Papéis Avulsos de Zoologia

THE INFLUENCE OF FORAGING MODE AND PHYLOGENY ON SEASONALITY OF TROPICAL LIZARD REPRODUCTION

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Abstract

A model incorporating foraging mode of tropical lizards, resource availability, and habitat patchiness predicts that sit-and-wait foragers should be seasonal in reproduction whereas widely foraging species should have prolonged reproductive seasons.

Data on sympatric tropical caatinga lizards of various ecologies reveal that 1) widely foraging species are habitat generalists and reproduce continually, 2) sit-and-wait species are habitat specialists and, with the exception of the gekkonids, exhibit seasonal reproduction, 3) among the seasonally reproducing sit-and-wait foragers, reproductive seasons are not synchronous, and 4) the sit-and-wait foraging gekkonids reproduce continually, possibly a consequence of low energy demands per episode for reproduction.

Data from other studies on tropical lizards are mostly supportive of the model. It is concluded that much of the variation in seasonal patterns of reproduction in tropical lizards may be explained by a resource availability model that incorporates foraging mode. Nevertheless, there is an interaction between foraging mode and phylogeny, and certain taxa appear constrained in their reproductive response to seasonality.

Introduction

Foraging mode in lizards has recently assumed central importance in the interpretation of such ecological and life history characteristics as prey types and amounts eaten (Huey and Pianka, 1981), energy utilization (Anderson and Karasov, 1981; Bennett and Gorman, 1979), escape mode (Huey and Pianka, 1981; Vitt and Congdon, 1978), and relative clutch mass (Vitt and Congdon, 1978; Vitt and Price, 1982). Even aspects of tail loss adaptations in lizards may be associated with foraging mode (Vitt, 1983a).

Differences in nearly every aspect of the biology of lizards should be at least partially influenced by the striking differences in foraging between sit-and-wait (ambush) and widely foraging lizards (see also Magnusson et al., 1985). This study investigates the relationship between foraging mode and seasonality of reproduction among lizards species. I first present a graphical model suggesting a mechanism by which foraging mode might be expected to influence seasonality of reproduction. Secondly, I test the fit of data on a taxonomically diverse community of tropical lizards studied simultaneously to eliminate error associated with

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temporally separated samples. Additional data from other tropical lizards studied are also considered. Finally, I consider specific assumptions of the model, particularly in respect to the confounding interaction of foraging mode and phylogeny (see Dunham and Miles, 1985).

<div align="center">METHODS</div>

The model

The model first considers resource (food) availability to individual lizards as a function of foraging mode. Specifically, it assumes that 1) food is distributed unevenly in the habitat and that sets of resources are associated with identifiably different habitat patches; 2) individual lizards that are sit-and-wait foragers spend most of their time in a habitat patch whereas a widely foraging individual encounters many patches during the course of its foraging activity; 3) resource availability, from the point of view of an individual lizard, directly influences reproductive investment *or* the interaction between immediate reproductive investment and current survival; and 4) foraging mode is relatively independent from other variables (see discussion).

Supportive data

Examining the relationship between foraging mode and seasonality of reproduction in temperate zone lizards would be difficult because season length and temperature become major limiting factors, thus obscuring seasonal variation attributable to foraging mode. The primarily carnivorous lizard fauna of the semi-arid caatinga of northeast Brazil is remarkably well suited for investigating this relationship because (1) the fauna is taxonomically and ecologically diverse, (2) the thermal environment is suitable year round for lizard activity and reproduction, and (3) due to seasonality in rainfall, there is potential for seasonal fluctuations in resource availability.

I rely primarily on two kinds of reproductive data: presence of oviductal eggs in female lizards as an indicator of immediate reproductive activity and size of fat storage organs (fat bodies) corrected for effect of body size (when necessary) as an indicator of the lizard's ability to gather resources and convert those resources to stored energy. Pertinent to this analysis, females were collected monthly from March 1977 through February 1978, necropsied, and examined for the presence of oviductal eggs or enlarged vitellogenic follicles. Presence of corpora lutea was also recorded. When females were killed (by injection of the brain with Nembutal or by shooting and placing carcasses on ice), measurements of snout-vent length (mm) and body mass (g) were taken and eggs and fat bodies (if any) were removed and preserved in 10% formalin. Upon return to the United States, preserved fat bodies and eggs were rolled dry and weighed to 0.001 g. In monthly samples where fat body mass (preserved) was correlated to female SVL, adjusted means were calculated by analysis of covariance with SVL as the covariate. Relative clutch mass was determined as:

<div align="center">total clutch mass (preserved) / total lizard mass (fresh)</div>

recognizing problems associated with use of preserved weights (Vitt et al., 1985).

These data represent a small subset of a much larger data set on reproductive tactics of caatinga lizards. Because the additional data are irrelevant to the points addressed here, they are not included. More complete data can be found elsewhere (Vitt, 1981, 1982a, 1982b, 1983a, 1983b, 1986; Vitt and Blackburn, 1983; Vitt and Goldberg, 1983; Vitt and Lacher, 1981).

To establish habitat specificity as an indicator of patch use, I calculated niche breadth as:

$$B = 1/\_ \sum p_i^2$$

where p is the proportional utilization of the ith resource (the resource being habitat or microhabitat; Simpson, 1949). Data on microhabitats and habitats were treated independently, and the habitats and microhabitats were chosen a priori. These data and other pertinent information have already been reported (Vitt, 1981, 1983a).

