distinguishable at that distance with a pair of low-power binoculars. The toads removed badly fitting bands within a few hours, but once a good fit was achieved bands remained in place for several days until they were removed by the observers. Once a toad was banded its movements could be followed from a distance, without further disturbance to its behaviour.

The remaining problem of locating the toad at rest, particularly during the day, has still not been satisfactorily solved and a remote detecting system is required. At present all radio tags and transponders are too large and heavy, but it is likely that their size will continue to decrease, though their cost will continue to rise. We investigated metal detectors, but their sensitivity is too low, and waste metal in the ground makes searching slow and laborious. Systems capable of identifying specific metal tags exist (as in anti shop-lifting equipment) but the cost, size and power requirements of the detection equipment prohibit their use. The only viable method found so far is the use of radioactive wire and scintillation counters (Beckinridge & Tester, 1961) but radioactive material cannot be recommended for normal use because of the problem of contamination.

The breeding behaviour of the common toad, *Bufo bufo*, has been studied many times, but the behaviour and movements outside the breeding season have only been studied by three authors (Heusser, 1968; Mathias, 1971; Haapanen, 1974). Heusser's work is an extensive five-year study near Zurich, during which he made 16 211 captures of 12 899 individuals. His data give forage ranges of 50–150 m, but he did not give detailed information on individual toads. Haapanen's results from a twelve-year study in Finland are based on 51 recaptures where less than one year has elapsed; these have a median distance between captures of 4 m. He also collected recaptures after more than one year, for which he had a median distance between captures of 15 m. Mathias's work is the only study from Britain, and was carried out amongst the dunes on the Ainsdale Sand Dunes National Nature Reserve. In all he had 25 recaptures outside the breeding season where less than one year had elapsed, 12 of which had moved less than 10 m. Of the other 13 the mean distance moved was 124 m, range 15–500 m. His very low recapture rate (7.2%) lead him to suggest that the actual distance normally moved was larger than his data indicated, and that his recaptures only represented the few individuals that had not moved too far for him to recover. He suggested, therefore, that their home range would be of the order of 200–600 m in diameter. This would agree well with the value for *Bufo hemiophrys* given by Beckinridge & Tester (1961) and for *Rana pipiens* given by Dole (1965). In both these cases the animals were observed to occupy only a small part of the home range for a time, and then to move to a new part of the range; this has yet to be observed in *Bufo bufo*. Mathias's low recapture rate could alternatively be explained if the

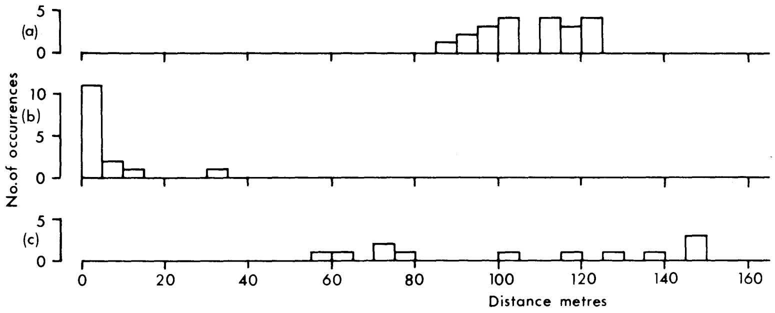

FIG. 1. Occurrence of resident toads on the drive. Toad (a). Seen 21 times, 8 June–6 July. Toad (b). Seen 15 times, 11 June–21 August. Toad (c). Seen 12 times, 25 June–17 August.

initial movement out from the breeding site to the summer quarters carried most of the toads out of his study area completely (Heusser (1968) gives 500–3000 m for this movement).

Throughout the summer of 1978 we monitored the drive of a cottage in Mid-Wales for the presence of toads. The drive, which is 165 × 3 m, was walked after dusk and the toads were located with powerful torches. During the period 8 June–7 September at least one toad was found on 65% of the nights on which observations were carried out ($n = 60$). Good nights for finding toads were mild and damp, and none was found when the temperature was below 5°C (c.f. Gittins, Parker & Slater, 1978), as compared with the value of 11°C given by Heusser (1968).

Altogether 34 individuals were marked and these fell into three groups:

(i) Three toads were recorded frequently over a period of a month or more and were considered as resident in the region of the drive.

(ii) 16 other toads were recorded more than once, median 3, with a median time span from first to last observation of 18 days. These were regarded as resident in the area but not living so close to the drive.

(iii) 15 toads were seen only once. It is not possible to be certain that these should not be included in (ii), but some probably represented transient individuals passing through the area.

Group (i) toads were found near the same place on the drive night after night, suggesting the presence of a home range (Fig. 1). Also 55% of the toads were seen more than once suggesting that toads are fairly sedentary outside the breeding season, as was found by Haapanen (1974), not mobile as Mathias (1971) suggests. The size of the home range is difficult to derive from our data, however, because of the influence of the drive. Toad (a) was seen on the drive 21 times in 29 days implying that the home range is either long and thin, more or less coincident with the drive or that the drive was strongly preferred to other parts of the home range during the period of observation. The lack of records for toad (a) after 6 July could indicate alternating use of different sectors of the home range similar to that described for *Bufo hemiophrys* (Beckinridge & Tester, 1961) and *Rana pipiens* (Dole, 1965).

The median length of the range measured along the drive for the three individuals in group (i) is 65 m (40–95 m). For group (ii) the median greatest distance between sightings for each individual is 12.5 m (0–118 m). From these findings, and reports from other observers, it appears that outside the breeding season at least some individuals in a toad population restrict their movements within a small home range. The diameter of this home range appears to vary considerably from a few tens of metres to a few hundreds of metres. Whether other individuals in the population are migratory outside the breeding season still remains to be determined.

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DEFENSIVE MECHANISMS AND PREDATION IN GEKKONID LIZARDS

H. ROBERT BUSTARD

Central Crocodile Breeding and Management Training Institute, Hyderabad, India

(*Received* 30 *December* 1978)

SUMMARY

Data are provided to demonstrate that defensive behaviour and/or morphological adaptations in Australian geckos of the genera *Diplodactylus, Nephrurus* and *Heteronotia* are effective in preventing or reducing predation by at least some potential predators.

INTRODUCTION

Numerous behavioural traits described in reptiles are claimed to have survival value. However, data on the effect of these displays on potential predators are usually lacking (Bustard, 1969a).

Defensive behaviour by the ejection of viscous liquid from the tail in *Diplodactylus williamsi* and *Diplodactylus elderi* and a form of defensive behaviour involving a continuous sequence of limb extension and retraction in *Nephrurus asper* were described by Bustard (1964, 1967). No data exist on the usefulness of either of these behavioural traits against potential predators.

OBSERVATIONS

This paper describes experiments carried out under simulated natural conditions in the laboratory using representatives of three Australian gecko genera and appropriate predators.

Diplodactylus elderi.—This small gecko (45 mm snout–vent length) lives exclusively within porcupine bushes (Bustard 1965; Kluge 1967) (*Triodia* spp.). The pygopod *Lialis burtonis* also occurs in this microenvironment and *Lialis* is probably the most important predator of *D. elderi* (Bustard, 1965). *Lialis burtonis*, a known lizard-eater, reaches a total length of at least 60 cm and can readily swallow lizards much larger than adult *D. elderi* (Bustard, 1970, plate 43). Both *Lialis* and *D. elderi* live well in captivity.

Three vivaria were prepared each containing a colony of 6 *D. elderi* and 2 or 3 *L. burtonis*. Both species of lizards were collected near Renmark, South Australia. They remained almost entirely within the *Triodia* clumps provided. Periodically these were inspected and the *D. elderi* counted. Colonies were maintained for 6 months and during this time no *D. elderi* disappeared even when the *Lialis* were denied food for periods of up to 6 weeks. The *Lialis* were fed mainly on the gecko *Gehyra variegata* or on other geckos including *Lucasium damaeum*.

Lialis has a more extensive distribution than *D. elderi*. Subsequent experiments were carried out using *Lialis* from North Queensland which would never encounter *D. elderi* under natural conditions. Although no *D. elderi* were eaten during these experiments they were attacked on several instances and then quickly relinquished. All were unharmed by the encounter.

On one occasion a *Lialis* from North Queensland jabbed at a *D. elderi*, which displayed by bending towards the *Lialis* and raising its tail. The *Lialis* did not attack it further. On another occasion a *Lialis* was seen to bite a *D. elderi* and hold its head firmly in its jaws for about one second before releasing it. The *D. elderi* remained passive during this encounter. On yet another occasion a *Lialis* grasped the body of a *D. elderi* in its jaws. The *D. elderi* writhed around at once and was released. It had exuded viscous liquid from its tail and rubbed it off on the throat region of the *Lialis*. It is not certain, however, that the discharge caused the *Lialis* to drop it.

The above observations suggest the presence of a skin toxin in *D. elderi* in addition to the liquid exudation mechanism from the tail. They also demonstrate, quite conclusively, that *D. elderi* is able to live in close proximity to *Lialis* with complete immunity although *Lialis* readily devours other geckos.

Diplodactylus williamsi.—The liquid ejected from the tail of this gecko can be fired for distances of 0.5 m and readily forms cobweb-like filaments which are very difficult to remove (Bustard, 1964). The effectiveness of this behaviour was tested against *Varanus gilleni* an arboreal pygmy monitor from Central Australia which feeds predominantly on geckos.

A pair of *V. gilleni* were maintained in the laboratory and fed *Gehyra variegata*. Each monitor consumed 1–2 geckos per week. They were grabbed wherever possible but always swallowed head first. *V. gilleni* can readily overpower and swallow geckos weighing 30–40% of its weight. Periodically one or two specimens of *D. williamsi* were added to the vivarium. These were never eaten. When attacked by the *V. gilleni* they fired liquid at the predator and then moved rapidly towards cover. The behaviour was most marked since *D. williamsi* is a very sluggish gecko. When initially approached by *V. gilleni, D. williamsi* unlike *G. variegata*, never attempted to flee. The following encounter is typical: a recently introduced *D. williamsi* was approached by a *V. gilleni* which grabbed it at the side of the head over one eye. The *D. williamsi* curved its tail forward (this gecko can "fire" in any direction, see Bustard, 1964) and "fired" twice at the head of the *V.*

gilleni, which immediately let go. The *D. williamsi* quickly moved for cover and the *V. gilleni* was left trying to remove viscous webs of exudation from its face and jaws. I have never seen a *V. gilleni* relinquish a struggling *G. variegata*.

The fact that *D. williamsi* is grabbed and then relinquished by *Varanus* (and presumably also by other predators such as the skink *Egernia striolata*) may explain the low level of autotomy (10.4%) recorded for this gecko (Bustard, 1969b).

Heteronotia binoei.—This gecko is often popularly called the prickly gecko due to its heavily keeled dorsal scales. Observations made in the course of feeding experiments using *Lialis burtonis* indicate that these keeled scales afford some degree of protection from *Lialis*, since individuals of *H. binoei* introduced to the vivarium were rarely eaten. The keeled scales probably afford similar protection against small lizard-eating snakes.

Nephrurus asper.—The behaviour of this gecko was observed when approached by (a) small mammals (laboratory mice), (b) small snakes (too small to swallow the gecko), (c) larger snakes capable of eating it, and (d) a giant cockroach 8 cm long.

Response to the laboratory mouse was the stereotyped display (Bustard, 1967). If the mouse came very near, the gecko opened its mouth and lunged at it or jumped towards it and vocalised. At no time was the mouse actually bitten. Either response caused the mouse to flee. The initial limb extension makes the gecko appear much larger than it is, which probably causes a small potential predator to hesitate before attacking (compare vertically elevated loops of the snake *Vermicella annulata*, Bustard, 1970). Alternate raising and lowering of the body probably serves to accentuate the size effect in *Nephrurus*. The forward lunge and/or vocalisation by the gecko, when closely approached, caused the mouse to withdraw. It seems likely that this behaviour is similarly effective against small, naturally occurring, mouse-sized, carnivorous marsupials such as *Sminthopsis* or *Antechnius*.

Small snakes (including the snake-mimicking pygopod, *Pygopus nigriceps*, (Bustard, 1968)) were treated similarly. However, the response to a 90 cm children's python (*Liasis childreni*) was completely different. Specimens of *N. asper* on seeing the small python never displayed. Instead they rushed to the furthest corner of the vivarium and crouched down or ran under the nearest cover. This behaviour was more remarkable since *N. asper* is a very sluggish species which readily displays to a human.

The response to the giant cockroach was ambivalent. Geckos tended to follow it when it moved away, showing feeding interest, although the cockroach was much larger than the maximum prey size. However, when the cockroach approached a gecko, the gecko displayed.

DISCUSSION

Individuals of *D. elderi* were frequently collected from porcupine bushes (*Triodia* spp.) inhabited by *Lialis*. Since the micro-environment provided no safe retreat for *D. elderi* from *Lialis* the defensive exudate of *D. elderi* may well provide protection against *Lialis*. The laboratory experiments offer confirmation of this hypothesis.

