

Population Density and Energetics of Lizards on a Tropical Island

Albert F. Bennett^{1*} and George C. Gorman²

¹ School of Biological Sciences, University of California, Irvine, Irvine, California 92717

² Department of Biology, University of California, Los Angeles, Los Angeles, California 90024, USA

Summary. 1. Population density, biomass, thermal relations and energetics of three common species of lizards (*Anolis bonairensis*, *Cnemidophorus murinus*, *Gonatodes antillensis*) were measured in a thornscrub community on the arid Caribbean island of Bonaire.

2. Population density and biomass estimates of these populations were 1318, 561, and 4200 individuals/ha and 4.2, 15.4, and 3.5 kg/ha, respectively. Although these densities are not exceptional for other Caribbean islands, they greatly exceed lizard densities reported for mainland communities.

3. Mean diurnal body temperatures are 33.4° C for *Anolis*, 40.4° C for *Cnemidophorus*, and 34.5° C for *Gonatodes*. Nocturnal temperatures average 27° C for all species.

4. Resting rates of oxygen consumption for all species were measured at naturally experienced diurnal and nocturnal temperatures. The values were used to calculate Minimal and more realistic Field Active estimates of the respiratory energy utilization of these lizard populations.

5. Minimal estimates of energy expenditure are 326, 950, and 268 kJ/(ha × day) for *Anolis*, *Cnemidophorus*, and *Gonatodes*, and Field Active estimates are 693, 2510, and 379 kJ/(ha × day), respectively.

6. These estimates greatly exceed values previously reported for other lizard populations. They also exceed reported values for the respiratory metabolism of populations of small mammals in temperate regions.

7. These values are probably not atypical of other tropical insular lizard populations, and the significance of these animals to energy flow in these communities has not generally been appreciated.

Introduction

It is a common observation that lizards are more abundant in tropical than in temperate areas, both in numbers of individuals and species. Likewise, they

* To whom offprint requests should be sent

appear also to be more abundant on islands than on adjacent mainland areas of comparable habitat (Soulé, 1966; Case, 1975; Scott, 1976; Wright, 1979). Where tropical and insular effects coincide, lizards may occur in dense and diverse assemblages, often forming the most conspicuous vertebrate faunal element of the ecosystem. This situation is particularly apparent on the islands of the Caribbean, where population densities as high as 20,000 animals/ha have been reported for a single species of anole (Gorman and Harwood, 1977). One would expect these populations to make a considerable contribution to energy flow in these communities. However, rates of energy utilization by individual reptiles are very low in comparison to mammals and birds of equal size (Bennett and Dawson, 1976; Bennett and Nagy, 1977) and the magnitude of their energetic impact on a community is not obvious. Observational data on the ecological energetics of such tropical insular communities are totally lacking.

We framed this study to estimate the energetic demands of the lizards in one such community. This study quantifies the biomass and energetics of a relatively simple lizard assemblage on the arid Caribbean island of Bonaire. For the three dominant species, we examined activity times, daily cycles of body temperature, and densities and biomass of the populations. We measured resting metabolic rates at normally encountered temperatures over a diurnal cycle and estimated minimal and more realistic field-active energy demands associated with respiratory metabolism by the lizards in this community. Data were gathered during June, 1976, and thus pertain only to that period and do not represent a yearly average. Our goal in this study was to document the high energetic demands of densely-packed lizard populations. The presence of seasonal cycles in energy utilization, determination of the fraction of community productivity channeled through these populations, and comparative examinations on other islands await further study.

Bonaire and its Biota

Bonaire is a Caribbean island of the Netherlands Antilles that lies approximately 74 km north of Venezuela and 50 km east of Curaçao (12° N, 68° W). The island is about 250 km² and is relatively flat (maximum altitude, 240 m). Bonaire is an arid island with an annual rainfall averaging 532 mm, but that is quite irregular. The wettest months are between October and December. The arid nature of the island is reflected in its vegetation. Most of the dominant species, such as cacti and the mesquite *Prosopis*, have pronounced xeromorphic characteristics. The dominant flora of the island has stronger affinities with that of the West Indies than that of the South American mainland (Stoffers, 1956).

Typical of an oceanic island, the fauna is relatively low in species diversity and has a large number of endemic forms. There are no native mammals except for bats, a single frog species (which appears to have been introduced by man), only one species of snake (*Leptotyphlops*), and fewer than 30 species of breeding land birds (Hummelinck, 1975). There are several dozen species of land snails and seven species of lizards, the majority of which are restricted to Bonaire and the adjacent islands of the Netherlands Antilles (Hummelinck, 1940).

Of all the land vertebrates on Bonaire, the lizards are by far the most numerous group. Three species are very widespread and abundant and comprise the focus of this investigation: *Anolis bonairensis*, *Gonatodes antillensis*, and *Cnemidophorus murinus*. *Anolis bonairensis* (Iguanidae) is a moderate-sized anole (2- to 10-g adults). It is arboreal, diurnally-active, and strictly insectivorous, primarily myrmecophagous. *Gonatodes antillensis* (Gekkonidae) is a small gecko (1-g adults). It is nocturnally active on the ground and occurs under rocks and litter during the day. It is also insectivorous, eating primarily insect larvae. *Cnemidophorus murinus* (Teiidae) is a terrestrial lizard (30- to 100-g adults) active only in the warmest periods of the day. It eats a variety of foods but is primarily herbivorous: plant parts constitute over 90% of the biomass in guts of dissected animals. Although unusual among small lizards (Pough, 1973), herbivory has previously been reported in other species of insular teiids (Schall, 1973; Janzen, 1973). Food relations of these lizards are taken from unpublished data (Gorman). These species are all endemic to Bonaire or Bonaire, Aruba, and Curaçao.