As an indirect indicator of seasonality of resource availability, I used climatic data summarized from the literature and collected during the period of the field studies. Past studies have shown a relationship between rainfall and insect abundance in tropical habitats (Janzen and Schoener, 1968; Stamps and Tanaka, 1981). Annual rainfall varies from 400-1000 mm and the long-term pattern is unpredictable (Jones and Kearns, 1976). The annual rainfall pattern during this study was similar to long-term averages, with the dry season (months receiving < 50 mm rain) extending from June through late November. The mean difference between maximum and minimum daily air temperatures was 10.19 ± 1.40 C ($\bar{x}$ ± SE) and there was no significant thermal difference between wet and dry seasons during this study (1977-78; Vitt and Goldberg, 1983).

Finally, I consider data collected independently by other investigators in various parts of the New and Old World Tropics.

<center>RESULTS AND DISCUSSION</center>

Model predicting seasonality in reproduction

A predictive model integrating foraging mode and seasonal resource availability in habitat patches can be generated as follows. Consider lizards A-D (Fig. 1) as individual sit-and-wait predators which feed on prey which enter their field of vision. Prey available to individual lizard A, B, C, or D depends on the frequency with which prey enter that particular habitat patch and the distance the individual lizard will move to capture a prey item. The latter is presumably determined by risk and energetic cost of capturing prey balanced by the energy gained from the prey. Also, because sit-and-wait foraging lizards rely primarily on vision to detect prey (Huey and Pianka, 1981), prey which might be under the surface of the substrate are essentially unavailable. From the perspective of the sit-and-wait foraging lizard, the environment is coarse grained with only specific patches (sites A-D) suitable for territorial defense, feeding, predator escape, and mate sequestering.

Lizard E is an individual of a widely foraging species. Widely foraging species tend not to defend perches or well defined territories (Stamps, 1977) and forage over relatively large areas searching for prey (Anderson and Karasov, 1981; Huey and Pianka, 1981). The same habitat that was coarse grained to sit-and-wait lizards is fine grained to the widely foraging lizards. An individual has the option of moving through the habitat in search of rich resource areas. Based on resource availability, it can adjust the amount of search time spent in any one area and consequently effect its own resource availability. This latter point is the critical difference between a sit-and-wait lizard and a widely foraging lizard in terms of the potential consequences to seasonal patterns of reproduction.

More explicitly, if we consider four sit-and-wait species, A-D (Fig. 2), each adapted to a particular kind of microhabitat (patches A-D), various hypothetical patterns of seasonal resource availability in these patches can be generated. These seasonal variations should be associated with the structural diversity of the patches and the particular vegetation or substrates which would provide a resource base for invertebrates used by lizards. For example, lizard species A might use rocks as perches and be restricted to resources available in the patch (A) associated with the rock. Species B might use tree trunks as perches and be restricted to resources available in the patch (B) associated with the tree trunk, and so on. Lizard species E, a widely foraging species, can, by shifting patches with season, spend most of the year in available patches having the highest resource availability. It can also find invertebrates in litter and the soil that may be unavailable to the sit-and-wait foragers.
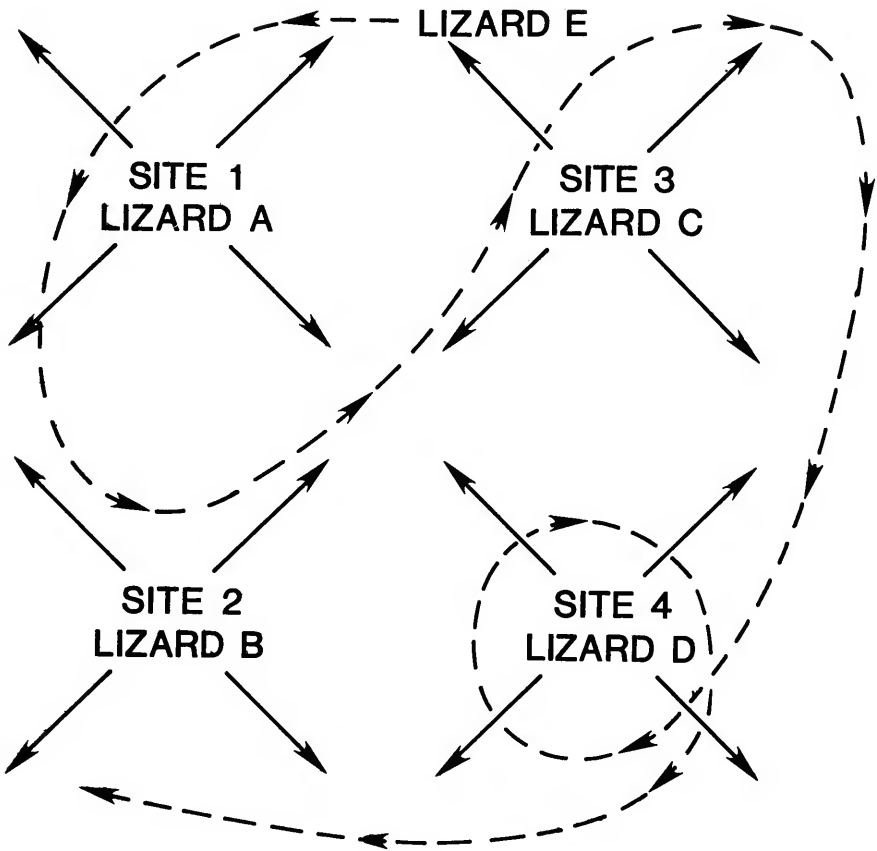
Fig. 1. Model describing hypothetical differences in spatial patterns of resource acquistion between sit-and-wait foraging individuals (A-D) and a widely foraging individual (E). See text for explanation.