The defensive behaviour provides complete protection from an important potential predator. However, the presence of a substantial level of regrown tails in *D. elderi* (40–50% of adult *D. elderi* near Renmark, South Australia, possess regrown tails) cannot yet be explained. Perhaps the inability of this species to exude the excretion immediately results in autotomy immediately the tail is grasped, that is before the defensive mechanism can operate. The defensive mechanism is less complete than in *D. williamsi* which fires the liquid. Bustard (1969b) noted that tail autotomy was uncommon in *D. williamsi*, only 10.4% of 127 individuals possessing regrown tails. *D. williamsi* and the other members of the *strophurus* group have evolved an extremely effective means of defence against a wide range of potential predators making tail autotomy almost unnecessary. *D. elderi* has a much less effective mechanism hence the much higher observed autotomy levels in this species.

Observations of *Lialis* dropping *D. elderi* which had not ejected liquid deserved further study since reptiles, unlike amphibians, lack skin glands (Maderson, 1964). Despite this, it seems most likely that the liquid ejected by *D. williamsi* and related species evolved from a simple skin exudation as occurs in amphibians. This generalised situation may still be present in *D. elderi*.

The behaviour of *Nephrurus asper* to the mouse and small snakes clearly has survival value. When faced with a larger snake *N. asper* makes no attempt to display but flees at once. It seems unlikely that display behaviour would be any deterrent to a snake capable of swallowing the stoutly built geckos thus fleeing offers the best prospects for survival. Mebs (1966) described the defensive behaviour of *Teratoscincus scincus* as a series of simple reactions. The first response is raising the body on all four legs and inflating the throat. This is followed by horizontal movements of the tail which produced a sound by specialised scales rubbing together. This behaviour has parallels in *N. asper* which also includes sounds in its repertoire. At higher display intensity, *Teratoscincus*, like *N. asper*, jumps at the enemy. Mebs noted that as a last resort the gecko flees. In devising a scheme of the defensive behaviour Mebs included a diagrammatic representation of the tendency to flee during all stages of the display. This was greatest (a) initially and (b) after the complete repertoire of defensive behaviour, including jumping at the enemy, had failed to overcome the threat.

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VARIABILITY IN CLUTCH SIZE IN AQUATIC CHELONIANS

J. Whitfield Gibbons, Judith L. Greene and Joseph P. Schubauer[1]

Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina, U.S.A. 29801 *and* [1]*Department of Biology, State University College at Buffalo,* 1300 *Elmwood Avenue, Buffalo, New York, U.S.A.* 14222

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INTRODUCTION

Clutch size is often cited as increasing as a function of body size within particular species of reptiles (Cagle, 1950; Einem, 1956; Avery, 1975; Plummer, 1977). Reproductive output and, consequently, average clutch size is theoretically expected to increase as a function of age in long-lived species (Williams, 1966; Hirshfield & Tinkle, 1975). Variability in clutch size may also result from responses of individuals to localised ecological and physiological factors, although this has not been confirmed.

Although intra-individual variability in clutch size occurs, the data have classically included only single measurements for individuals (Tinkle, 1961; Christiansen & Moll, 1973). Thus, only inter-individual variability has been considered in establishing the relationship between clutch size and selected independent variables in previous studies. However, recent developments of an X-ray technique for determining clutch size in chelonians (Gibbons & Greene, 1979) has permitted us to record the clutch sizes of particular individuals for as many as three years. The objective of this paper is to compare clutch size variability within particular individuals with that in chelonian populations as a whole.

METHODS

Turtles used to determine intra-individual variability in clutch size were from marked populations on the U.S. Department of Energy's Savannah River Plant (SRP) near Aiken, South Carolina, U.S.A. The populations have been under study since 1967. The ranges in clutch size of the SRP species are similar to those given in general works on aquatic turtles (Carr, 1952; Ernst & Barbour, 1972).

Females were photographed by means of a standard medical X-ray machine following each capture from 1976 to 1978. The technique is 100% effective in establishing clutch size (Gibbons & Green, 1979). Some individuals were collected with aquatic traps but most were captured terrestrially by pitfall traps (Gibbons, 1970) as they left aquatic sites to lay eggs. In most instances individuals were released immediately following clutch size determination and are presumed to have deposited their eggs in normal fashion.

RESULTS

One hundred and ninety-three individual females containing eggs of six species have been X-rayed. Of these, two clutches were observed in 19 recaptures representing two species, *Deirochelys reticularia* (chicken turtle) and *Kinosternon subrubrum* (eastern mud turtle). Three clutches have been observed in a female *K. subrubrum* (Table I).

The greater intra-individual variability was observed in *D. reticularia* in which subsequent clutches in individuals had a mean difference of 3.5 (range 1–10; Table I). Subsequent clutches within 12 *K. subrubrum* were much less variable. No consistent trend of increase or decrease in subsequent clutches was apparent for either species (Table I).

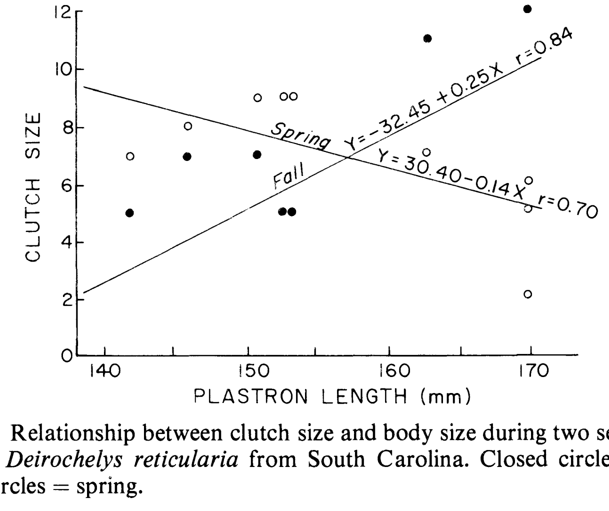

FIG. 1. Relationship between clutch size and body size during two seasons in female *Deirochelys reticularia* from South Carolina. Closed circles = fall; open circles = spring.

TABLE I. Subsequent clutch sizes of two species of aquatic turtles in South Carolina as determined by X-ray photography during different years. Length (in mm) is for time of original capture S = spring (February–June). F = fall (late August–October)

Deirochelys reticularia

Plastron length	1977 S	1977 F	1978 S
142		5	7
146	8	7	
151		7	9
153		5	9
153		5	9
163	7	11	
170		12	2
170	6		5
Annual $\bar{X}$	7.0	7.4	6.9
Range	6–8	5–12	

Kinosternon subrubrum

Carapace length	1976 S	1977 S	1978 S
83		3	3
84	3		4
85	3		3
87	3	2	
89		2	3
89		4	2
90	2	3	
90	3	3	3
91	4	4	
93	2	3	
95	4		3
95			
Annual $\bar{X}$	3.0	3.0	3.0
Range	2–4	2–4	2–4

The variability in the clutch size–body size relationships potentially attainable with *D. reticularia* depending on when they were sampled is indicated in Fig. 1. Use of the spring samples suggests an increase in clutch size as a function of body size whereas the fall (autumn) sample could be construed as demonstrating the opposite trend.

DISCUSSION

Clutch size in aquatic chelonians is clearly related to factors other than merely age or size as indicated by the variation occurring among different sized individuals and within the same females in different years and seasons. An indication that clutch size within an individual can vary slightly over a season has been suggested by counts of subsequent sets of *corpora lutea* (Webb, 1961; Ernst, 1970; Iverson, 1977). However, inter-annual clutch size variation has not been determined using this technique, as counts of waning *corpora lutea* do not allow confident statements to be made about clutch size variation between, or even within a season.

Present data from the SRP turtle populations indicate the general trend that clutch size increases with body size. That the relationship is a fragile one that can be influenced by sampling error is clearly shown by comparison of clutch size–body size trends in *D. reticularia* (Fig. 1) taken during two seasons.

Clear patterns of clutch size variation have yet to be revealed for any species of turtle. However, the present information emphasises the need for consideration of other factors, besides age or size, that can influence clutch size. Attention to measurable variables such as clutch sequence, length of the previous growing/feeding period, season, and reproductive output in the previous year, as well as body size and age, may prove to be an instructive approach to unravelling and interpreting the patterns of clutch size variation in aquatic turtles.

ACKNOWLEDGEMENTS

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SOME PROBLEMS IN REPTILIAN PATHOLOGY

E. Elkan

Department of Histopathology, Mount Vernon Hospital, Northwood, Middlesex

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SUMMARY

Reptilian and amphibian histopathology presents particular problems. Most of the animals cannot be collected in large numbers or subjected to comparative experiments. They seldom arrive fresh from their natural habitat, but are sent in either by those who keep them as pets or by institutions which keep lower vertebrates for display, breeding or acclimatisation trials. Much of the material submitted is not well preserved and, therefore, can only be subjected to a cursory examination. The following cases are submitted to readers in the hope that some of them may be able to be resolved as more cases accrue.

SHED TEETH IN A GABOON VIPER

The specimen of *Bitis gabonica* arrived at a British zoo as a hatchling; in four years it reached a length of 1.4 m. It fed regularly and seemed in excellent health up to the day of its death. The only abnormal organ seen was the pancreas which contained a large central abscess. The lung showed a moderate degree of inflammation and on the whole it seemed that the snake had died from septicaemia. The likely origin of the sepsis was found. In the small gut, at the level of the pancreas, two fangs were found lying side by side, each 2.5 cm long, and both of exactly the same type as the snake's own fangs. They were needle-sharp and not decalcified. If their presence had been due to cannibalism other evidence would have been found. Therefore, it must be assumed that the snake shed these fangs and swallowed them. It is apparently normal for snakes to swallow their discarded teeth but these should then be decalcified in the stomach in order that they can be digested. In this case the teeth passed the stomach and pierced the wall of the gut, setting up inflammation of the pancreas and the start of general septicaemia. We are left to wonder how snakes usually survive the swallowing of their sharp teeth.

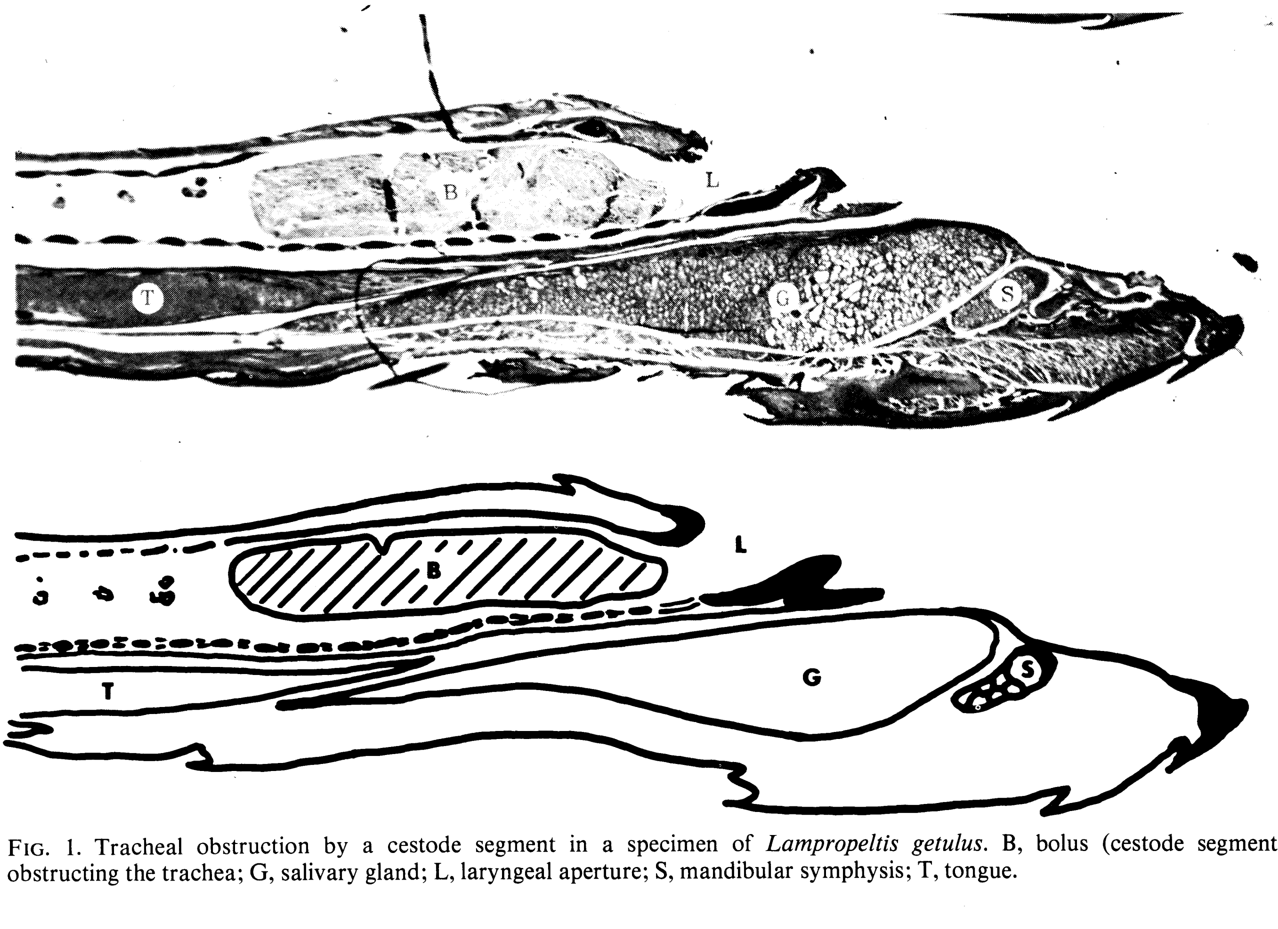

Fig. 1. Tracheal obstruction by a cestode segment in a specimen of *Lampropeltis getulus*. B, bolus (cestode segment) obstructing the trachea; G, salivary gland; L, laryngeal aperture; S, mandibular symphysis; T, tongue.