The other lizards of the islands have more patchy distributions and are far less abundant. These include two arboreal geckos, *Thecadactylus rapicauda* and *Phyllodactylus martini*, which are associated with large trees or man-made structures; a microteiid, *Gymnophthalmus lineatus*, that was only rarely seen by us; and the large herbivorous *Iguana iguana*. The latter is hunted by man and eaten on the island.

Materials and Methods

The Study Site

We estimated the abundance and biomass of the lizard community in a relatively undisturbed area of natural vegetation in a nature reserve on the northwest part of the island. Our primary study site was a 15 m × 30 m plot of gently sloping thornscrub near Playa Funchi in Washington National Park. The site was dominated by the mesquite *Prosopis juliflora* (13 trees, most with multiple trunks) and stands of the cactus *Lamaierocereus griseus* (13 large cacti or stands of cacti). Also present were *Casearia tremula* (3 trees), *Capparis cynophallophora* (one tree) and a single *Opuntia wentiana*. Small shrubs such as *Croton flavens* were abundant, and there were patches of heavy ground cover composed of creeping prickly pear, *Opuntia curassavica*. Canopy height was approximately 6 m. The area is far from any human habitation or disturbance; however, goats roam freely through the National Park, as they do throughout the island. *Anolis*, *Gonatodes*, and *Cnemidophorus* were abundant in our study area. No *Iguana* were found in the area during this study, but two were seen the previous year in essentially the same location. *Thecadactylus*, *Phyllodactylus*, and *Gymnophthalmus* were absent from the study quadrat. Population density of the lizard populations was estimated in this area. Observations on activity times, thermal relations, and activity budgets were made in areas adjacent to the study plot.

Population Study and Biomass

No single sampling technique was adequate to estimate individual and biomass densities of the lizard species on the study quadrat. Differences in vagility, visibility, and habitat dictated a variety of sampling methods to estimate the number of individuals. To estimate biomass, we captured a large number of animals in areas directly adjacent to the quadrat and measured their snout-vent length and body mass. We grouped animals into discrete size classes (adult male, adult female

and young male, and juvenile) and used the mean body mass of each size class and the frequency of that size class on the study quadrat to estimate biomass densities on the quadrat.

For *Anolis*, which is readily visible and has a high degree of site fidelity, we used a Lincoln Index estimate of population density. Anoles were caught by slip noose or by hand. They were weighed, measured, given a unique color code with three small dots of paint, and released within 2 min at their site of capture. We censused the study area twice daily for 5 days, counting the proportion of marked animals in the total number of animals sighted. Previously unmarked animals were caught, marked and released after each census. The census period is sufficiently short so that the influences of mortality, immigration, and emigration on our estimates are probably negligible. A total of 26 anoles were marked on the study area; 17 of these were subsequently resighted.

Gonatodes were very abundant in the quadrat. However, because of their subterranean habitat, determination of population density required complete dismantling of ground cover, rocks, and logs in relatively small areas. We destructively sampled two smaller quadrats (25 m² each) directly east of, and of similar composition to, our study quadrat. Each gecko seen was collected, weighed, and measured.

The assessment of the population density of *Cnemidophorus* posed several problems. Free-ranging teiids are very wary, difficult to capture, and will run at high speeds if pursued. Animals captured once become even more difficult to approach subsequently. On the other hand, these animals are readily attracted to almost any bait and will converge from a large area if food is available. Thus, they seem to range freely over considerable areas, and their numbers are greatly influenced by the presence of humans. The previous censusing methods were consequently inadequate for *Cnemidophorus*. Instead, we conducted a series of visual censuses by three observers walking rapidly through the quadrat when we first arrived at the study site in the morning. Animals were counted and classified according to size group on each census period. These lizards were not captured or otherwise disturbed.

The censusing methods employed for *Gonatodes* and *Cnemidophorus* almost certainly underestimate population density, since it is unrealistic to assume that all animals in a given area will be observed (Turner, 1977a). Although our study area was relatively small, the lizards were very abundant and they appeared equally numerous in all areas of adjacent thornscrub.

Thermal Relations

Daily cycles of body temperature of the three species in our study area were measured to permit construction of energy budgets for these populations. Diurnal cloacal body temperatures of the three species were measured with a Wescor model TH-50 thermocouple thermometer immediately after capture by hand or noose. Temperatures of animals on our study quadrat were measured when initially captured, but to avoid disturbance of the census area, many supplementary observations were gathered on animals at sites immediately adjacent to the quadrat. These areas were similar in plant cover and temperature. Nocturnal body temperatures were estimated with measurements of soil and air temperature, measured with the thermocouple thermometer and a Taylor recording thermograph. Air temperature was measured at a height of 5 cm from the ground. Soil temperatures were monitored in the quadrat under logs, rocks, and cactus pads under which individual *Gonatodes* and *Cnemidophorus* had previously been found.

Metabolic Measurements

To estimate the energetic requirements of these populations, we measured resting metabolic rates diurnally and nocturnally at the appropriate body temperature for each species (i.e., that experienced under field conditions). A range of body sizes was examined, and the demographic and metabolic data were used to construct daily energy budgets for each species.