The essence of this model lies in the association between foraging mode and predator escape tactics. Sit-and-wait species tend to be cryptic in coloration, morphology, and behavior, and consequently closely match the habitat patches they occupy. They rely on crypsis to avoid detection by predators, or if crypsis fails, they usually need to move only short distances to refugia for escape. Consequently, foraging away from their patch, or even moving excessively within the microhabitat should greatly increase risk of predation for sit-and-wait species. Associated with considerable movement during foraging in widely foraging species is the ability to detect potential predators (wariness) and move rapidly over considerable distances to escape attacks (Huey and Pianka, 1981; Vitt and Congdon, 1978). These adaptations presumably counter-balance the risk of mortality associated with this foraging mode. Thus, only when resourse availability in all patches is low would a response of reduced reproduction be expected in the

widely foraging species. It is notable that actual burst speed is greater in sit-and-wait lizards as compared to widely foraging species (Huey et al., 1984) suggesting the importance of rapid short movement when crypsis has failed and a predator is at close range.

The assumptions of this model (see Methods) appear reasonable, based on published empirical data. Numerous studies have addressed the issue of prey distribution, either directly or indirectly. These studies (Janzen and Schoener, 1968; Dunham, 1981; Stamps and Tanaka, 1981; Vitt et al., 1981) indicate that prey are not distributed evenly in space or time. A large body of data (reviewed by Stamps, 1977) reveals that most sit-and-wait lizards are territorial and use relatively small home ranges compared to widely foraging species which patrol large home ranges (see also Anderson and Vitt, in press).

It is well known in temperate zone lizards that resource availability can influence clutch size, clutch frequency, and even egg size in different parts of the reproductive season (Ballinger, 1977; Dunham, 1981; Martin, 1977; Nussbaum, 1981).

Caatinga lizard reproduction

Of the 11 caatinga species for which I have complete data, seven are sit-and-wait predators, three are widely foraging predators and one appears to use a combination of sit-and-wait and widely foraging tactics (Table 1). I consider species which use distinct perches, spend most of their time not moving, and pursue prey items sighted from the perch as sit-and-wait predators. Species which continually move through the habitat, spend most of their time actively searching
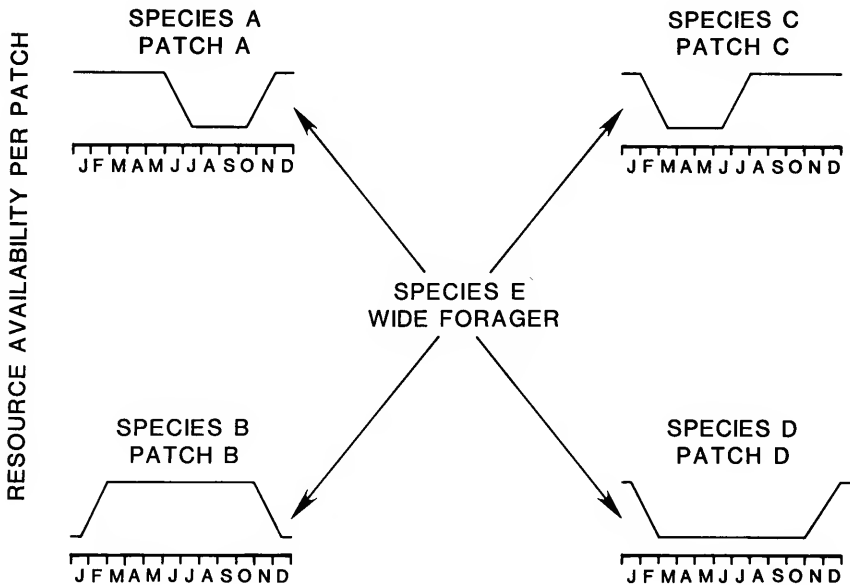

Fig. 2. Model showing that given seasonal resource variation in different habitat patches (A-D) occupied by different species of sit-and-wait predator (A-D), a widely foraging predator (E) should be capable of enhancing its own resource availability by seasonally choosing patches with high resource availability (see text).

Table 1. List of species of caatinga lizards including information on foraging mode, general occurrence, and niche breadth based on Simpson's (1949) index.

Family and Species	Foraging Mode	Niche Breadth		Occurrence
		Habitat	Microhabitat	
Gekkonidae				
Gymnodactylus geckoides	Sit-and-wait	low	low	Saxicolous-Terrestrial
Hemidactylus mabouia	Sit-and-wait	1.00	1.00	Buildings
Lygodactylus klugei	Sit-and-wait	1.26	1.25	Arboreal
Phyllopezus pollicaris	Sit-and-wait	1.15	1.33	Saxicolous
Iguanidae				
Tapinurus semitaeniatus	Sit-and-wait	1.09	1.21	Saxicolous
Polychrus acutirostris	Sit-and-wait	1.13	1.13	Arboreal
Tropidurus hispidus	Sit-and-wait	2.65	3.17	Ubiquitous
Scincidae				
Mabuya heathi	Mixed	——	——	Terrestrial
Teiidae				
Ameiva ameiva	Widely foraging	3.78	3.24	Terrestrial
Cnemidophorus ocellifer	Widely foraging	3.51	2.94	Terrestrial
Gymnophthalmus multis-cutatus	Widely foraging	1.47	3.83	Terrestrial

[1] All individuals sighted and/or collected were found in piles of relatively small rocks.
[2] All individuals of this introduced gecko were found on sides of buildings.

for prey, and generally do not use distinct perches I consider to be widely-foraging predators. The categorical classification, in the absence of quantitative data on salient aspects of foraging are warranted here for the following reasons. First, I am interested in potential differences between species which are near the endpoints of a hypothetical continuum, and I am not interested in species which might fall somewhere near the nebulous center of the continuous. Thus the variation between my categories is great enough to mask variation within categories (and such variation certainly occurs; Magnusson et al., 1985). The species and higher taxa that I include within each category are representative of those which other researchers have independently categorized similarly. For example, Dunham and Miles (1985) recently performed an analysis of lizard reproductive and life history data from the extant literature using foraging mode as a binary variable. The groups of lizards and species (where overlap occurs) placed in each foraging mode category are identical to those I independently assigned. There are other examples like the latter, but suffice it to say that there appears to be general agreement among researchers who conduct field studies on complex lizard communities.