SUFFOCATION OF A KING SNAKE

A specimen of *Lampropeltis getulus* behaved normally during several months of captivity until it displayed convulsions and died rapidly. The small intestine of this fully grown and well-nourished snake contained some tapeworms, probably *Ophiotaenia* sp., but these do not cause death unless they become so abundant as to cause intestinal obstruction. No clue as to the cause of death was found until the trachea was opened. It was then found that a bolus of apparently half-digested tissue was lodged below the laryngeal aperture where it obviously acted like a ball valve and asphyxiated the snake. Microscopic examination showed that the bolus was not an article of food but a disintegrating segment of a large tape worm, very much larger than those found in the snake's intestine (Fig. 1).

It is not easy to visualise how a cestode segment of that size could have entered the trachea. Even assuming the snake had swallowed the segment, it would hardly be sufficiently mobile to pass through the laryngeal slit without being rejected by the snake. This case demonstrates the distintegration of the cestode segment in the trachea in the absence of digestive enzymes. Apparently, therefore, such enzymes are not a prerequisite for the disintegration of the strobila.

TUMORAL CALCINOSIS IN A SNAKE

According to Slavin, Klenermann, Darby and Bansal (1973) tumoral calcinosis is, "an uncommon condition of obscure aetiology, characterised by lobulated calcified cystic masses, containing structureless calcified debris". The literature on human cases is scanty, and in veterinary medicine the disease is so far unknown. One would therefore be reluctant to describe what was found in a snake (*Lampropeltis getulus*) as tumoral calcinosis, yet no other diagnosis seems to fit equally well.

The female snake lived and bred in a zoo; a male kept in the same cage has remained healthy. After several years, the female developed subcutaneous tumours which, on removal, proved to consist of agglomerations of cystic masses. Later, the snake developed further tumours but at different sites. This material was examined histologically. The results almost completely matched the descriptions given in cases of tumoral calcinosis. The cysts were multilocular, the largest 4 × 2 × 2 cm in size (Fig. 2). They had no well-defined lining and were not adherent to the surrounding tissues; their contents were sterile and consisted entirely of calcified debris (Fig. 3). Other identical tumours have since been removed from the same snake. No parasites or other foreign bodies which might have caused the condition were found.

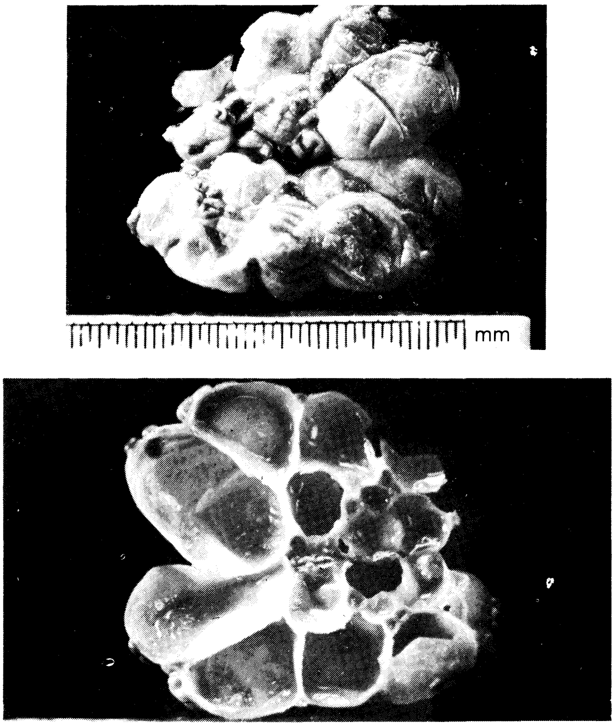

FIG. 2. Tumoral calcinosis in *Lampropeltis getulus*. Top, whole tumour after excision; bottom, tumour bisected.

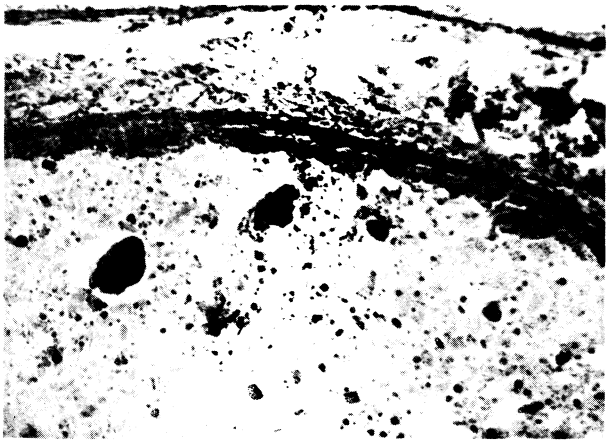

FIG. 3. Tumoral calcinosis (as in Fig. 2). Section showing cyst wall and calcified contents.

UNUSUAL GIANT CELLS IN *PSEUDEMYS ORNATUS CALLIROSTRIS*

Giant cells which may contain over a hundred nuclei result from the agglomeration of mononuclear monocytes produced in the bone marrow. They form part of the defence system. In reptiles they are most commonly seen in infections by fungi, helminths or acid-fast bacilli. An unusual formation of giant cells was found in two, otherwise completely unconnected specimens of *Pseudemys ornatus callirostris*. In one case it was the spleen, in the other the kidney, which was affected. In both, the diseased organs were the seat of numerous granulomata or micro-abscesses filled with structureless detritus. Each of these granulomata was lined by a thick layer of elongated giant cells arranged in palisade formation. In most of these cells the nuclei were strung out in a single line, starting at the periphery where the cell was anchored to the parenchyma of the affected organ and ending at the centre where the cell fused with the debris filling the granuloma (Fig. 4).

Since this condition has so far only been seen in one species of chelonian one might speculate that it might be the presence of one particular parasite in this species that elicits this peculiar giant cell formation. Unfortun-

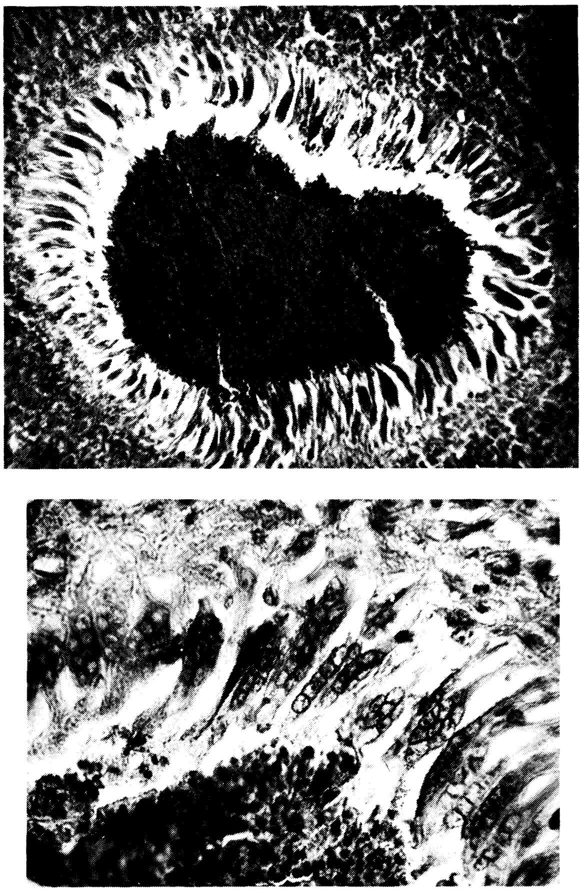

FIG. 4. Splenic granuloma in *Pseudemys ornatus callirostris* showing giant cells in palisade formation (top), with giant cells at higher magnification (bottom).

ately, in both cases, the disintegration of the debris at the centre of the granulomata was too advanced to allow identification of the causative organism. The eosinophilia which usually accompanies cases of this kind was only moderate.

A CONDITION CLOSELY RESEMBLING SARCOIDOSIS IN A DESERT COBRA

Sarcoidosis is a group of diseases of unknown origin in which numerous small granulomata appear in various organs. Macroscopically, the lesions resemble those of miliary tuberculosis but in sarcoidosis acid-fast bacilli are never found. It has been suggested that the disease may be due to a viral infection (Anon, 1973). It has not so far been described in veterinary medicine.

The present case occurred in a fully grown desert cobra (*Walterinnesia aegyptia*). Other snakes kept in the same cage of the collection at the Department of Zoology, University of Tel Aviv, were not affected. There was no difference in the histological appearance of the renal and pulmonary lesions. The granulomata, 4–6 mm in diameter, were ovoid or spherical, filled with epithelioid monocytes and surrounded by a thin fibroid capsule (Fig. 5). At the centre there was usually some fibrinoid degeneration but caseation was never seen. In the kidneys, the reticular pattern of the parenchyma was sharply disrupted, as if dissolved by the granulomata. Plasma cells were predominant in the pulmonary material whereas lymphocytes prevailed in the kidneys. Most of the foci contained large giant cells of both the "foreign-body" and Langhans types; in many of these cells the nuclei were too numerous to be counted.

FIG. 5. Possible renal sarcoidosis in *Walterinnesia aegyptia* showing macroscopical (top) and microscopical (bottom) appearance.

Asteroid or Schaumann bodies, as described from human sarcoid material, were not seen. Equally, no bacteria of any kind could be detected, but it must be mentioned that since the material had been received in formalin, only staining methods could be employed to identify bacteria.

In comparing this case with human sarcoidosis, the following points might be considered. In both cases the disease was systemic, but whereas human sarcoid has a tendency to heal, the snake died. Disseminated granulomata, surrounded by a thin fibrous capsule, plasma cells and lymphocytes were found in this case just as in human material. In both, the granulomata contain epithelioid monocytes and giant cells with central fibrinoid degeneration but no caseation. Conforming with human sarcoid, no acid-fast bacteria were found in the reptilian material. The similarity of the two conditions is impressive but more material is needed to confirm the diagnosis of sarcoidosis in a reptile.

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THE COMPARATIVE ABUNDANCE AND RESOURCE PARTITIONING OF TWO GREEN-GECKO SPECIES (*PHELSUMA*) ON PRASLIN, SEYCHELLES

R. S. THORPE AND C. M. CRAWFORD*

Department of Zoology, University of Aberdeen, Scotland

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SUMMARY

The two species of day-gecko *Phelsuma* on Praslin, Seychelles, would appear to be potential competitors. Although atypical for diurnal lizard communities, the macrohabitat (vegetation) is more important in resource partitioning than the daily activity or microhabitat. In this sense their community is organised like that of their nocturnal gecko ancestors rather than that of diurnal lizards. This generalisation conforms to other aspects of their mode of life such as their thermoregulation.

Phelsuma astriata appears to be most abundant in natural plant communities with high vegetation, *i.e.* natural lowland forest and hillside forest. *P. madagascariensis* is more abundant in lowland areas whether the plant communities are artificial, *i.e.* gardens and coconut groves, or "natural", *i.e.* lowland forest. Neither species was abundant on eroded hillside or in casuarina plantations.

INTRODUCTION

Phelsuma are green diurnal geckos which live in arboreal habitats. The genus contains over twenty species, the exact number depending on the author (Rendahl, 1939; Loveridge, 1942; Mertens, 1962, 1966; Vinson & Vinson, 1969 and Blanc, 1972). These species are distributed on Madagascar and other Indian Ocean islands including Praslin, Seychelles.

Praslin is the second largest of the granitic Seychelles. It lies in the Indian Ocean just south of the Equator and approximately 1000 km north-east of Madagascar. Praslin is approximately 11 km long and up to 5 km wide. There are several hilly ridges from 250 to 350 m above sea-level and coastal strips of lowland ground. The rainfall can be heavy (over 2 m per annum at sea level) with a high average humidity (76%) and stable temperature (24–30°C).

There are two species on Praslin, the large *Phelsuma madagascariensis* (approximately 20 cm long) and the smaller *Phelsuma astriata* (approximately 11 cm long).

P. madagascariensis *was originally named* P. sundbergi *by Rendahl* (*1939*) *but changed to* P. madagascariensis sundbergi *by Mertens* (*1962*). P. sundbergi *has recently been resurrected by Borner* (*1972*).