Animals were transported to our laboratories in the United States and were maintained in glass aquaria equipped with photothermal gradients. All metabolic measurements were made within 2 weeks of field capture. Animals were fasted 2 days before measurement. Oxygen consumption of *Anolis* and *Cnemidophorus* was measured by open circuit paramagnetic oxygen analysis; details of the procedure are given in Bennett and Gleeson (1976). Animals were placed in individual

metabolic chambers, equipped with air ports and thermal sensors, at midnight the day before metabolic measurements. These were housed in a dark, controlled temperature cabinet which regulated body temperatures at 27° C at night and, during the day, at 33° C for *Anolis* and 40° C for *Cnemidophorus*. Diurnal temperatures were maintained from 0600–1500 local time. Excurrent air samples were removed and analyzed at 1100–1400 and 2200–2400 to estimate diurnal resting metabolic rate at field-active temperatures and standard metabolic rate at nocturnal temperatures. Oxygen consumption (corrected to STPD conditions) was determined with a Beckman model E-2 oxygen analyzer, according to the method of Depocas and Hart (1957). Oxygen consumption is equated to energy utilization by assuming an equivalent of 20.11 J per ml of oxygen consumed.

Individuals of *Gonatodes* are too small to permit measurement of metabolism by these methods. Oxygen consumption was determined manometrically in a Gilson respirometer equipped with a controlled temperature water bath. Animals were placed individually in Warburg-type flasks which were connected to micrometer manometers. The side arm of the flasks was blocked with mesh screening and contained 10N KOH for absorption of carbon dioxide. The flasks were placed in the water bath at 34° C at 0800 local time, and air was metered through the chamber. At 1400, the chambers were sealed and the decrement in volume (equivalent to oxygen consumption) was measured at 15 min intervals for 1 h. The temperature of the bath was then lowered to 27° C and the chambers reventilated with room air. At 2100, oxygen consumption was measured again with the previous protocol. The bath was covered with a dark plastic cloth during the entire experimental period. Decrements were corrected to STPD conditions and were used to calculate oxygen consumption.

Results

Population Density and Biomass

Anolis

In each of our 9 censuses, approximately half of the animals observed had been previously tagged. The mean estimate was 59.3 animals (range 43.3–84.5) (standard error of these 9 estimates = ± 5.12) on the study quadrat, equivalent to a density of 1318 individuals per hectare.

Body mass is related to snout-vent length by the following least squares relation:

$$\log(\text{mass in g}) = -1.0388 + 0.0296(\text{SV length in mm}) \quad (1)$$

$$n = 43 \quad r^2 = 0.96 \quad p < 0.0001 \quad 35 \leq \text{SV} \leq 75.$$

Individuals on our study area were divided into three discrete size classes – adult males: 19% of individuals, 65–69 mm SV, 5.4–8.9 g, mean 7.8 g; adult females and young males: 38% of individuals, 45–53 mm SV, 2.1–4.1 g, mean 3.0 g; juveniles: 42% of the individuals, 36–42 mm SV, 0.9–1.9 g, mean 1.2 g. The population densities and biomass of these size classes are reported in Table 1. No hatchlings were present during our study period and no females were in reproductive condition.

Cnemidophorus

An average of 25.0 animals (± 2.5 S.E., range 12–35) was observed on the 11 walking censuses on our study quadrat. This estimate is equivalent to 556

Table 1. Population densities of three species of lizards in a thornscrub community on Bonaire in June, 1976

Species and size class	Density Individuals/ha	% of Individuals	Mean Mass (g)	Biomass (kg/ha)
<i>Anolis bonairensis</i>				
Adult ♂	253	19	7.8	1.97
Adult ♀, young ♂	507	38	3.0	1.52
Juvenile	558	42	1.2	0.67
Total	1,318	—	—	4.16
<i>Cnemidophorus murinus</i>				
Adult ♂	67	12	77	5.16
Adult ♀, young ♂	344	61	28	9.63
Juvenile	150	27	4	0.60
Total	561	—	—	15.39
<i>Gonatodes antillensis</i>				
Adult ♂, ♀	3,000	71	1.1	3.30
Juvenile	1,200	29	0.2	0.24
Total	4,200	—	—	3.54
Grand Total	6,079	—	—	23.09

individuals per hectare. Animals were censused in three visually-distinct size categories: large males, >120 mm SV; adult females and young males, 80–100 mm SV, and juveniles, <60 mm SV. These represented 12%, 63% and 27%, respectively, of the individuals sighted.

Body mass of individuals collected off our study quadrat was related to snout-vent length according to the following relationship:

$$\log(\text{mass in g}) = -0.2181 + 0.0161(\text{SV length in mm}) \quad (2)$$

$$n = 44 \quad r^2 = 0.94 \quad p < 0.0001 \quad 50 \leq \text{SV} \leq 150.$$

The average mass of the three size classes taken from this relation was 77 g for adult males, 28 g for adult females and young males, and 4 g for juveniles. Biomass and population density of these size classes are reported in Table 1. Adult animals were not in reproductive condition, and the absence of any individuals in the population between 60 and 80 mm SV length indicates that reproduction is seasonal in this species.

Gonatodes

Twenty-one geckos were found in the smaller quadrat. This density is equivalent to 4200 individuals per hectare. Six of these animals (29%) were hatchlings (18–20 mm SV; 0.2 g) and 15 were adults (71%, 33–38 mm SV, 0.9–1.4 g, mean