Species which are sit-and-wait foragers tend to have relatively narrow habitat and microhabitat niche breadths whereas species which are widely foraging have relatively wide niche breadths (Table 1). The iguanid lizard *Tropidurus hispidus* superficially appears to be an exception in that it is a sit-and-wait foraging species yet it has a wide habitat and microhabitat niche breadth (in previous publications I have called this species *T. torquatus*. A recent revision of the taxonomy of *torquatus* group of *Tropidurus* [Rodrigues, 1987] assigns the populations I studied in Pernambuco to the species *T. hispidus*). Individuals of *T. hispidus* do, however, remain

in specific patches, but different individuals select different kinds of perches thus yielding high breadth values. This is quite different from the situation found in the widely foraging species. Given individuals of all of the widely foraging species can be observed in a large number of patches and there do not appear to be any sort of patches that are defended from conspecifics as is usually the case in the sit-and-wait foraging species (see Stamps, 1977). Thus sit-and-wait species are habitat and microhabitat specialists whereas widely foraging species are habitat and microhabitat generalists (see also Vitt and Price, 1982). Thus empirical data on caatinga lizards support the second assumption of the model. Note also that there is an apparent phylogenetic bias; iguanids and gekkonids are sit-and-wait foragers and teiids are wide foragers.

Data on egg production (Fig. 3) reveal that local populations of gekkonids and teiids produce eggs nearly year round. The three iguanids are seasonal in reproduction, but to varying degrees even though all are active year round. Data for *Mabuya heathi* are not included in Fig. 3. *Mabuya heathi* is an exceptional species reproductively. Females synchronously ovulate tiny ova, there is little growth in the ova for the first 4-5 months of development, a chorioallantoic placenta forms, rapid embryonic growth takes place during the 6th-10th month following ovulation, and broods are produced synchronously by all females in the population (Vitt and Blackburn, 1983). Thus, all females of this viviparous species produce broods during a relatively short time period (late September - mid November). These lizards are therefore highly seasonal in reproduction.

The sample sizes for *Hemidactylus mabouia, Phyllopezus pollicaris,* and *Gymnophthalmus multiscutatus* are relatively small and the first two are not included in Fig. 3. Female *H. mabouia* contained oviductal eggs in January and near ovulatory-sized vitellogenic follicles during October, January, February, May, and June. On a return trip in March of 1982, females with oviductal eggs were also collected. Female *P. pollicaris* contained oviductal eggs during December, June, July, August, September and near ovulatory-sized follicles during December and from March-September. Thus, it appears that reproduction in the gekkonids and the microteiid is continuous for the most part. During November-January no *Ameiva ameiva* contained oviductal eggs; however, 14.2, 12.5, and 15.4 per cent, respectively, of the females contained corpora lutea suggesting recent deposition of eggs. Thus, I consider reproduction continuous for this species as well. Females of *Cnemidophorus ocellifer* contained oviductal eggs during every month except June and thus reproduction is continuous even though the proportions of females breeding at any one time varies.

In summary, all of the widely foraging species reproduce nearly continuously. Within the sit-and-wait foragers, the gekkonids appear to reproduce continually whereas the iguanids are seasonal with *Tapinurus semitaeniatus* (formerly *Platynotus semitaeniatus;* Rodrigues, 1984) and *T. hispidus* reproducing over an extended time period, but *Polychrus acutirostris* reproducing within a very restriced time period. The one species of viviparous skink produces broods over a very short time period.