Whether or not an allopatric island population deserves specific status is a difficult question beset by many conceptual problems (*Sokal 1973, Sneath & Sokal 1973, Thorpe 1979*). *It is not sufficient for recognition of species status to indicate that an allopatric population is different because conspecific populations may also differ considerably due to raciation. Consequently, the specific status of the Praslin population of* P. madagascariensis *can only be judged adequately by comparing its relative degree of divergence with that associated with speciation in the rest of the genus.*

Since no such scientific study is available, a conservative view is taken and the name P. madagascariensis *is used throughout this study.*

Even though young *P. madagascariensis* appear superficially like *P. astriata* and had been confused by previous field workers (1976 University of Aberdeen Expedition to Praslin, Seychelles) they could be distinguished with some confidence by the shape of their snout, the colour of their flanks and the presence of bars across the neck (Crawford & Thorpe, in preparation).

These two species exist on Praslin in high numbers in a stable environment with a low reproductive rate, producing two relatively large offspring at a time, and with a relatively long life span. They will therefore tend to be K-selected (MacArthur & Wilson, 1967) and subject to keen interspecific competition. Consequently one would usually expect a tendency for a reduction in niche overlap so that interspecific competition is reduced (Pianka, 1978). Such resource partitioning has been studied in wide range of lizards (see references in Schoener, 1974, 1977; Pianka, 1973, 1978) and has shown a tendency for sympatric conspecifers to partition various aspects of their resources such as time, space and food.

Various facets or "dimensions" of these resources can be defined under headings such as macrohabitat, microhabitat, daily activity, seasonal activity and food, and the so-called niche overlap and niche breadth (Sensu Pianka, 1973) along these dimensions can be quantified.

Niche breadth is quantified as

$$B = \frac{1 \Big/ \sum_{i}^{n} P_i^2}{n}$$

where P_i is the proportion of the *i*th resource (category) used where the niche dimension, *e.g.* daily activity is divided into *n* categories.

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* Present address: School of Biological Sciences, University College of Wales, Aberystwyth, Wales.

Niche overlap between two species is quantified as:

$$O_{jk} = O_{kj} = \frac{\sum_{i}^{n} P_{ij} P_{ik}}{\sqrt{\sum_{i}^{n} P_{ij}^{2} \sum_{i}^{n} P_{ik}^{2}}}$$

where P_{ij} and P_{ik} are the proportions of the ith resource (category) used by the jth and kth species.

These statistics are discussed by Pianka (1973).

MICROHABITAT, DAILY ACTIVITY AND OTHER "DIMENSIONS"

METHODS

The microhabitat and daily activity were studied by Crawford during July–September 1976 (1976 University of Aberdeen Expedition to Praslin, Seychelles) in a coconut grove at Amitie (Fig. 1, locality 7).

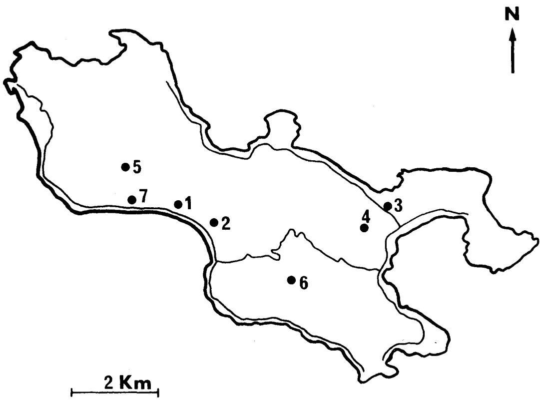

FIG. 1. Location of study areas on Praslin. The roads are indicated by thin lines and the study areas by the following numbers: (1) Coconut groves, (2) Garden, (3) Casuarina plantations, (4) "Natural" lowland forest, (5) Eroded hillside, (6) Hillside forest, (7) Coconut grove at Amitie.

The coconut grove had a mixture of three sizes presumably reflecting three stages of plantation. The three sizes of tree, which were intermixed with one another were: (i) juvenile trees without trunk or fruit, (ii) medium trees of 8–10 m, and (iii) large trees of 20 m.

In this section of the study the adult geckos were identified to species but the juveniles were not. Therefore the analyses ignored the juveniles.

The aspect of the microhabitat that was considered was the structural (or spatial) niche. This was expressed in terms of several "dimensions", *e.g.* tree size and position in tree, which were not necessary mutually exclusive. These dimensions were then divided into several nominal or ordinal categories.

The dimensions considered were as follows:

1. Tree size, three categories (as above): (i) juvenile, (ii) medium, (iii) large.
2. Position in large tree, seven categories: (i) trunk, (ii) lower leaves, (iii) middle leaves, (iv) upper leaves, (v) bract, (vi) flower, (vii) matting.
3. Position in medium tree, seven categories as for dimension 2.
4. Position in juvenile tree, four categories: (i) lower leaves, (ii) middle leaves, (iii) upper leaves, (iv) matting.
5. Position on leaf (large tree), three categories: (i) midrib, (ii) petiole, (iii) frond.
6. Position on bract (large tree), four categories: (i) low (old) bract, (ii) medium bract, (iii) high bract, (iv) new bract.
7. Position on flower (large tree), three categories: (i) new (male) flower, (ii) female flower and young fruit, (iii) ripe fruit.
8. Position on leaf (medium tree), three categories as for dimension 5.
9. Position on bract (medium tree), four categories as for dimension 6.
10. Position on flower (medium tree), three categories as for dimension 7.
11. Position on leaf (juvenile tree), three categories as for dimensions 5 and 8.
12. Daily activity, five categories recorded at three-hour intervals, *i.e.* 6.00, 9.00, 12.00, 15.00 and 18.00.

The niche breadth and overlap were not computed if there were less than 10 observations per species per dimension. In Table I the number of observations for *P. madagascariensis* is given before those for *P. astriata.*

RESULTS AND CONCLUSIONS

Table I reveals two points. That *P. astriata* tends to have a narrower "niche breadth" than *P. madagascariensis.* And, more importantly, that their

TABLE I

Dimensions	No. of observations per species	Niche breadth *P. madagascariensis*	Niche breadth *P. astriata*	Niche overlap
1. Tree size	632/66	0.72	0.54	0.87
2. Position in large tree	248/too low	0.79		
3. Position in medium tree	349/51	0.47	0.40	0.97
4. Position in juvenile tree	35/10	0.51	0.46	0.99
5. Position on leaf (large tree)	82/too low	0.73		
6. Position on bract (large tree)	47/too low	0.62		
7. Position of flower (large tree)	50/too low	0.71		
8. Position of leaf (medium tree)	113/12	0.50	0.47	1.00
9. Position on bract (medium tree)	171/27	0.66	0.58	0.94
10. Position of flower (medium tree)	53/12	0.91	1.00	0.95
11. Position on leaf (juvenile tree)	25/10	0.77	0.76	0.90
12. Diurnal activity	372/36	0.95	0.87	0.91
13. Macrohabitat (vegetation)	45 × 5 counts/36 × 5 counts	0.58	0.47	0.68

"niche overlap" is generally very high for the microhabitat and daily activity.

Other aspects of their ecology also indicate that they are potential competitors. Although there may be quantitative differences in their diet they are both nectivorous and insectivorous. Their behaviour and thermal ecology are also very similar. They are both, inactive, largely shade dwelling and maintain their temperature about 2–5°C above ambient as well as having very similar mean cloacal temperature of around 29–30°C (Crawford & Thorpe, 1979).

MACROHABITAT AND ABUNDANCE

INTRODUCTION

The similar ecological requirements of these two species as exemplified by their considerable "niche overlap" in facets of their structural microhabitat and daily activity, etc., begs the question: Is interspecific competition reduced by partitioning the macrohabitat?

METHOD

The ability to identify these two species at a distance makes it possible to attempt to answer the above question. Nevertheless, several problems remain in attempting to estimate the population density in various habitats.

The various capture–recapture technique used to estimate the population density of small mammals, etc. (Delany, 1974) were not applicable in this study because *Phelsuma* are not readily trapped. Although they could be captured by noosing up to 7 m above ground this was very time consuming and not applicable to the habits with high vegetation.

Consequently we were obliged to rely on straight counts. Ornithologists are faced with similar problems when attempting to estimate the relative abundance of bird species in woodland. One method they frequently use is that of strip transects (Yapp, 1962; Driscoll, 1977). The individuals are recorded from a set distance either side of a straight line whilst walking along it. They are recognised either by sight or voice. This method was not suitable for *Phelsuma* because, unlike birds, they do not draw attention to themselves by vocalisation or movement.

Therefore the method adopted was to mark out quadrats and search them intensively. Three people, using binoculars searched the quadrat five times throughout the day. Adult, subadult and juveniles were recorded for each species and the population density was estimated as the sum of the maximum count for adults and juveniles. The quadrats were 900 m^2 (except where stated below) and each tree was closely searched for several minutes. This was carried out by the authors during the 1978 University of Aberdeen Expedition to the Seychelles in August.

The effectiveness of this method was checked in one macrohabitat, the garden. The *Phelsuma* in one coconut tree and an associated clump of bananas within the quadrat were studied intensively for 12 hr. The activity of each individual during this time was noted and the data are presented in Crawford & Thorpe (1979).

An analysis of the above diurnal activity data shows that between 7.15 and 17.15 (when the quadrat searches were conducted) that even if each tree was searched for an hour one is most likely only to see 60% of the individuals. Since this was also the percentage of the individuals recorded during the quadrat study increasing the search intensity would not be likely to give a much better estimate of the population density.

On the other hand, at any one instant, one is most likely to see only 20% of the individuals so a more superficial search of a larger area would tend to give a much greater underestimate of the population density.

There are obviously difficulties in extrapolating from this estimate of search efficiency in the garden habitat to search efficiency in other habitats. Nevertheless it does enable one to judge approximately how large a quadrat can be for a given time limit and show that one is unlikely to count all the individuals in an area. On the latter point it is evident that we probably saw only about half of those present so that the quadrat counts are likely to be a considerable underestimate of the actual population density. In terms of resource partitioning this matters less than if there is a bias in the counting efficiency of the two species that varies between vegetation types. If there is such a variable bias it is unlikely to be of a magnitude to have any substantial influence on the results.

VEGETATION TYPES

The macrohabitat is described in terms of vegetation types.

The vegetation has been considerably altered by man since his arrival on the island in 1770 and few, if any, entirely natural areas remain. Nevertheless, some areas are more natural than others and have fewer introduced species of plants.

Although there have been several studies of the Seychelles vegetation (Vesey-Fitzgerald, 1940; Jeffrey, 1962; Bailey, 1971; Procter, 1974) we are unaware of any scientific analysis and classification of the vegetation types on Praslin. Vesey-Fitzgerald (1940) only briefly mentions the Praslin vegetation in relation to that of Mahe.

Since there was no plant community analysis on which to base our study, we recognised six vegetation types representing lowland and hillside areas as well as "natural" and artificial communities. These are listed and described below:

(1) Coconut grove (lowland, artificial)

These are common on Praslin and other Indian Ocean islands since they have a commercial significance, *i.e.* copra production. The site studied (Fig. 1) contained eighteen mature coconut trees (*Cocos nucifera*) planted in rows, three juvenile coconut trees and two casuarinas (*Casuarina equisetifolia*). The trees were well spaced and the fronds, as a rule, did not form a complete canopy but were separate. The undergrowth was kept low by grazing cattle.

(2) Garden (artificial, lowland)

There can be no such thing as a typical or representative garden since they vary so much. Nevertheless, it is worthwhile including this type of area in the study since subsistence gardens account for a significant proportion of the lowland area. The area studied was an irregular shape (635 m^2) in the village of Grande Anse. It contained two mature and two immature coconuts (*Cocos nucifera*), two large golden apple trees (*Spondias dulcis*), a medium-sized bread-fruit tree (*Artocarpus altilis*), around thirty banana plants growing in clumps (*Musa* sp.), a paw-paw (*Carica papaya*) and various shrubs. There were also open areas with grass or sweet potatoes.

(3) Casuarina plantation (lowland, artificial)

The study area was on the edge of a fairly large plantation and contained 80 casuarina trees (*Casuarina equisetifolia*) growing in regular rows with approximately 150 takamaka saplings (*Calophyllum inophyllum*) interspersed between them. The casuarinas were around 18–27 m high whilst the takamaka saplings were around 1 to 3 m high. The ground was covered with grass.

The casuarina plantations provide firewood and construction material.

(4) "Natural" lowland forest

There is a small strip of lowland forest with few introduced trees (Fig. 1) on Praslin. A section of the forest strip was selected as natural lowland forest but it bears little or no floral resemblance to the lowland forest described in the report of the 1976 University of Aberdeen Expedition to Praslin. The quadrat had a very dense undergrowth of grass, ferns and creeper with some wild pineapple, *Randia* shrubs, paw-paw and small bead trees (*Adenanthera pavonina*). The large trees were growing in clumps with an interlocking canopy separated by some open areas. There was only one casuarina (*C. equisetifolia*), the area being dominated by four large (20 m) and 12 medium (6–15 m) takamaka trees (*Calophyllum inophyllum*) together with one large and six medium badamier trees (*Terminalia catappa*). The introduced species, *i.e.* wild pineapple and paw-paw etc. represent only a very small proportion of the vegetation.