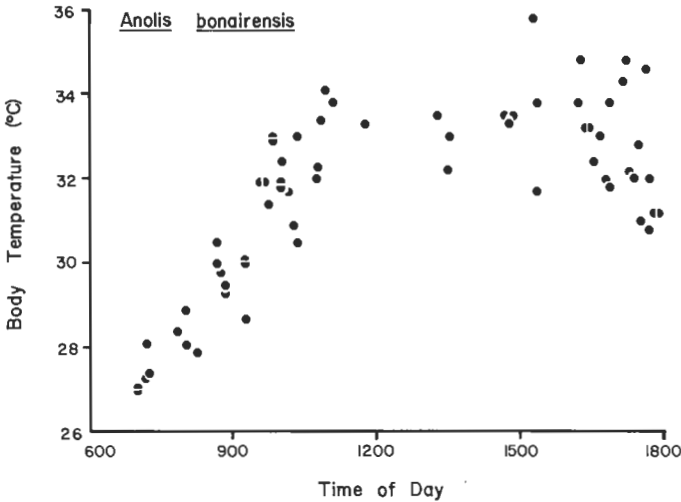


Fig. 1. Diurnal body temperatures of *Anolis bonairensis* on or immediately adjacent to our census quadrat during June 1976

1.1 g). Snout-vent length and mass relations for animals collected on the quadrat are reported by the following relation:

$$\log(\text{mass in g}) = -1.5152 + 0.0438 (\text{SV length in mm}) \quad (3)$$

$n = 18 \quad r^2 = 0.96 \quad p < 0.0001 \quad 18 \leq \text{SV} \leq 40$

Biomass and population densities are reported in Table 1. Hatchling animals were just emerging from eggs during our study and females were still carrying oviducal eggs. No geckos with a snout-vent length of 21–32 mm were found, indicating seasonal reproduction, with a different timing than that of *Anolis* or *Cnemidophorus*.

Thermal Relations

The determination of thermal relations of the lizards was facilitated by the impressive constancy of environmental temperature cycles during our study period. The daily maximum and minimum were 36° C and 27° C on each day of our study. Diurnal soil temperatures were slightly more variable, but since the ground area receives only filtered sun, there was very little differential in temperature between sites at any time during the day (maximum differential = 2.5° C, generally less). Soil temperatures were approximately 2° C cooler than air temperature during the morning and 2° C warmer in the afternoon; they were identical at night.

Body temperatures of individual *Anolis* captured in the field are reported in Fig. 1. Animals are active in the lower portion of the tree canopy from sunrise to sunset. They climb down from the tops of the trees when the sun rises and sit in patches of sun on the trunks. Body temperature exceeds air temperature then stabilizes at an average value of 33.4° C (± 0.18 S.E., $n = 31$)

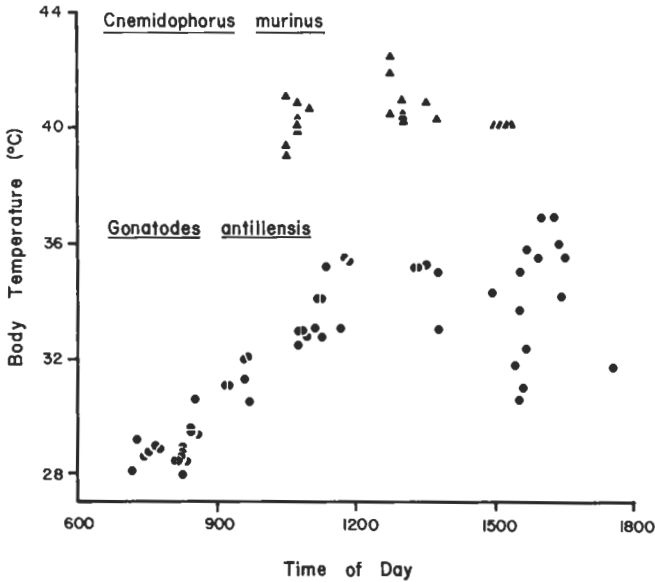


Fig. 2. Diurnal body temperatures of *Cnemidophorus murinus* (triangles) and *Gonatodes antillensis* (circles) on or immediately adjacent to our census quadrat during June 1976

between 1030 and 1730. At sunset, the animals climb to the tree tops and sleep. Animals are assumed to be at air temperature overnight.

Cnemidophorus spend the night in burrows or under stones or logs. Soil temperature is a good approximation of body temperature during this time. Activity is restricted to the hottest part of the day, and the animals are not seen during the earliest and latest daylight hours. Their period of activity was between 0900 and 1500, and this coincided with the appearance of animals on our quadrat. A high and stable level of body temperature was maintained throughout this period: 40.4°C (± 0.16 S.E., $n=21$) (Fig. 2).

Gonatodes are active on the surface between dusk and dawn, with the greatest levels of activity at the crepuscular periods. Animals were observed active on the surface between 1730 and 0630. Body temperature was approximated well by ground-level air temperature (27°C) during this time. During the day, however, animals remain below the surface, under rocks or bark. The animals become very active when suddenly uncovered. Body temperature is higher during this "inactive" period than during the nocturnal foraging time (Fig. 2). In the morning, body temperature rises with the soil temperature until 1100. It remains fairly constant from 1100 to 1700 with an average value of 34.5°C (± 0.33 S.E., $n=25$). The range of field temperatures during this period was not unexpectedly broad: $30.6\text{--}36.8^{\circ}\text{C}$.

Metabolic Measurements

The rates of minimal oxygen consumption for *Anolis*, *Cnemidophorus*, and *Gonatodes* are reported as a function of body temperature and mass in Figs. 3–5.