Caatinga lizard fat cycles

None of the gekkonids, nor the microteiid *G. multiscutatus,* contained fat bodies at any time of the year. There were varying degrees of seasonality in fat storage in the macroteiids, (*A. ameiva* and *C. ocellifer*), the three iguanids (*P. acutirostris, T. semitaeniatus,* and *T. hispidus*), and the skink (*M. heathi*) (Fig. 4). Although fat storage in all of these species was cyclical to differing degrees, it is clear that the species with seasonal reproduction (*P. acutirostris, T. semitaeniatus, T. hispidus,* and *M. heathi*) also exhibited the greatest seasonal variation in fat storage often including time periods with near zero fat storage. The macroteiids that reproduced continually showed *relatively* low variation in fat storage with season when compared to the iguanids and the scincid. Among the caatinga species that store fat in abdominal fat bodies, it is apparent that during peak reproductive periods, fat bodies tend to be smaller than during non-reproductive periods (compare Figs. 3 and 4).
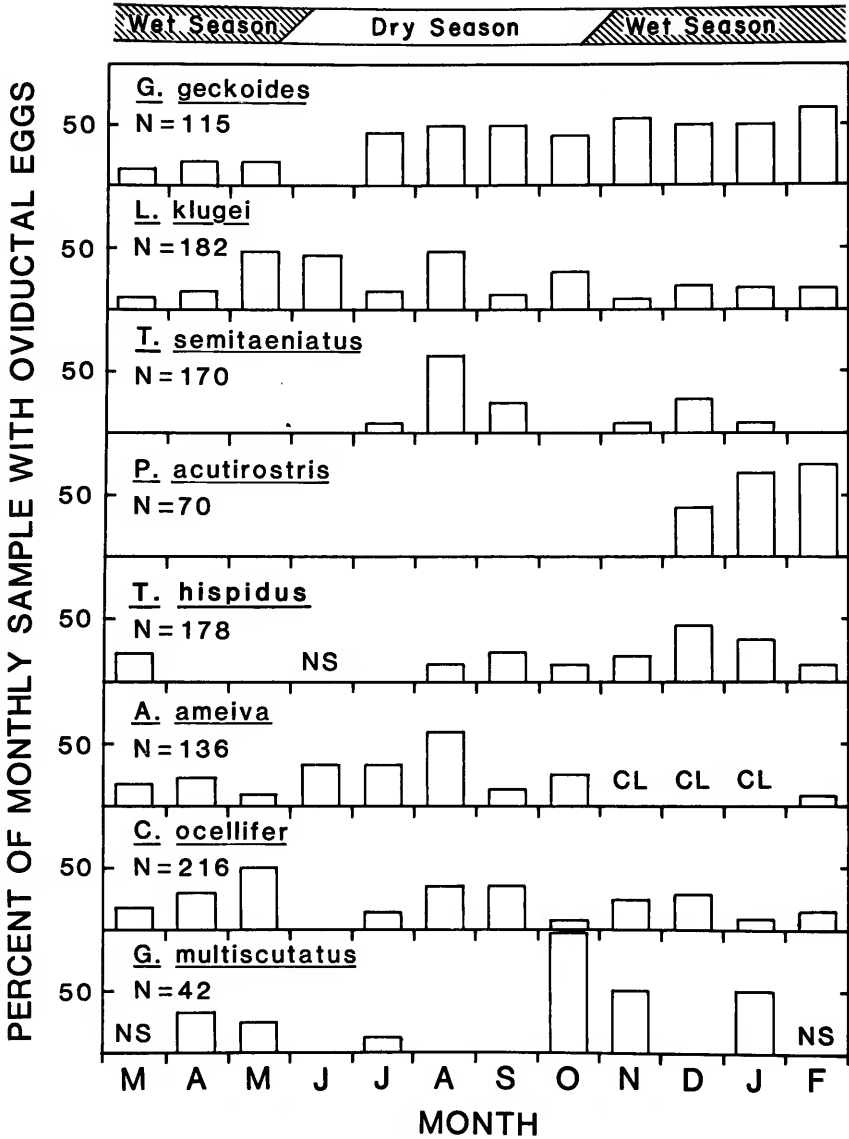
Fig. 3. Seasonal distribution of the percentage of monthly female lizard samples containing oviductal eggs in eight sympatric tropical lizards. The total number of adult females sampled per month is shown above each bar. NS indicates no sample for a given month, and CL indicates that females contained corpora lutea, indicative of recent clutch production.
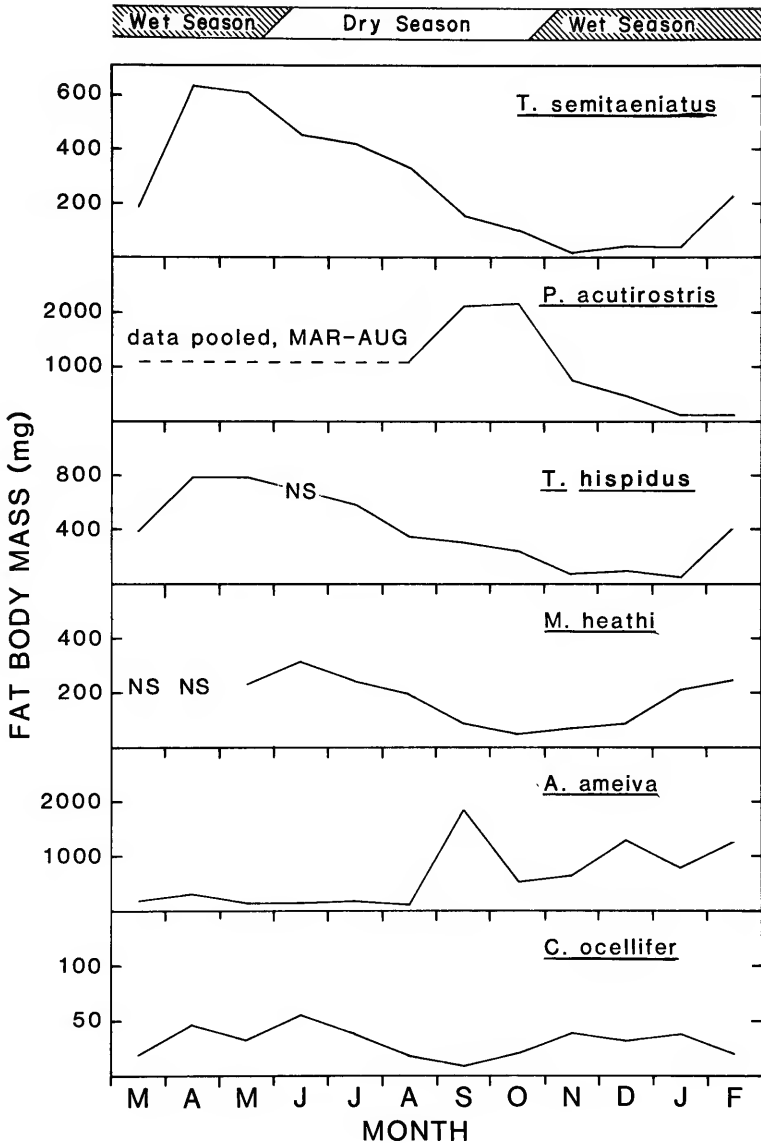
Fig. 4. Seasonal cycle of fat bodies in females of six sympatric tropical lizards. Sample sizes are the same as in figure 3. NS indicates no sample for a given time period.