(5) Eroded hillside (artificial, upland)

Praslin has suffered from fire-induced erosion on several hillsides. Once the fire has destroyed the natural forest the soil is quickly eroded by the high rainfall. Reclamation of the eroded areas is attempted by planting coco-plum (*Chrysobalanus icaco*) which may inhibit further erosion but does not appear to be readily replaced by the original vegetation. The hillsides also have contoured drainage channels and palm leaf water breaks so that the soil is retained.

It is thought that the study area (about 150 above sea level) was burnt out around five years ago, there having been no obvious change in the vegetation over the last two years. The coco-plum had formed dense patches, 1 to 2 m high, separated by stretches of bare soil with some grass. One small and a few juvenile thief palms (*Phoenicophorium borsigianum*), a small bois rouge (*Dillenia ferruginea*) and the occasional *Randia* sapling were present.

(6) Hillside forest (upland, natural)

An area (400 m^2) over 300 m above sea level, just below the peak of Fond Azore, was selected for study, being one of the highest areas on Praslin. This area would be classified as "intermediate forest" in Vesey-Fitzgerald's (1940) classification of the Mahe vegetation, and may bear some resemblance to the *Deckenia-Memecylon* society of Mahe.

This area is likely to be fairly natural since it is as remote as any on the island and contains the endemic palms rather than introduced species. The area studied was only 400 m^2 since the dense trees and large boulders made intensive searching of a larger area impracticable.

The forest had an extremely dense interlocking canopy and little or no undergrowth, the ground being covered with dead fronds. The vegetation was dominated by the following three endemic palms, *Deckenia nobilis* (20 trees), *Nephrosperma vanhouteana* (6) and *Phoenicophorium borsigianum* (6). Several broadleaf trees were present, *Dillenia ferruginea* (3), *Randia sericea* (3) and several unidentified hardwoods. Only one possible introduction was present, *Adenanthera pavonina* (1).

RESULTS AND CONCLUSIONS

The density of the two species within the six vegetation types are expressed in "numbers per hectare" for ease of comparison (Table II).

It can be seen that the density of both species of *Phelsuma* varies considerably according to the type of vegetation. Using a χ^2 goodness-of-fit test, the hypothesis that the maximum count of geckos should be equal (or proportional to the size of quadrat) in each type of vegetation can be tested. This hypothesis has a $P < 0.001$ of being correct for both species—(*P madagascariensis*, $\chi^2 = 36.84$, 4 degrees of freedom; *P. astriata*, $\chi^2 = 16.91$, 3 degrees of freedom). These analyses excluded hillside forest for *P. madagas-*

TABLE II

Vegetation	Estimated density per hectare		Lowland/ upland	Natural/ artificial	Significant difference in the counts between species
	P. madagascariensis	*P. astriata*			
1. Coconut grove	233	67	Lowland	Artificial	Yes
2. Garden	158	79	Lowland	Artificial	Yes
3. Casuarina plantation	0	0	Lowland	Artificial	No test
4. "Natural" lowland forest	122	144	Lowland	Natural	No
5. Eroded hillside	0	33	Hillside (150 M)	Artificial	No
6. Hillside forest	75	225	Hillside (300 M)	Natural	Yes

cariensis and both hillside forest and garden for *P. astriata* because of the low expected frequency in these quadrats.

It can be seen that the two species do not always show comparable densities in the various types of vegetation. If one takes the vegetation types one at a time the number of each species seen during the five counts can be compared by a "paired *t* test". These tests indicate that the counts were significantly higher (with at least a 95% probability) for *P. madagascariensis* than *P. astriata* in both the coconut groves ($t = 13.65$ with 4 degrees of freedom) and garden ($t = 3.34$). There was no significant difference between the counts of the two species for the lowland forest ($t = 1.81$) or eroded land ($t = 1.58$). The counts of *P. astriata* were significantly higher than those of *P. madagascariensis* in the hillside forest ($t = 3.28$). No *Phelsuma* were observed in the casuarina plantation; therefore no test was done.

Two of the artificial types of vegetation, *i.e.* casuarina plantation and eroded land, support few or no geckos of either species. The other four vegetation types support fairly large numbers of geckos and include both artificial and natural vegetation types as well as hillside and lowland types.

Comparing the densities of both species in these four types of vegetation reveals that *P. madagascariensis* is found in high numbers in the lowlands in both artificial (coconut groves and garden) and natural (lowland forest) vegetation. *P. astriata* on the other hand is found in high numbers only in natural forest vegetation (lowland and hillside forest) particularly the high hillside forest.

DISCUSSION

Resource Partitioning

Schoener reviewed the relative importance of various niche dimensions in resource partitioning for both animals as a whole (Schoener, 1974) and for reptiles in particular (Schoener, 1977). Resource partitioning in lizards features strongly in both studies. The dimensions he considered were food, macrohabitat, microhabitat, daily activity and seasonality. This study did not consider food or seasonality.

Our study indicates that the *Phelsuma* community did not conform to some of the trends for diurnal lizards indicated by Schoener. Schoener (1974) considers, terrestrial poiklotherms relatively often partition food by being active at different times of the day and (Schoener, 1977) separation of species by daily activity period is common in diurnal lizards ... but is unreported in strictly nocturnal lizards.

The two *Phelsuma* species, although diurnal, appear to have very similar activity periods and there is no evidence that they are avoiding competition by partitioning this resource. In so far as this dimension is concerned the *Phelsuma* community is organised like that of their nocturnal ancestors rather than like a typical diurnal lizard community.

One group of lizards that might be expected to have similar ecological community structure to *Phelsuma* are *Anolis* from the Caribbean Islands which, like *Phelsuma*, are essentially green in colour, small, diurnal and arboreal. The *Anolis* communities have been studied in some detail (Rand, 1967; Schoener & Schoener, 1971a, b; Schoener & Gorman, 1968; Wingate, 1965; Rand & Williams, 1969; Moermond, 1974; Ruibal, 1961, 1964) and Schoener's (1974, 1977) review of this work indicates that microhabitat is generally of prime importance in resource partitioning whilst macrohabitat tends to be less important or unimportant. The opposite situation is found in *Phelsuma*. From Table I, it can be seen that the microhabitat is not partitioned between the species whilst the macrohabitat has by far the lowest degree of "niche overlap" between species with a highly statistically significant difference in the abundance of the species in the different vegetation types.

Whilst it is atypical for the macrohabitat to be more important in resource partitioning than the microhabitat in diurnal lizards such as *Anolis* it is typical of other (nocturnal) geckos. This is apparent from the studies referred to by Schoener (1977) (Pianka & Pianka, 1976; Huey, 1969; Greer, 1967). Therefore the *Phelsuma* community is organised like a nocturnal gecko community rather than a typical diurnal lizard community in relation to both the relative importance of macro- and microhabitat partitioning and its failure to partition the "daily activity dimension". This is in accordance with our studies on thermoregulation (Crawford & Thorpe, 1979) which indicates that *Phelsuma*, like nocturnal geckos are essentially thigmotherms and are not, like most diurnal lizards, particularly heliothermic.

Abundance

The factors that influence the disparate abundance of *Phelsuma* throughout the various vegetation types are likely to include shade availability, cover for geckos and their eggs and food supply.

Phelsuma having evolved from nocturnal stock, spend a large proportion of their time in the shade (Crawford & Thorpe, 1979) it being important in their thermoregulation. They have only a thin outer epidermis (1 mg per cm^2 in an adult *P. madagascariensis*) and may dehydrate in strong sunlight at a greater rate than an outright heliotherm.

Cover is also important in its own right. Both species tend to seek cover to sleep and also when disturbed during the day. Moreover, the eggs of both species are laid under coconut matting or other such cover and support in a tree or shrub rather than being buried in the ground.

Food may also be an important factor. Whilst both species are insectivorous and nectivorous, *P. madagascariensis* was more frequently observed licking nectar and *P. astriata* catching flying insects.

Of the four vegetation types where *Phelsuma* were abundant, *P. madagascariensis* was prevalent in two of the three areas with abundant nectar and *P. astriata* was abundant in the two forest areas with high vegetation that would support a large number of flying insects.

Only two of the vegetation types did not have an abundance of *Phelsuma*; the eroded hillside and casuarina plantation.

It is not surprising to find a paucity of *Phelsuma* in the eroded hillside because it provides little cover, shade or nectar. The absence of *P. madagascariensis* but the presence of a few *P. astriata* may be because this smaller species can find just enough cover and food to support a low biomass.

The lack of *Phelsuma* in the casuarina plantation, confirmed by observations outside the quadrat area, is quite striking considering their abundance in adjacent coconut groves and lowland forest. Although the casuarina plantation provides adequate shade there is no cover close to the perches for a sleeping gecko, no cover for the eggs and no nectar for food.

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BODY TEMPERATURES OF TWO GECKOS (*PHELSUMA*) AND A SKINK (*MABUYA*) IN PRASLIN, SEYCHELLES

CAROLINE M. CRAWFORD* AND ROGER S. THORPE

Department of Zoology, University of Aberdeen, Scotland

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SUMMARY

1. Data on body temperatures of two diurnal geckos, *Phelsuma astriata* and *P. madagascariensis*, and a skink, *Mabuya seychellensis*, were collected on Praslin, Seychelles.

2. The mean body temperatures of *P. astriata* and *P. madagascariensis* were found to be 29.42°C and 29.9°C, respectively, while mean Tb of the skink, *M. seychellensis*, was considerably higher, 34.67°C.

3. *M. seychellensis* was found to become more active towards the middle of the day, when mean Tb was also highest. The majority of the day was spent basking in sunny sites on the ground or on rocks.

4. Both species of *Phelsuma* showed low levels of activity during the day, and spent most of the time in the shade on trees.

5. It is concluded that *M. seychellensis* is a heliothermic lizard and shows similar thermal behaviour to other members of the genus.

6. It seems likely that *Phelsuma* is largely thigmothermic and the explanation for recorded body temperatures being higher than environmental temperatures is that substrate temperatures are in fact higher than were recorded, but were not measured accurately by the equipment used, and also *Phelsuma* spends short periods basking in the sun.

INTRODUCTION

Many studies have now been made of the thermal ecology of lizards—*e.g.* Bradshaw & Main (1968), Bustard (1967), Heath (1965), Heatwole (1970) and Ruibal (1961), but there is little published information on the thermal ecology of diurnal, arboreal geckos. Furthermore, few studies have been made of thermal relations of lizards in forest habitats where contrasts in environmental temperatures are less extreme than in desert areas. It was thus hoped that a study of the body temperatures of two spp. of arboreal, diurnal geckos—*Phelsuma madagascariensis* (Gray), approximately 20 cm long, and *Phelsuma astriata* (Tornier), approximately 11 cm long; and a skink *Mabuya seychellensis* (Dumeril & Bibron) approximately 15 cm long, would contribute further towards the understanding of lizard thermal ecology.

The genus *Phelsuma* is predominantly Madagascan and is composed of 26 species, of which 19 occur in Madagascar—the others being found on many of the Indian Ocean islands, the Tanganyikan coast of Africa and the Andaman Islands in the Bay of Bengal (Vinson & Vinson, 1969).

Mabuya has a widespread distribution.

The three species of lizard in the present study are closely sympatric on Praslin, Seychelles, and there is also some ecological overlap in that *Mabuya* is also to some extent arboreal.

The main aims of the study were:

1. To determine the relationship between body temperatures of the lizards and those of the surrounding air and substratum.
2. To compare the body temperatures of the three species.
3. To try and relate body temperatures of the lizards to their daily activity and behaviour.

STUDY AREA AND METHODS

The field work was carried out during August 1978. All data on *P. madagascariensis* and *P. astriata* are from individuals captured in the Vallee de Mai National Park, Praslin, at a height of about 200 m above sea level. Most of the trees in the area were Coco de Mer palms, *Lodoicea maldivica*, in a slight clearing in the forest. This area was selected mainly because it provided a site where both species of *Phelsuma* were fairly abundant and could be caught quite easily. Data on *M. seychellensis* were from individuals caught in a garden, where they were common. The area was at sea level and contained coconuts, *Cocos nucifera*, a grove of banana trees, *Musa* sp. and various shrubs. There were also open grassy areas and large rocky outcrops of granite boulders. There was no obvious difference in temperature between the two study areas, and both species of *Phelsuma* were also found in the garden, though *P. astriata* occurred here in low density (Thorpe & Crawford, 1979).

Continuous observation of *Phelsuma* activity and records of tree temperatures were taken in a coconut palm in the garden, and on the adjacent banana trees.

Geckos were captured in the field using a long pole with a noose fitted to the end, which enabled the quick capture of animals at a height of up to 7 m in the trees, causing minimal disturbance. Data from individuals which were disturbed in their activity and could not be easily caught were rejected. Skinks were readily captured with a baited line. Lizards were observed

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* Present address: Department of Botany, University College of Wales, Aberystwyth, Wales.

immediately prior to capture to ascertain their activity. Temperatures were taken quickly on capture using a small mercury cloacal thermometer with a 2 mm bulb, with care being taken in handling the animal to avoid the investigators temperature affecting that of the lizard. The following data were recorded at each capture—date, time and place of capture; species; weight; substratum type and temperature (Ts); air temperature (Ta); cloacal temperature (Tb), activity, and also whether the lizard was in sun or shade at the time of capture.