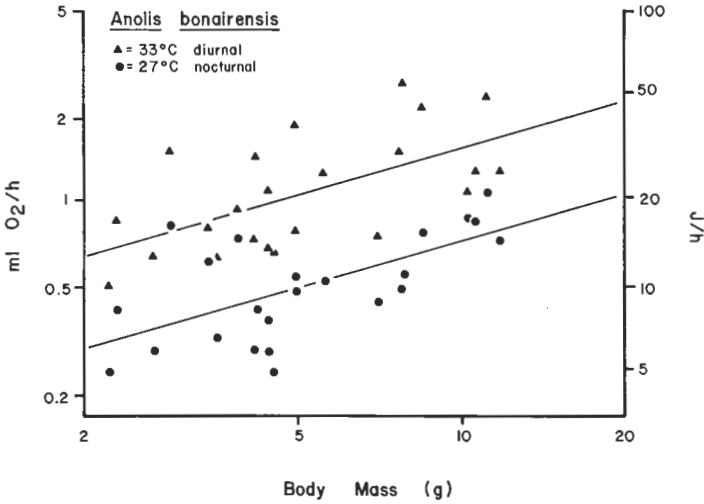


Fig. 3. Minimal (resting) metabolic rate of *Anolis bonairensis*. Triangles indicate diurnal measurements of $T_B=33^\circ\text{C}$; circles, nocturnal measurements at $T_B=27^\circ\text{C}$

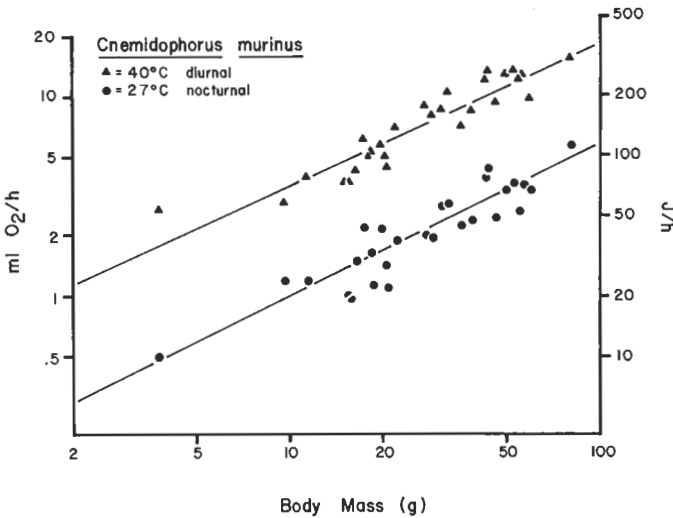


Fig. 4. Minimal (resting) metabolic rate of *Cnemidophorus murinus*. Triangles indicate diurnal measurements at $T_B=40^\circ\text{C}$; circles, nocturnal measurements at $T_B=27^\circ\text{C}$

The following least-squares power regressions were fit to these data; these equations are of the form $y=ax^b$ where y is oxygen consumption in ml O₂/h and x is body mass in g.

Anolis

33° C diurnal	$y=0.430 x^{0.554}$	$n=23$	$r^2=0.36$	(4)
27° C nocturnal	$y=0.201 x^{0.548}$	$n=23$	$r^2=0.40$	(5)

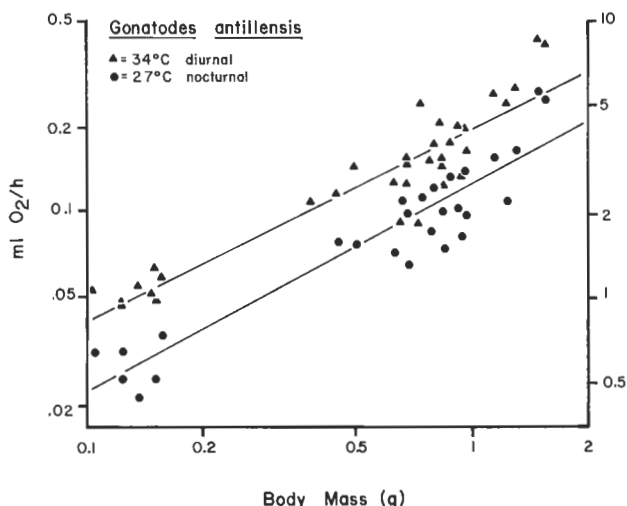


Fig. 5. Minimal (resting) metabolic rate of *Gonatodes antillensis*. Triangles indicate diurnal measurements at $T_B=34^\circ\text{C}$; circles, nocturnal measurements at $T_B=27^\circ\text{C}$.

Cnemidophorus

$$40^\circ\text{C diurnal} \quad y = 0.680 x^{0.705} \quad n = 28 \quad r^2 = 0.86 \quad (6)$$

$$27^\circ\text{C nocturnal} \quad y = 0.168 x^{0.761} \quad n = 28 \quad r^2 = 0.84 \quad (7)$$

Gonatodes

$$34^\circ\text{C diurnal} \quad y = 0.199 x^{0.695} \quad n = 34 \quad r^2 = 0.86 \quad (8)$$

$$27^\circ\text{C nocturnal} \quad y = 0.127 x^{0.753} \quad n = 27 \quad r^2 = 0.88 \quad (9)$$

Metabolic rate may be expressed in J/h by multiplying a values by 20.1. All these regressions are significant ($p < 0.01$), indicating that metabolic rate is allometrically related to body mass in all three species. Analysis of covariance indicates that the regressions relating metabolic rate of 27°C and body mass are not significantly different among these species ($p = 0.18$). Therefore, all three species possess a similar resting level of metabolism, and the differences among the minimal energetic requirements of these animals are primarily related to differences in body temperature and mass.