Caatinga lizard synthesis

Seasonality in rainfall should have an overall effect on resource availability with the dry season having relatively low insect resources compared to the wet season (Janzen and Schoener, 1968; Stamps and Tanaka, 1981). The sit-and-wait foragers exclusive of the gekkonids (see below), show distinct seasonality in fat storage and reproduction. This is consistent with the hypothesis that resource availability for these sit-and-wait species in not constant throughout the season. In addition, the non-synchrony in reproduction among these species suggests that the seasonality in resources is different among patches that lizards use. For example, *P. acutirostris* is an arboreal and relatively sedentary species which reproduces over a very short time period (Fig. 3). Its fat storage is highest during September and October. Fat storage in *T. semitaeniatus* and *T. hispidus* is highest in April-June, and in the mixed forager, *M. heathi*, which is seasonal in reproduction, fat storage is highest in June.

The widely foraging macroteiids, *A. ameiva* and *C. ocellifer,* are not only able to reproduce continually, but can also store fat while reproducing even though the caatinga habitat is seasonal. This is consistent with the hypothesis that there was nearly always energy available to these species during the study period. The same is undoubtedly true for the microteiid, *G. multiscutatus,* but fat is not stored in abdominal fat bodies (the tail is very large and most likely is an important fat storage organ as in certain other lizards [Bustard, 1967; Congdon et al., 1974; Vitt et al., 1977; Vitt and Cooper, 1985]). Also, based on the diversity of fat storage cycles shown here, the expected patterns cannot possibly be as simple as previously thought. Derickson (1976; p. 721) for example stated "In tropical latitudes, lipids may be stored during the dry season and utilized for reproduction during the wet season." His conclusion was based on a portion of the small amount of data available at the time and a lack of familiarity with literature on tropical lizards (see for exemple Alcala, 1967; Alcala and Brown, 1967; Inger and Greenberg, 1966). Consequently he underestimated the diversity of reproductive and fat cycle patterns in tropical species.

Extraneous variables

The reproductive patterns of caatinga gekkonids clearly cannot be explained simply on the basis of foraging mode. There are, however, several aspects of the biology of gekkonids which partially explain their divergence from other sit-and-wait foragers in northeast Brazil (and most likely elsewhere). All known gekkonids produce clutches of one or two eggs, dependent on subfamily (Fitch, 1970). Thus, clutch size and relative clutch mass are small (see Vitt and Price, 1982; Vitt, 1986). There is no evidence that egg size varies with body size within a gekkonid species. Because neither clutch size nor egg size within a species can be increased by a body size increase, there should be a selective advantage to remaining just large enough to produce eggs, investing little or no energy in growth, and producing eggs as rapidly as resource levels allow. These are the opposite expectations as those for species which can vary clutch or egg size with body size (see Trivers, 1972). This would partially explain the lack of fat bodies in females, although fat storage in gecko tails is well known (Dial and Fitzpatrick, 1981; Vitt et al., 1977).

Relative investment per clutch may also provide a partial explanation for the disparity of results in geckos as compared to the other sit-and-wait foragers. Generally, relative clutch mass is high in sit-and-wait foragers and low in widely foraging species (Huey and Pianka, 1981; Vitt and Congdon, 1978; Dunham and Miles, 1985). However, species such as gekkonids with low and fixed clutch sizes tend to have low relative clutch mass, at least partially a consequence of a small and fixed clutch size (Vitt and Price, 1982). Relative clutch masses for the caatinga gekkonids are: *G. geckoides*, 0.084; *H. mabouia*, 0.139; *L. klugei*, 0.169; *P pollicaris*, 0.114. Values for the other threee sit-and-wait species and the skink are: *P acutirostris*, 0.401; *T. semitaeniatus*, 0.195; *T. hispidus*, 0.258; *M. heathi*, 0.326; and for the widely foraging species: *A. ameiva*, 0.159; *C. ocellifer*, 0.207; and *G. multiscutatus*, 0.161. The low value for the sit-and-wait forager *T. semitaeniatus* is atypical and part of a suite of adaptations associated with crevice dwelling (Vitt, 1981).

The relatively high value for *M. heathi* presumably is associated with viviparity (Tinkle and Gibbons, 1977; Vitt and Price, 1982). The low investment per clutch, presumed low investment in somatic growth, and relatively low energy demands associated with low metabolic rates in geckos, as compared to other lizards (Bennett and Gorman, 1979; Putnam and Murphy, 1982) apparently buffers these to some extent from resource fluctuations making it possible for them to reproduce over very extended periods. The low metabolic rates might partially explain why geckos can reproduce continually in seasonal tropics (caatinga) whereas certain *Anolis* (Iguanidae), which also produce clutches of only one egg (Smith et al., 1972), often exhibit seasonal egg production (Gorman and Licht, 1975) in seasonal environments. This may reflect differences in energy utilization between geckos and anoles (Bennett and Gorman, 1979). I would expect geckos to show a decrease in frequency of clutch production associated with low resource periods, and this may partially explain some of the seasonal variation apparent in Fig. 3 for *G. geckoides* and *L. klugei*.

The above summary of reproductive and fat storage data on species comprising a community of tropical lizards indicates that sit-and-wait foraging iguanid lizards and a viviparous scincid lizard that has a mixed foraging strategy exhibit seasonal reproductive and fat storage patterns. Lizards in the family Teiidae, which are widely foraging, exhibit nearly continuous reproduction and store fat through most of the year. The lizards in the family Gekkonidae are sit-and-wait predators, reproduce continuously, and do not store fat, at least in the same manner as sympatric iguanids and teiids. The exceptional situation in geckos is presumably a consequence of relatively lower metabolic rates and relatively low investment per clutch. This difference would be even more striking if the differences in maintenance energy utilization between widely foraging and sit-and-wait species were incorporated (see Anderson and Karasov, 1981).