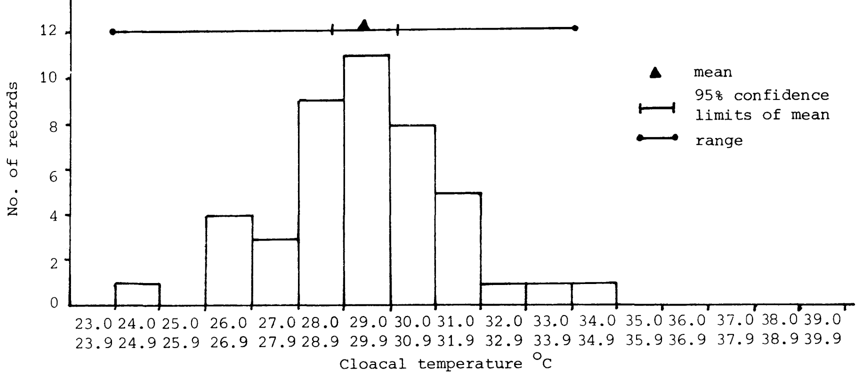
Generally, each record was taken from a separate individual, with the possibility of a few exceptions, but the records are statistically independent and therefore testable, because they were taken at different times under different conditions, rather than being taken from the same individual in consecutive recordings.

In order to ascertain the daily fluctuations in temperature in relation to the activity of the geckos, thermometers were set up in a coconut palm and temperatures recorded at half-hourly intervals from 0600 to 1800 hours from four different positions—the air temperature about 2 m from the ground; trunk temperatures 0.6 m from the ground; substratum temperature of a frond in direct sun; and that of a frond in the shade. At the same time, continuous observation was kept on the positions and activities of all geckos seen in the tree from 0600 to 1800 hours.

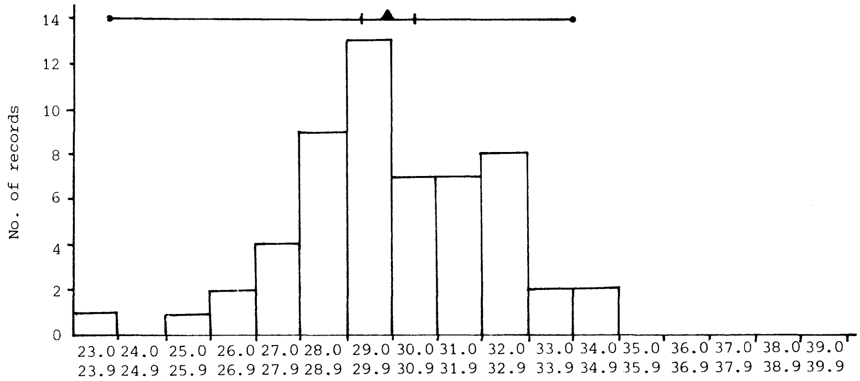
RESULTS

A total of 44 cloacal recordings were obtained from *Phelsuma astriata*; 56 for *P. madagascariensis* and 83 for *Mabuya seychellensis*. The frequencies of temperatures recorded for each species, with the means and ranges, are shown in Fig. 1. The mean Tb for *P.*

(a) Phelsuma astriata



(b) Phelsuma madagascariensis



(c) Mabuya seychellensis

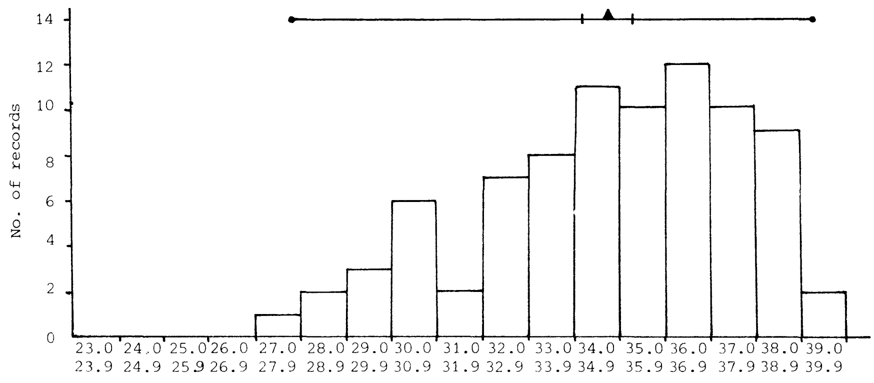


FIG. 1. Frequency of Recorded Cloacal Temperatures.

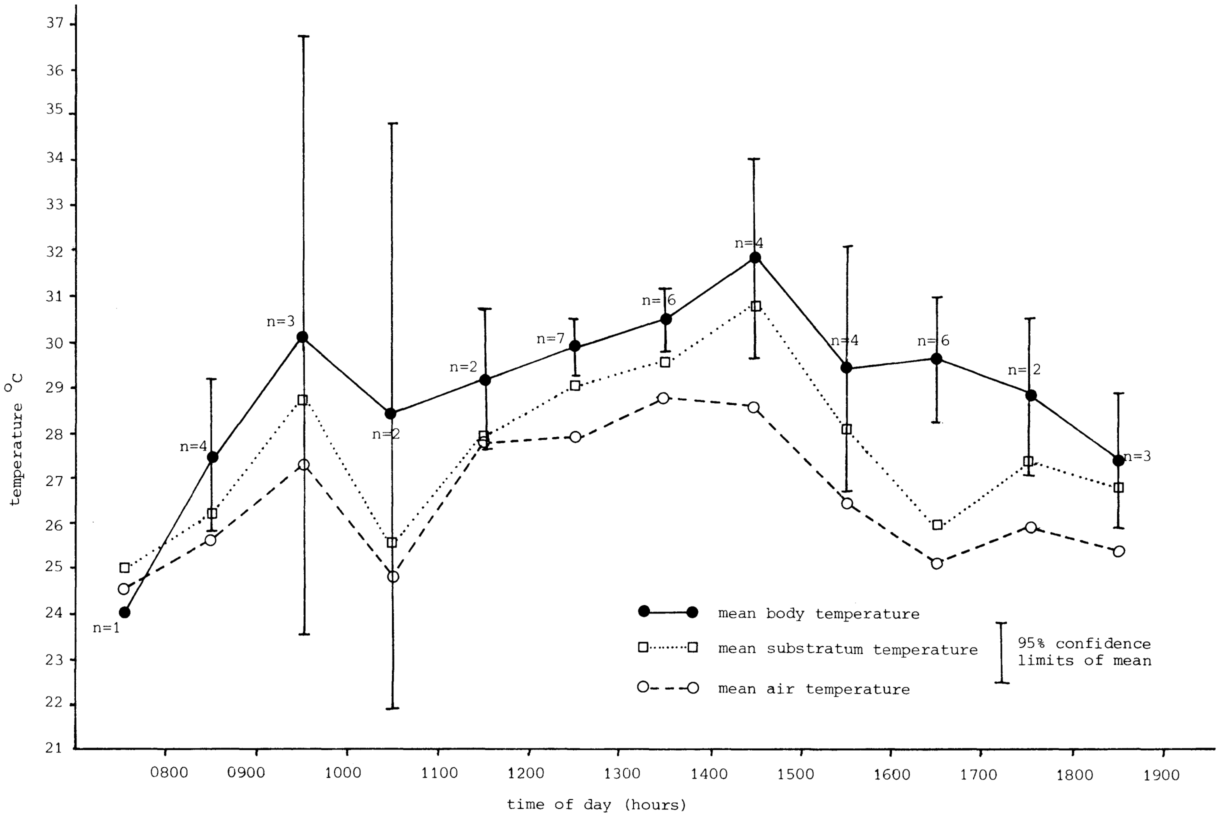


FIG. 2. *Phelsuma astriata*—mean body, substratum and air temperatures during day.

astriata (29.42 ± 0.59°C) is very similar to that of *P. madagascariensis* (29.9 ± 0.59°C), whereas the mean for *Mabuya seychellensis* is 34.67 ± 0.63°C. Statistical comparison of the means using the *t* test shows that the mean Tb of *Mabuya* is significantly higher than that of both *Phelsuma* species ($P < 0.001$ in both cases), which are not significantly different to each other.

In Figs. 2, 3 and 4 the variations in cloacal temperatures compared to those of air and "substratum" are shown for each hour of the day for each species ("substratum" will be referred to in inverted commas as, for reasons discussed later, it is not considered to be an accurate measurement of substratum). The values shown represent the mean of all recordings taken within

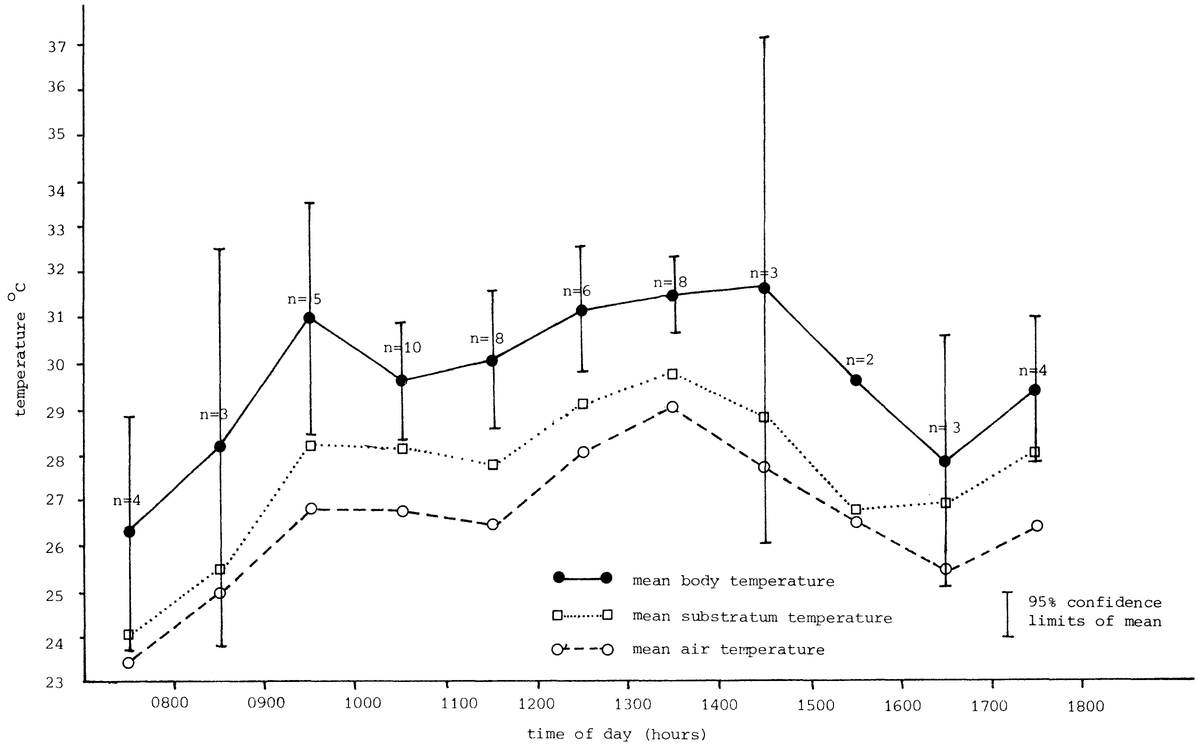


FIG. 3. *Phelsuma madagascariensis*—mean body, substratum and air temperatures during day.

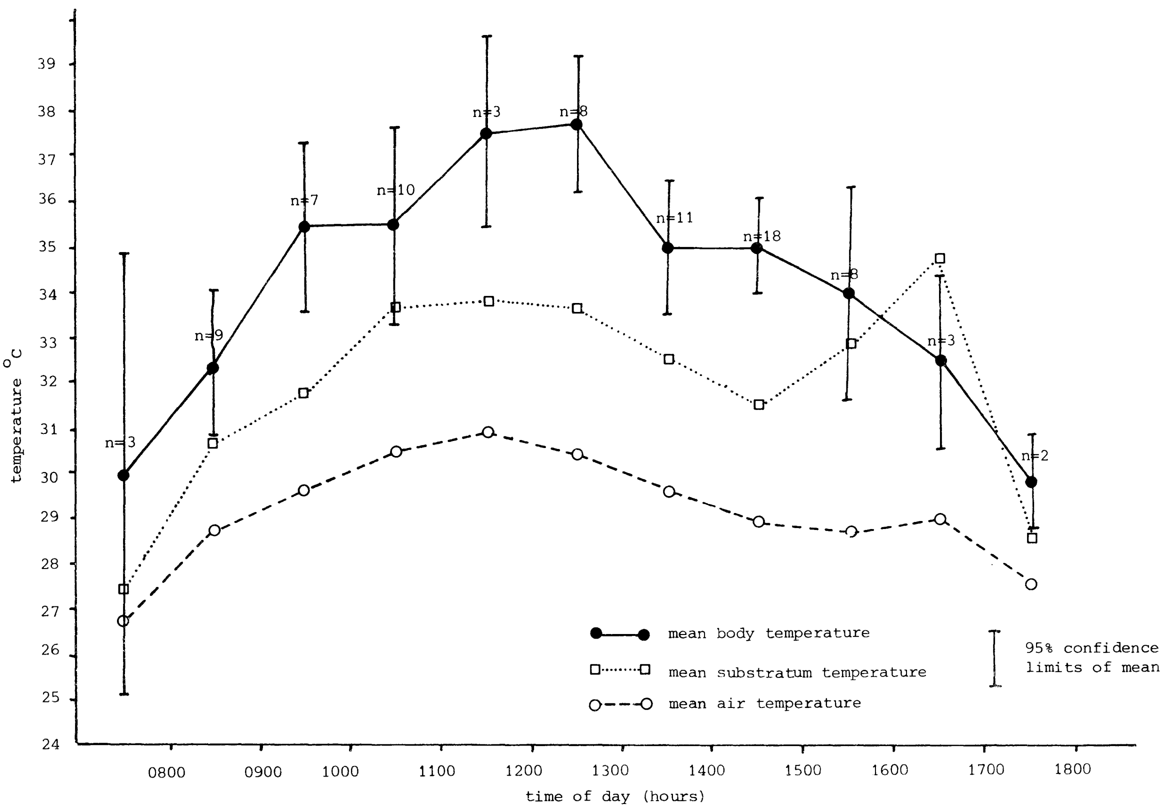


FIG. 4. *Mabuya seychellensis*—mean body, substratum and air temperature during day.

that hour, with data grouped from different days. Even so, the number of records for some time periods are low, and the 95% confidence limits shown for Tb are consequently large. Tb appears higher than both Ta and Ts for all three species, and also varies throughout the day.