Estimated Energy Budgets

Two estimates of the energetic demands associated with respiratory metabolism are calculated from the previous data. The first (Minimal) budget is based upon measurements of resting metabolism alone and thus represents an absolute minimal baseline of the energetic requirement of these populations. The second (Field Active) makes assumptions concerning the metabolic increments associated with field activity and thus is a more realistic estimate of the actual

Table 2. Energy expenditure (respiratory metabolism) of 3 common species of lizards in a thornscrub community on Bonaire in June, 1976. Mean body mass and population density of each size class are reported in Table 1

Species and size class	Individual energy expenditure J/(day × individual)		Population energy expenditure kJ/(ha × day)	
	Minimal	Field active	Minimal	Field active
<i>Anolis bonairensis</i>				
Adult ♂	435	922	110	233
Adult ♀, young ♂	256	545	130	276
Juvenile	155	330	86	184
Total	—	—	326	693
<i>Cnemidophorus murinus</i>				
Adult ♂	3,830	10,010	257	671
Adult ♀, young ♂	1,820	4,820	626	1,658
Juvenile	444	1,204	67	181
Total	—	—	950	2,510
<i>Gonatodes antillensis</i>				
Adult ♂, ♀	80	113	240	339
Juvenile	23	33	28	40
Total	—	—	268	379
Grand Total	—	—	1,544	3,582

energetic demands. It should be emphasized that increments associated with storage terms (growth and reproduction) are not taken into account and thus these represent underestimates of total energy demands.

Minimal Energy Budget

Measurements on daily fluctuations in body temperature are combined with measurements of resting metabolic rate to produce an estimate of the minimal metabolic rate per day. Values of resting metabolic rate are calculated for an individual of average mass for each size class. These calculations assume the following cycles of T_B : *Anolis*, 27° C at 2200–0800, 33° C at 1100–1700; *Cnemidophorus*, 27° C at 2200–0900, 40° C at 1000–1700; *Gonatodes*, 27° C at 2200–0800, 34° C at 1100–1800. At intermediate times, metabolic costs are estimated by interpolation of log metabolic rate to the body temperature experienced in the field at that time. These daily integrated measurements for individuals of average size are reported in Table 2. Minimal daily metabolic rates of *Anolis bonairensis* are very similar to those previously estimated for other species of Caribbean anoles (McManus and Nellis, 1973; Andrews and Asato, 1977). The individual daily estimates are then combined with demographic measure-

Table 3. Observations on locomotory activity in two species of lizards on Bonaire

	<i>Anolis bonairensis</i>	<i>Cnemidophorus murinus</i>
Number of animals observed		
< 10 min	1	19
10–20 min	5	9
20–30 min	7	1
	13	29
Number of observation minutes	250	246
% time in activity		
Stationary	56	23
Postural adjustment	12	
Locomotion	32	77
Speed of locomotion		
meters/locomotory min	0.39	2.08
meters/observation min	0.13	1.60

ments given in Table 1 to estimate metabolic rate of the size classes and of the total populations on a per hectare basis (Table 2). A minimal energetic demand of over 1500 kJ/(ha × day) is estimated for these lizard populations.

Field Active Budget

Animals expend metabolic energy at levels greater than resting rates according to the amount of physical activity in which they are engaged. We made observations on the time and level of activity of these lizards under field conditions and estimated the metabolic increments associated with these normal levels of activity.

Anolis and *Cnemidophorus* are active, diurnal animals and were easily observed. We constructed time-activity budgets for these species based on several hours of direct observation in the field. Each minute of observation was categorized as either "stationary", in which the lizard did not move; "postural", in which the lizard adjusted its position or moved less than a body length; or "locomotory", in which the lizard moved more than a body length. Every time the lizard moved, an estimate of distance was made. If the lizard fled, observations were terminated and the final minute of observation was not scored.

Table 3 contrasts the activity patterns of *Anolis* and *Cnemidophorus*. The difference between the species in the amount of locomotion is striking: the teiid moves over 10 times as far as does the anole in the same period of time. These data provide a quantification for the observation that *Anolis bonairensis* is a typical sit-and-wait predator while *Cnemidophorus murinus* is a much more actively foraging animal.

Gonatodes is more difficult to observe since it is active on the surface only at night. The activity component during the daytime is unknown: uncovered animals are alert and flee rapidly. However, when abroad this gecko is much less active than the other species. Several individuals observed continuously remained completely motionless for long periods of time (in excess of 1 h). They seem to travel rapidly only when attempting to avoid capture.

Field activity generally results in metabolic rates which are 2- to 4-times those of resting animals. During their activity periods in free-living existence, small rodents and birds expend metabolic energy at approximately 4 times basal rates (assuming they are close to basal levels during their inactive periods) (Mullen, 1970, 1971; Utter and LeFebvre, 1970). These animals are generally much more active than small lizards with sit-and-wait behavior patterns. *Sceloporus occidentalis*, a small iguanid lizard which has an activity level very similar to that of *Anolis bonairensis*, has a field-active rate which is 2.5–3 times resting metabolic rate at the same temperature (Bennett and Nagy, 1977). Because of the relative activity levels maintained by these species, we estimate that *Anolis* and *Gonatodes* have metabolic rates 3- and 2-times, respectively, resting metabolic rates at foraging body temperatures.

Cnemidophorus is a more actively foraging animal, moving most of the time, although at rather slow rates. When walking at normal foraging speeds (0.13 km/h) on a treadmill, *Cnemidophorus murinus* has an oxygen consumption of 0.9 ml/(g × h) (40° C, 71 g mean mass) (Bennett and Gleeson, 1979). This metabolic rate is 4.6 times minimal oxygen consumption at this temperature (Eq. 6). If three-quarters of the active period is spent foraging with this energy expenditure (Table 3) and the remainder is spent in postural adjustments and rest, requiring a doubling of minimal rates, field-active metabolic rate during the day is approximately 4 times minimal metabolic rate.