Additional supportive data

An ideal test of the model would require good seasonal samples of several lizard species of varying ecologies studied during the same time period and at the same locality, in addition to data on seasonal availability of resources in patches used by lizard species. Furthermore, such a study would need to take place in a tropical environment exhibiting seasonality. Unfortunately no such data set exists. There are several studies that include reproductive data on many sympatric species studied over long time periods (Dixon and Soini, 1975; Duellmam, 1978; Fitch, 1973; Schwaner, 1980). Even though these studies contain large amounts of data, the data sets are inadequate for testing the model for one or more the following reasons: 1) in some cases the habitat is not seasonal, 2) seasonal samples are not complete, 3) samples from different years or localities are pooled obscuring patterns that might be associated with resource fluctuations, 4) data on resource availability were not collected, and 5) sample sizes for critical species are too small.

The best comparative data set comes from a seasonal tropical habitat in Cumana, Venezuela. The habitat is considered thorn forest and receives about 500 mm of rain per year. Several lizard species were studied simultaneously or in sequence; two (*Cnemidophorus lemniscatus* and *Ameiva bifrontata*) are wide foragers and the other (*Tropidurus hispidus*) is a sit-and-wait forager. *Ameiva bifrontata* (Leon and Ruiz, 1971) and *C. lemniscatus* (Leon and Cova, 1973) were found to reproduce continually whereas *T. hispidus*, the sit-and-wait species, produced eggs during the wet season only (Prieto et al., 1976). Thus the wide foraging species appeared relatively unaffected by climatic seasonality whereas the sit-and-wait species was drastically affected. These data are particularly enlightening when compared to Caatinga lizard data. The two tropidurine iguanid lizards of caatinga (*T. hispidus* and *T. semitaeniatus*) are seasonal in reproduction (Vitt and Goldberg, 1983) but reproduce during the dry season, opposite to the season during which reproduction occurs in Venezuelan *T. hispidus*. Thus it appears that seasonality rather than the nature of that seasonality determines when reproduction will occur. In other words, immediate climatic conditions alone cannot account for the seasonality in

reproduction exhibited by tropidurine iguanids in general. In both habitats, the wide foraging species reproduced continually.

There are additional data that are peripherally supportive. Inger and Greenberg (1966) presented exceptionally complete reproductive data on four species of agamid lizards and two gekkonids in addition to incomplete data on the other species. Their study took place in an aseasonal rain forest in Borneo. Based on the model, I would predict on the basis of a lack of seasonality alone that all of the species would reproduce continually (but see Caveat), regardless of foraging mode. The agamids *Draco melanopogon, D. quinquefasciatus, Gonyocephalus grandis*, and *G. liogaster* and the gekkonids *Cyrtodactylus malayanus* and *C. pubisulcus* all reproduced throughout the year.

A perusal of data presented by Dixon and Soini (1975), Duellman (1978), and Fitch (1973) also adds some support (and lack thereof) even withstanding problems identified above. Although these studies took place in habitats with varying degrees of seasonality (wet most of the year), the sit-and-wait iguanid lizards tended to have more restricted breeding seasons than the widely foranging teiid lizards in the same habitat. Notably, as with caatinga gekkonids, the geckos in these studies also had relatively extended breeding seasons. In a relatively complete study by Alcala and Brown (1967), the widely foraging skink, *Emoia atrocostata* was shown to breed continuously in a seasonal tropical environment. Several independent studies on widely foraging tropical teiid lizards in seasonal and aseasonal environments reveal that these lizards have either very extended or continuous breeding seasons. In relatively aseasonal tropics, various species of *Ameiva (A. ameiva* in Ecuador, Dixon and Soini, 1975; *A. festiva* and *A. quadrilineata* in Costa Rica, Smith, 1968) were shown to have extended (9 mo or greater) or continuous breeding seasons. Hirth (1963a) has shown that *A. quadrilineata* in Costa Rica has an extended or continuous breeding.

There are additional examples that offer support, as well as some examples which do not seem supportive. Those which are not supportive (e.g., *C. deppii* in Costa Rica, Fitch, 1973; *Kentropyx pelviceps* and *Ameiva ameiva* in Amazonian Peru [Dixon and Soini, 1975] and Amazonian Ecuador [Duellman, 1978], both tropical forest habitats) may represent sampling bias or populations in extremely fluctuating environments where factors other than foraging mode become important, such as egg survival (see caveat). Extremely fluctuating environments explain the restricted breeding season reported for beach populations of *C. deppi*. Duellman (1978) presented a composite of his data and that of Dixon and Soini (1975) showing that a pattern of nearly continuous reproduction may exist in *A. ameiva* and *K. pelviceps* from Amazonian Peru.

A particularly interesting study (Magnusson, 1987) on reproduction in widely foraging macroteiids in tropical savannah of Brazil also contains relevant data, but no comparative data on sit-and-wait foragers from the same habitat are available. Pertinent to this study, Magnusson found that female *Cnemidophorus lemniscatus* and *Ameiva ameiva* had extended breeding seasons with at least some females reproductive during most of the year and relatively little seasonal variation in fat storage. Reproduction was reduced or curtailed during early dry season in both species. The temporal similarity in reproductive response to low rainfall (or a correlate) and continued fat storage suggesting that at least some food was available, are consistent with the model presented here. Synchronous reduction of reproduction or fat storage among sympatric widely foraging species would be expected when resource availability across all patches is lowest. The lack of data on resource availability for this savannah habitat and alternate explanations (Magnusson, 1987) leave this unresolved.