Figure 5 compares the percentage of each species in the shade at different times of day. This was recorded for each individual immediately prior to capture. Comparing shade histograms for *P. astriata* and *P. madagascariensis* using χ^2 no statistical difference is found between these two species. However, when data from both species of *Phelsuma* is combined and compared to that of *Mabuya*, significant differences ($P < 0.01$) are found between these genera for each two-hour period from 0700 to 1700 hours. *Mabuya* is evidently a much more heliothermic lizard than *Phelsuma*, which spends a considerable proportion of each day in the shade.

In order to compare activity of each species during the day, the proportion of lizards active—*i.e.* walking—and resting at each time of day is represented in Fig. 6. Feeding was also occasionally observed in geckos immediately prior to capture, but as numbers were low, these figures have been omitted. In *Mabuya*, using χ^2 to test activity/resting against hours from midday—*i.e.* 1100–1300 compared to 1300–1500 + 0900–1100 and 1500–1700 + 0700–0900—significant associations are found ($P < 0.001$). In other words, skinks are significantly more active between 1100 and 1300 hours, when their Tb is also greatest (Fig. 4). It is not possible to test this in *Phelsuma* as the number of active individuals is too low.

A comparison of activity level between *Phelsuma* and *Mabuya* using χ^2 reveals that geckos are significantly less active between 0900 and 1500 hours than skinks ($P < 0.001$).

Attempting to relate *Phelsuma* activity to environmental temperatures, continuous observation results are plotted in Fig. 7a. The activity of five different individuals, 3 of one species and two of the other, were studied throughout the day, though all individuals were not always visible to the observer. Each gecko is plotted as being either in the sun or in the shade or unobserved. Environmental temperatures generally increase during the morning and cool down again during the afternoon. The figure illustrates that individuals operated between the sun and shade and suggests a slight degree of heliothermy. This is further indicated by Fig. 7b for which data have been extracted from 7a, showing an increasing amount of time spent in shade in the middle part of the day when environmental temperatures were highest.

DISCUSSION

Field data indicate the different thermal preferences of the two genera of lizards studied. All three species were found to have Tb higher than Ta most of the time. The skink, *Mabuya seychellensis*, emerges as a heliothermic lizard which can often be observed basking in the open sun, and shows increasing activity as Tb rises, suggesting that elevated body temperatures are required for efficient activity. However, it did not obviously exhibit discrete behaviour patterns for temperature regulation, as has been shown for example in *Amphibolurus inermis*, the desert dragon (Heatwole

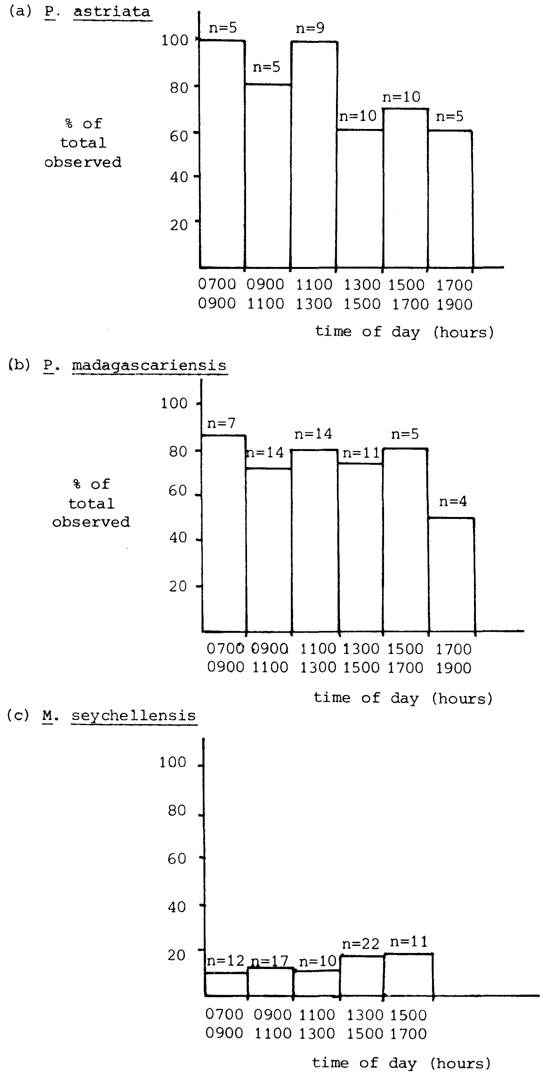


FIG. 5. Per cent of animals observed in shade during day.

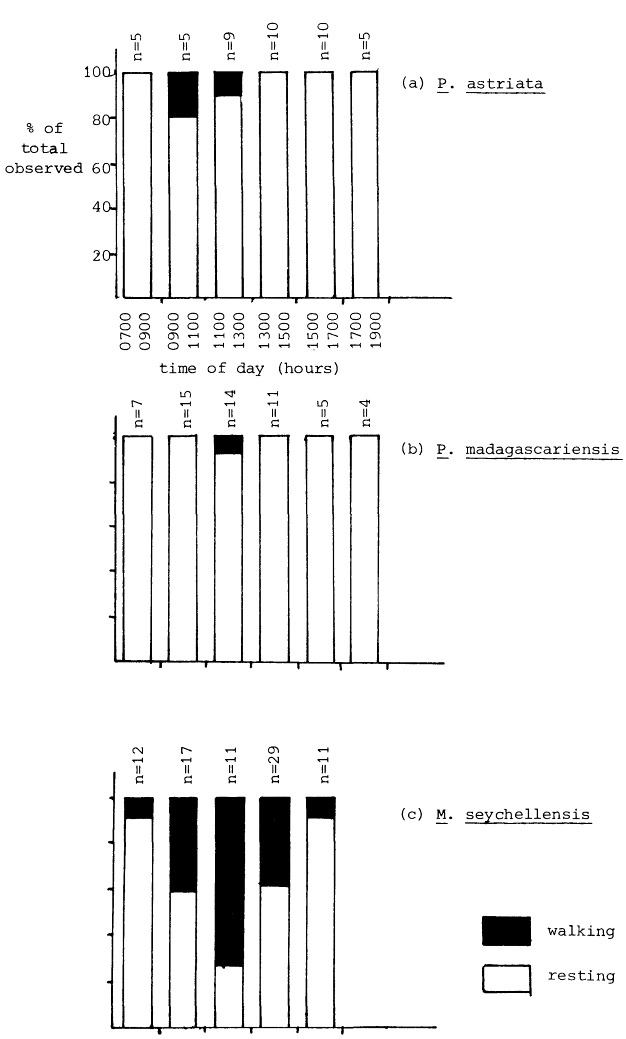


FIG. 6. Activity during the day.

1970), and did not apparently attempt to keep Tb between narrow limits for most of the day, although Fig. 1 shows a sharp cut-off at high temperatures (over 39°C). However, Tb continued to rise as air temperature increased in the middle of the day, without evidence of the skink seeking shade at this time to "cool off". This may indicate that during the study period, temperatures in the area never became sufficiently high, even in the middle of the day, to cause the skinks to actively regulate temperature by shuttling between sun and shade. In fact August is a relatively cool, windy month of the south-east wind season in Praslin, with temperatures rising during November–March in the north-west wind season. It is thus possible that thermal behaviour varies in different seasons of the year. Balinger *et al.* (1970) in their study of *Anolis limifrons* in Panamanian forests, found significant differences between mean Tb in the dry season compared with mean Tb in the wet season.

The mean temperature found for *M. seychellensis* is comparable to that found by Inger (1959) for *M. rudis* (32.76 ± 0.66°C) in forest vegetation in Borneo, where they were mainly observed along the edges of wide trails through the forest. Like *M. seychellensis*, *M. rudis* is a diurnal inhabitant of the floor stratum, though occasionally climbing up to about 2 m. In Praslin, as well as being found in garden vegetation and coconut plantations, *Mabuya* also occur in the hillside palm forest where open sunny areas for basking are less available. Temperature data for skinks in habitats with denser vegetation could indicate whether *Mabuya* is able to maintain an equally high mean Tb in such places. Bogert (1949) found a striking similarity in the means and extremes of body temperatures of lizards of the same genus in widely different habitats. This was also observed by Licht *et al.* (1966) in their study of western Australian lizards.

If lizards are to be categorised according to their thermal relations, as suggested by Ruibal, 1961, then *Mabuya seychellensis*, is clearly in the category defined as "heliothermic species that bask in the sun, absorb radiant heat, and are characterised by having a high body temperature (above 31°C)."

Following the same classification for lizard thermal relations, both species of *Phelsuma* studied would be categorised as "non-heliothermic lizards that do not bask and have low mean Tb (below 31°C)". This apparently conflicts with results actually obtained in the field, which suggested that, rather than being purely thigmothermic, the geckos are somehow maintaining a mean Tb higher than that of both the "substrate" and

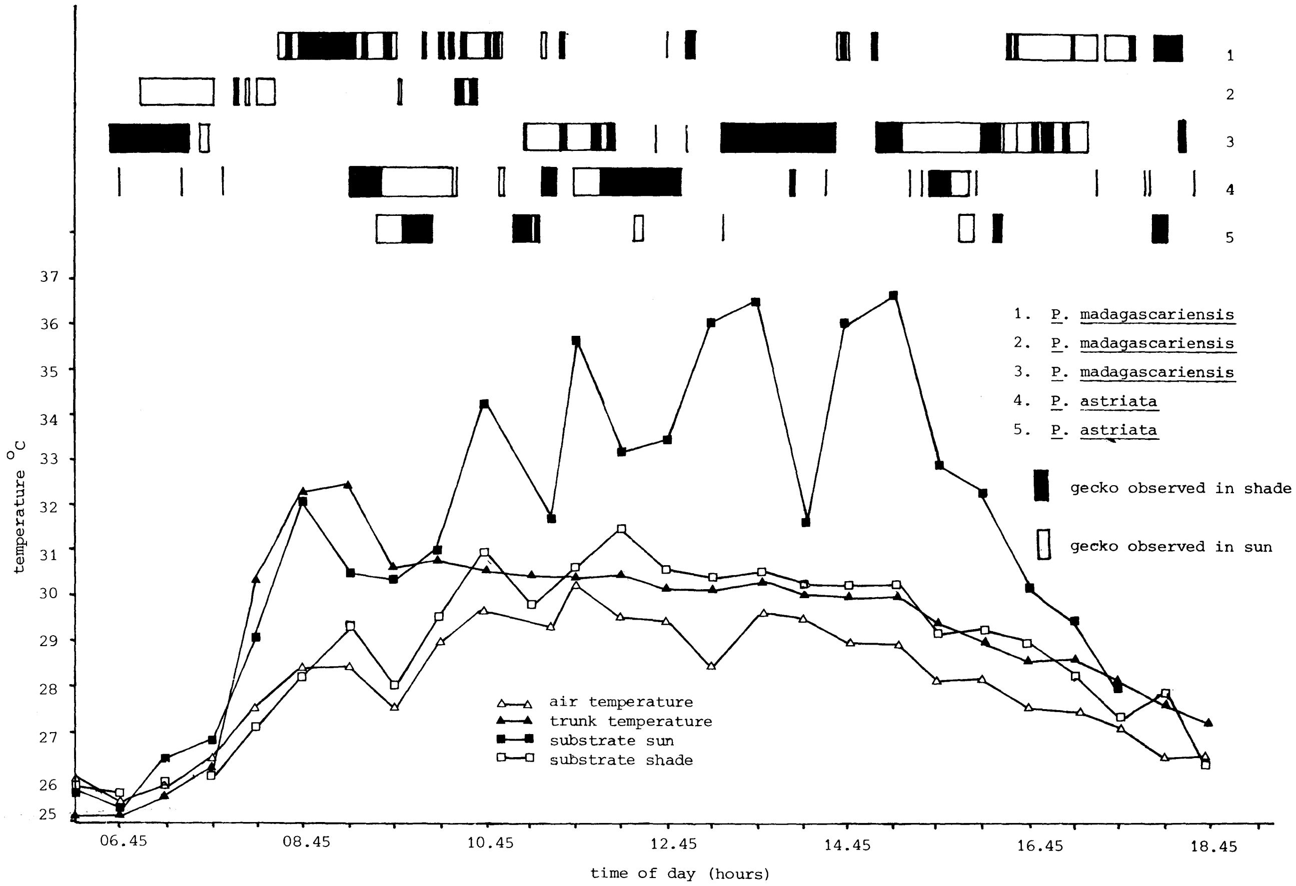


FIG. 7a. Daily course of temperature and activity of geckos in study tree.