These estimates are used to construct more realistic energy budgets for the metabolic requirements of these populations. During the active period, resting metabolic rates are multiplied by the factorial increments appropriate to each species. For the inactive period of the daily cycle, we estimate that all these species metabolize at resting rates. *Anolis* and *Cnemidophorus* are inactive in the tree tops and under rocks, respectively, during this period. Estimates for daily Field Active metabolic rates are given in Table 2. These values are 1.4–2.6 times Minimal estimates.

Discussion

The Lizard Community of Bonaire

Division of Resources. There are pronounced differences in time of activity, preferred thermal levels, and microhabitat selection among the lizard species of Bonaire. Combined with food preferences, these differences result in an almost total lack of interspecific overlap in resource exploitation except for the two nocturnal arboreal geckos that were absent from our study site. Among the lizard species, nearly all the available feeding niches are represented (Table 4).

Table 4. Habitual partitioning by lizards in the thornscrub community of Bonaire

Niche	Species
Diurnal-tree-insectivore	<i>Anolis bonairensis</i>
Diurnal-tree-herbivore	<i>Iguana iguana</i>
Diurnal-ground-insectivore	<i>Gymnophthalmus lineatus</i>
Diurnal-ground-herbivore	<i>Cnemidophorus murinus</i>
Nocturnal-tree-insectivore	<i>Phyllodactylus martini</i> <i>Thecadactylus rapicauda</i>
Nocturnal-tree-herbivore	None
Nocturnal-ground-insectivore	<i>Gonatodes antillensis</i>
Nocturnal-ground-herbivore	None

Four species are mainly restricted to arboreal foraging. *Anolis* is a diurnally-active insectivore which forages only in shrubs and trees. The geckos *Phyllodactylus* and *Thecadactylus* were not observed on our study site but are not uncommon elsewhere on the island and occur on the same trees diurnally occupied by *Anolis*. All species are insectivorous, but the geckos are active only nocturnally. *Iguana*, observed the previous year on our quadrat, is a diurnally-foraging herbivore. There are three ground dwelling species. *Cnemidophorus* is active only during the hottest part of the day and is primarily herbivorous but will also take insects when available. The microteiid *Gymnophthalmus* is also diurnally active and insectivorous. However, it was seen only very rarely and then only when we were raking deep in the litter or turning logs. This species does not appear to forage actively on the surface. The surface foraging activity of *Gonatodes*, another insectivore, is nocturnal. Only the nocturnal-herbivore niche is not occupied in this community, but we are unaware of any nocturnally active herbivorous lizards.

Although the *Cnemidophorus* population has the lowest density of individuals of the three species in our study plot, its biomass per unit area is nearly 4 times that of either of the other species. This high biomass density, combined with high active body temperatures and greater levels of sustained activity, requires a large amount of energy expenditure, over twice that of the combined populations of *Anolis* and *Gonatodes*. Considering the large number of insects consumed daily by these latter species (see below) and the relative paucity of insects in this community in comparison to most Caribbean islands (Gorman, unpublished data), it is doubtful that the teiids could sustain these metabolic demands on insect material alone. These high population densities may be possible only because of the adoption of a herbivorous diet by these animals (Janzen, 1973).

Gonatodes is by far the most populous species in the community. However, due to its small body size, its total biomass is nearly equal to that of the less numerous *Anolis*. Because of its nocturnal foraging behavior and low levels of activity, the Field Active metabolic rate of this gecko population is only half that of the anole. It should be borne in mind that anole and

gecko harvest energy at a higher trophic level than does the teiid. Consequently, they consume a greater fraction of the primary productivity of the community than these estimates would otherwise indicate.

Juvenile animals (hatchlings up to 1 year old) of all three species are numerous and account for about one-third of the total individuals present in the population during June. However, their small body size minimizes their impact on the population biomass and energy demand, being only about 10% of the total in each case. In those species which show a marked size-sexual dimorphism for adult animals (*Anolis*, *Cnemidophorus*), the adult males make a much larger contribution to biomass and energetics than is indicated by their numerical abundance.

Estimates of Food Consumption and Total Energy Demand

It is possible to estimate the food consumption required to support these Field Active estimates of respiratory metabolism. For the strictly insectivorous species, *Anolis* and *Gonatodes*, we assume an assimilation efficiency of 80%, an average value measured for several species of small insectivorous lizards (Bennett and Dawson, 1976). A food intake of 866 kJ/(ha × day) and 474 kJ/(ha × day) are consequently required by these populations of *Anolis* and *Gonatodes*, respectively. Assuming an energy content of 23.1 kJ per g dry mass and a water content of 70% in the insect prey, we estimate an average field consumption of 125 g insects/(ha × day) by *Anolis* and 68 g insects/(ha × day) by *Gonatodes*. Since the prey of these animals is small, this represents a very large number of individual prey items, approximately 20,000–100,000 insects/(ha × day). *Cnemidophorus* is primarily herbivorous. Assuming an assimilation efficiency of 57% as measured by Nagy and Shoemaker (1975) for two species of herbivorous lizards, we estimate 4400 kJ of plant material/(ha × day) are ingested by this population. This corresponds to a food consumption of approximately 420 g of plant material/(ha × day) (21.0 kJ/g dry mass; 50% water content). To supply a neutral energy budget, the lizards of this community require approximately 195 g insects and 420 g of plant material/(ha × day).

These estimates assume no growth (storage) during this period, and this assumption is almost certainly incorrect for the juveniles of all species and for adult geckos, which were reproducing in June. Consequently, these values will be underestimates of actual consumption. Efficiencies of secondary productivity in small lizards range from 20–40% (Golley, 1968; Mueller, 1970; Turner et al., 1976), and our values may underestimate actual food intake accordingly. McNeill and Lawton (1970) provide general relations for the estimation of productivity of ectotherms on the basis of respiratory energy expenditure. Their equation (Eq. 2) for poikilotherms estimates an average productivity of 1130 kJ/(ha × day) for this community. Assuming previously-stated assimilation efficiencies, we estimate the average food consumption of this lizard community, accounting for both respiration and production, averages nearly 7550 kJ/(ha × day).