I have not considered *Anolis* even though many data exist (see for example, Andrews and Rand, 1974; Fitch, 1970, 1973, 1982; Gorman and Licht, 1974, 1975). My reasons for not including these lizards are 1) they are unusual among iguanids in that they produce a single egg at a time, i.e., their reproductive investment per episode is low (Andrews and Rand, 1974) and 2) two studies exist which make seasonal comparisons keeping taxa constant. Sexton et al., (1971) showed that *Anolis limifrons* exhibited seasonal reproduction in a seasonal habitat in the Panama Canal Zone, but only a short distance away (60 km) in an aseasonal environment reproduction

was continuous. These data are supportive in that they demonstrate the capability of a sit-and-wait forager to respond reproductively to some correlate of tropical seasonality patterns.

Rose (1982) also demonstrated that *Anolis* lizards in a relatively dry seasonal environment (east St. Croix) reproduced less than those in a relatively wet seasonal environment (west St. Croix). However, even though increasing resource availability resulted in an increase in fat storage in females of east St. Croix *Anolis,* a reproductive response was not apparent (Rose, 1982). It is possible that females in east St. Croix would use their stored fat to produce eggs if conditions for egg deposition (moisture) were available. This remains to be resolved. The immediate cue for egg deposition in many anoles appears to be rainfall, which in addition to triggering egg production (Stamps, 1976) presumably translates into higher resource levels (Janzen and Schoener, 1968). Seasonal aspects of physical characteristics of potential nest sites may also play a role (see Muth, 1980). Fitch (1982) provided data on *Anolis* in his Table 1 which are also supportive. In most instances, *Anolis* in seasonal tropics are seasonal in reproduction whereas those in aseasonal tropics reproduce nearly continually.

Even though literature data provide some support for a model based on foraging mode influencing reproductive seasonality in tropical lizards, most of the data on lizards in seasonal habitats are not complete enough to provide an adequate test of the model presented here.

The hypothesis, presented in model form, could be tested in a seasonal tropical habitat by first determining the patch distribution of lizards and then devising a sampling scheme to determine seasonal abundance of resources in the patches. The sit-and-wait foraging lizards would be expected to exhibit seasonal reproduction associated with seasonal abundance of resources within their respective patches. Concurrent time-energy budgets on widely foraging species would determine the degree to which widely foraging species are capable of switching to high resource patches and thus effecting their own resource availability.

CAVEAT

I have throughout this paper emphasized the significance of foraging mode in affecting seasonality of reproduction in tropical lizards to the near exclusion of other potential factors. Even though I am convinced that foraging mode may be one of the more important factors responsible for the seasonal diversity in reproduction of lizards in tropical environments, there are certainly other factors which may explain part of the diversity. Certain species, for example, may show highly seasonal patterns regardless of their habitat. This seems to be the case with the herbivorous iguanid lizard *Iguana iguana*. In all localities where *I. iguana* has been studied, the breeding season is restricted to a relatively small portion of the year (Alvarez del Toro, 1982; Fitch, 1973; Hirth, 1963b; Rand, 1982). This is also true in Brazilian caatinga (Vitt, unpubl.).

There are certain patterns associated with specific taxa that must be considered. I have already provided some examples (the family Gekkonidae; the genus *Anolis,* Iguanidae). Lizards in the family Teiidae that are considered microteiids (some of which are placed in a separete family, the Gymnophthalmidae) represent another example. These have relatively small bodies and all studied species have a clutch size of two (Dixon and Soini, 1975; Duellman, 1978; Fitch, 1970; Sherbrooke, 1975; Telford, 1971; Vitt, 1982b). Thus, even though many of these are widely foraging, and fit the model, there may be other aspects of their biology (fixed clutch size) that influence any predictions. In addition, I have restricted my considerations to adult animals. It is reasonable that resource availability for hatchling lizards may partially explain seasonal patterns in the sit-and-wait foraging species (except gekkonids). This would not, however, be inconsistent with the resource availability model presented here.

Other factors, such as body size, may also play a role. Lizards of very large adult body size generally reproduce only once per year and this does not appear associated with foraging tactics. Examples include *Iguana iguana* (see above for citations), *Cyclura carinata* (Iverson, 1979), and *Varanus komodoensis* (Auffenberg, 1981).

Finally, as Dunham and Miles (1985) have pointed out, it is difficult to separate foraging mode from "phylogeny." My examples suggest that most iguanid lizards are relatively seasonal

in reproduction whereas most teiids and gekkonids are aseasonal. Therefore, this attribute, like certain others, can be explained to a large degree simply as a lineage effect. Such an explanation does not however, provide a tenable evolutionary mechanism explaining the origin of such an attribute. If foraging mode is primitive to the differentiation of currently recognized lizard families, we would expect sister families to contain a majority of species with relatively similar foraging modes. As suggested by Dunham and Miles (1985), members of the sister families Agamidae and Iguanidae are primarily sit-and-wait foragers whereas members of the sister families Teiidae and Lacertidae are primarily wide foragers.

Note Added in Proof

Two stimulating papers relevant to mine have appeared since my paper was accepted and I briefly comment on them here. James and Shine (1988) have shown that among congeneric Australian agamid and scincid lizards, differences in life history characteristics are minimal between temperate and tropical species, with greatest variation attributable to phylogeny. James and Shine (1985) also suggested that biogeographic history of taxa may be the best predictor of seasonality in reproduction of certain Australian lizards. Similar to my studies, they observed high diversity of life history chacarcteristics and patterns of seasonality within localized faunas. I see little inconsistency between their findings and mine. Foraging mode follows lineages, is most likely primitive to family level differences used for taxonomy, and should influence entire lineages in similar ways. My paper deals with the ultimate causes of the differences, theirs deal with correlates of differences and conclusions are for the most part consistent. Hopefully, these papers taken together will stimulate students of lizard life history evolution to carefully consider foraging mode, phylogeny, and biogeographic history in attempting to interpret life history data.

Acknowledgments

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