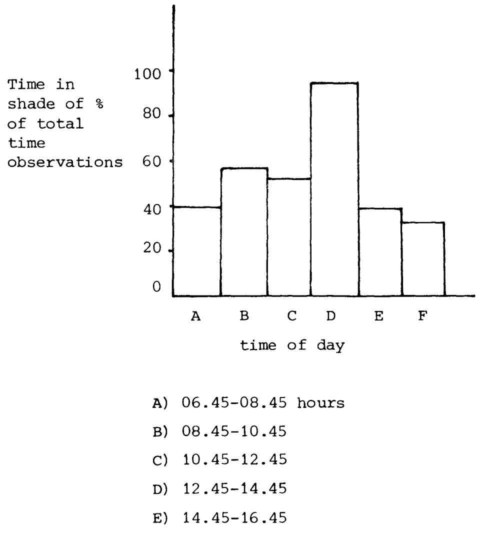


FIG. 7b. Analysis of gecko observations in Fig. 7a

the air. There are several possible explanations for this discrepancy.

1. The geckos may be spending time basking out of view. This would be most likely during the early morning and in the evening, when there are fewer field recordings anyway. In the forest type of vegetation where *Phelsuma* was studied, most of the available basking sites are high up amongst the leaves, and geckos would be less likely to be observed and caught there, so that the data may be biased. The fact that Fig. 7a suggests more time spent in the sun than Fig. 5 may indicate that geckos in basking sites in the palm forest vegetation were under-recorded. However, this explanation seems unlikely in view of the fact that data collected in the early morning in the Vallee de Mai already suggested that mean Tb of the geckos was above that of air and "substrate", at a time when, at the study area, the sun was not in a position to illuminate the area, therefore no basking sites were available.

2. The other possible explanation comes from the recording of the so-called "substratum" temperature. Almost all the "substratum" data, taken at the site of capture, were on the surface of the petiole or frond of palm leaves, or on the wooden supports of the viewing lodge. In all cases it was impossible to actually insert the bulb of the thermometer into the "substratum", as would be possible in say, sand or earth, so that the temperature recorded was really a compromise between that of the surrounding air and that of the "substratum". "Substratum" temperature was in fact air temperature adjacent to "substratum". "Substratum" temperatures were thus subject to inaccuracy, and true substratum temperatures were probably considerably higher than the data actually suggest, and probably were very similar to the recorded body temperatures of the geckos. Heatwole (1970) also points out the difficulty of obtaining accurate substratum temperature recordings in this situation. More reliable recordings of substratum temperature could be obtained by actually inserting a fine probe into the substratum and connecting it to a thermorecorder.

This would appear to be the most likely interpretation of the data. If accurate substratum temperatures could be obtained they would probably be very similar to that of the body temperature of the geckos. Thus *Phelsuma* are probably largely thigmothermic and are simply assuming the temperature of the substratum, with Tb consequently varying in relation to this during the day. Any elevation of Tb above that of the substratum is probably due to spending short periods on sunlit substrates as observed in Fig. 7a. Ruibal (1961) in his discussion of lizards in this category, suggests that most thigmothermic lizards will probably be facultative heliotherms, capable of basking to raise body temperatures when air temperatures drop below 25 °C. However, since temperatures in the study area were rarely recorded this low, this may not be necessary for *Phelsuma*. Results from continuous observation (see Fig. 7a) did show that the geckos operated between sun and shade sites.

Transmitters attached to the geckos and giving continuous accurate information on body temperatures in the field under varying weather conditions, could produce some interesting results. However, there is little evidence for a complex repertoire of thermoregulatory behaviour in *Phelsuma*, such as basking, changing posture, perching, shade seeking, burrowing, flattening, panting and colour change as is seen in some heliotherms (Heatwole, 1970). In many respects, they seem similar to lizards of the genus *Anolis*, as studied by Heatwole *et al.* (1969) in various Caribbean islands, Panama and Venezuela. Daily activity is observed to begin almost with first light and may continue until almost dusk. Most daylight hours are spent in stationary resting positions on various parts of the tree. They are thus characterised by ill-defined activity periods, nearly coincident with the duration of light and by spending inactive periods in exposed situations demanding quick responses to disturbance. Thermoregulation is not precise and body temperatures vary with time of day. Forest-living *Anolis allogus* and *Anolis lucius* in Cuba (Ruibal, 1961) were found to have mean Tb of 29.2°C and 29.3°C, respectively—almost identical to those of *Phelsuma*.

There is little data available for comparison with other members of the gekkonidae. Field measurements of body temperatures for the desert banded gecko, *Coleonyx variegata* give a mean Tb of 24.7°C, for *Phyllodactylus tuberculosus* 22.7°C and for *Chondrodactylus angulifer* 26.2°C (Brattstrom, 1965), but there is little information as to how this relates to the general ecology of the species. Bustard (1967) showed active thermoregulation of the nocturnal *Gehyra variegata*, under cover during the day. In general geckos are confined to the warmer areas of the world where temperatures remain sufficiently high after darkness to permit activity. Although there is little data on nocturnal geckos in the field at night, observations by Licht *et al.* (1966) suggested that there was a close correspondence between mean Tb and air temperature. Observations by the present authors on *Gehyra mutilata* in Praslin also indicated this.

It seems likely that diurnal geckos have evolved from nocturnal forms, thus *Phelsuma* apparently has thigmothermic ancestors. Thus although *Phelsuma* appears to be largely thigmothermic, it appears to have a higher mean Tb than nocturnal forms which have been studied, and also spends some time in the sun. It is thus possible that *Phelsuma* is evolving towards a more heliothermic form, which is feasible for a diurnal gecko.

ACKNOWLEDGEMENTS

The field work was carried out during the 1978 University of Aberdeen Seychelles Expedition and we would like to thank the numerous sponsors of this expedition.

We would also like to thank Gordon Steele for help with the field work and Martin Nicoll for logistic support.

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LETTER TO THE EDITOR

COLOUR VARIATION IN THE NATTERJACK

In his excellent survey, *The British amphibians and reptiles* (London: Collins, 1951), M. Smith noted that no specimens of the natterjack toad, *Bufo calamita*, completely lacking the yellow vertebral stripe, so characteristic of this species throughout its range, had been recorded from the British Isles. The discovery of a stripeless natterjack in 1970 while I was engaged in field-work on this species in Scotland may therefore be of interest.

The specimen, an adult male with a snout-vent length of 5.2 cm, was found on the coast of Dumfreisshire (the map reference is known to the Editor) in August 1970. Although the median raphe was evident on close inspection, the yellow vertebral stripe was completely absent. The specimen was photographed and then released at the point of capture.

Although, as Smith noted, the vertebral stripe may occasionally be absent in individuals of *B. calamita* from southern France and the Iberian Peninsula, this specimen of a stripeless British natterjack is the only one I am aware of.

M. J. Boyd
Department of Natural History
Kingston upon Hull Museums
Kingston upon Hull
North Humberside
16 March 1979

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 35–36

BOOK REVIEWS

INTERNATIONAL ZOO YEARBOOK, Volume 19. Edited by P. J. S. Olney (1979). 434 pp. London: The Zoological Society of London. £17.

A common, and well-justified, complaint is that no modern book exists which deals in detail with the husbandry of reptiles. Volume 19 of the authoritative International Zoo Yearbook should do much to satisfy this demand. As in volume 9, published in 1969, the first section of this year's edition (130 pages) is dedicated to Reptiles in Captivity. The range of topics covered in the twenty-nine papers presented varies from the esoteric, "The western Australian swamp tortoise *Pseudemydura umbrina* in captivity", to the general, but very pertinent, "Notes on reproductive patterns of reptiles in relation to captive breeding".

Although the Zoo Yearbook is a well-established series in professional zoological circles, it is not so readily accepted by the amateur. This may be due to the erroneous assumption that the text is too technical or scientific for the general reader. In fact, the Yearbook is eminently readable and offers excellent value to anyone who professes interest in the care and breeding of animals in captivity.

D. R. BLATCHFORD

LIZARDS—A STUDY IN THERMOREGULATION. By R. A. Avery (1979). 56 pp. (Studies in Biology Series, No. 109). London: Edward Arnold. £1.80 (paperback).

While one advantage of the mini-book approach to knowledge may be that it allows the student to buy only that subject matter which he can actually get around to reading; another, and perhaps far more important one, is that it gives us all a good and reasonably priced opportunity to widen our horizons. With the publication of this splendidly clear and concise account of thermoregulation in the lizards, no student of mammalian thermoregulation, even a medical student, will have a valid excuse for thinking that the capacity to thermoregulate is confined to the birds and mammals.

The text reads well, and almost covers the full span of the salient features of subject matter. In two areas the text seems to be deficient. Dr Avery might have indicated that while much of the central nervous component of thermoregulation seems to have existed already in the reptilian ancestors of the mammals and birds, there is little or no evidence in contemporary reptiles of a progression, within the class, from bradymetabolism and tachymetabolism, which made the transition from ectothermy to endothermy possible. The similarity of the higher levels of metabolism of birds and mammals is intriguing since the upward shift would seem to have occurred independently in the two post-reptilian evolutionary lines. The other omission is any mention of the evidence of a pyrogen-induced upward shift in the preferred body temperature in reptiles. This evidence supports the contention that the basic central nervous machinery for thermoregulation, including the capacity to respond to pyrogens, is well established in contemporary reptiles, and may have existed already in the reptilian ancestors of the birds and mammals.

Notwithstanding these comments, Dr Avery's book makes informative and enjoyable reading. The British Herpetological Society wants the review copy back for its library, so I am buying my own copy. Since we have no lizards in Alaska, this surely constitutes a strong recommendation. (Incidentally, are there really lizards in Norway above the Arctic Circle—as is stated on page 41?)

JOHN BLIGH

SYSTEMATICS AND NATURAL HISTORY OF THE AMERICAN MILK SNAKES, *Lampropeltis triangulum*. By Kenneth L. Williams, (1978). 258 pp. Milwaukee Public Museum Publications in Biology and Geology No. 2. £14 (paperback).

Quite simply this is the most comprehensive and exhaustive treatise on this species ever to be published. The text is detailed and meticulous, and covers all the known subspecies of the wide-ranging snake. Although only ten subspecies are illustrated in colour plates, all twenty-three are shown in elegant line drawings; a very useful complement to the diagnostic keys.

Interest in these snakes, which must rate amongst the most beautiful in the world, is high and this volume is an essential addition to the libraries of all students of American herpetofauna.

D. R. BLATCHFORD

BOAS AND OTHER NON-VENOMOUS SNAKES. By Werner Franck (translated by U. Erick Friese) (1979). 95 pp. TFH Publications. £1.

The original German edition of this book was reviewed by Dr Elkan in the previous issue of the journal. The translated version of this reputable text has been inflicted with a whimsical and wholly-inappropriate title that exemplifies the dual nature of the end-product since a large proportion of the book is devoted to illustrations and lists of venomous snakes. The numerous colour and monochrome illustrations vary from excellent to abysmal but it is the captions that will cause most confusion. The incorrect naming of species, although annoying, is forgiveable but the legends rarely complement the text and at times seem in direct conflict; the final result is a lop-sided debate.

D. R. BLATCHFORD

Second Revised Annotated Checklist With Keys to the Snakes of Hong Kong. By J. D. Romer (1979). 23 pp. Memoirs of the Hong Kong Natural History Society, No. 14.

Copies of this publication may be obtained on application to: The Hong Kong Natural History Society, c/o Department of Zoology, University of Hong Kong, Hong Kong. A crossed postal order for £2 should be enclosed to cover the cost of a single copy sent by surface mail.

ANNOUNCEMENTS

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

The required six months' notice is given of the possible use of plenary powers in connection with the following names listed by case number: (see *Bulletin of Zoological Nomenclature* **35,** part 3, 19 February 1979).

1704 *Coluber chiametla* Shaw, 1802 (Reptilia, Serpentes): revived proposal for suppression under the plenary powers.

Comments should be sent in duplicate to R. V. Melville, The Secretary, International Commission on Zoological Nomenclature, c/o British Museum (Natural History), Cromwell Road, London SW7 5BD.

The following *Opinion* has been published recently in the *Bulletin of Zoological Nomenclature* **35,** part 4, 31 May 1979.

1117 (p. 209) Refusal of request for two rulings concerning the names of species of *Sphaerodactylus* (Reptilia, Lacertilia).