Comparison With Other Communities

Biomass and Density of Other Lizard Populations

The density of lizards in this community is impressive, both in numbers of individuals (6000/ha) and biomass (23 kg/ha) (Table 1). Data on population densities of lizards have recently been summarized by Turner (1977a, Table III): each of the three species examined here is more than an order of magnitude more abundant than the mean value reported in Turner's summary (51 individuals/ha). However, the densities measured here are not unusual and are in fact low in comparison with those reported for lizards on other Caribbean islands.

The density (1318/ha) and biomass (4.2 kg/ha) of this population of *Anolis bonairensis* is less than that of anoles on other Caribbean islands. Values summarized by Andrews (1979) for six species of island anoles of body size similar to *A. bonairensis* range from 1450–10,900/ha with a median density of 4700/ha. The biomass represented by these numbers may also be very great: J. Roughgarden (unpublished data) has measured maximal biomass values ranging from 4.0–22.7 kg/ha (median=8.1 kg/ha) for five species of *Anolis* on three wetter Caribbean islands. The greatest density of biomass (*A. richardi* on Grenada) is nearly equivalent to that of all three species of lizards on Bonaire. Wright (1979) estimates biomass values of 2.6–19.3 kg/ha for *Anolis* in dry forest areas on seven Caribbean islands. These greater lizard densities may be the result of much greater densities of insects on these islands: captures of insects on sticky plates under similar conditions are 10 times as great on St. Vincent and Puerto Rico as on Bonaire (Gorman, unpublished data). It is clear that anole populations on other islands may be expected to have an even greater energetic demand and to account for an even greater proportion of the community metabolism than does *A. bonairensis*. This species has a density which is much more similar to that of anoles on the tropical mainland, where the median density of six species is 1175/ha (range 60–1910/ha) (summarized by Andrews, 1979).

The densities of *Cnemidophorus* are very similar to those measured by Schall (1975) for the herbivorous *C. arubensis* in optimal habitats (550–710 vs. 561/ha for *C. murinus*) on Aruba, an arid island near Bonaire. These densities are greater than estimates reported for insectivorous *Cnemidophorus* on the continental mainland (Turner, 1977a). Likewise, our estimates of the density of *Gonatodes antillensis* greatly exceed those reported for *G. albobularis* in Panama (maximum density=130/ha) (Heatwole and Sexton, 1966). Although detailed observations are generally lacking, local concentrations of geckos on islands may be very high (Cagle, 1946).

There are very few comparable measures of number of individuals and biomass of lizards within a single community; previous investigators have generally concentrated on only one species rather than on the total herpetological fauna. Estimates of the total biomass of lizards in other arid-zone areas are reported in Table 5. On the basis of these unfortunately limited data, both the tropical and temperate mainland communities previously examined support a substantially smaller biomass of lizards than does this tropical island.

Table 5. Estimates of lizard biomass in arid regions

Area	Habitat	No. of Species	Biomass kg/ha	Reference
Bonaire	Thornscrub	3	23.4	This study
Kenya	Arid scrub and desert	2-9	0.2-4.0	Western, 1974
Ivory Coast	Savannah	8	0.1-0.3	Barbault, 1967
Western U.S.	Desert	5	0.4-0.7	Turner, 1977b

Table 6. Estimates of field maintenance energy requirements (respiratory metabolism) of populations of small vertebrates

Maintenance metabolism				
	Habitat	No. of Species	kJ/(ha × day)	Reference
Lizards	Thornscrub	3	3,580 ^a 1,544 ^b	This study
Small mammals	Desert	13	1,150	Chew and Chew, 1970
	Taiga	5	2,050	Grodziński, 1971
	Alpine meadow	2	687	Grodziński et al., 1966
	Old field	2	2,010	Golley, 1960
	Old field	2 ^c	1,750	Odum et al., 1962

^a Field Active^b Minimal^c One bird species; active period of year

Energy Utilization

The energetic demand (respiratory metabolism) of the lizard community of Bonaire is high: approximately 3600 kJ/(ha × day) [1500 kJ/(ha × day) minimal estimate]. This value is considerably above that previously assumed to be the upper limit of energy intake by lizard populations [1400 kJ/(ha × day) by Darevskij and Terentev (1967)]. It also greatly exceeds the maximum monthly values measured for populations of individual species of North American desert lizards: *Uta stansburiana* [49 kJ/(ha × day), Turner et al., 1976], *Sauromalus obesus* [193 kJ/(ha × day), Nagy, 1971]. It is also much greater than that reported for populations of salamanders in a temperate-zone forest community [~40 kJ/(ha × day); ~100 kJ/(ha × day) including production] (Burton and Likens, 1975).

The rate of respiratory metabolism of these lizard populations is even greater than that estimated for populations of small mammals in temperate areas (Table 6). These comparisons are even more striking considering that the rate of field metabolic expenditure of individual small lizards is less than 3% that of a bird or mammal of the same size (Bennett and Nagy, 1977). Consequently, it is the very great density of animals and not high individual metabolic rates which is responsible for the high metabolic expenditure of these populations.

These lizards are clearly major consumers in their community and, because of their much greater efficiencies of secondary productivity (Engelmann, 1966; Golley, 1968; McNeill and Lawson, 1970), may account for even greater levels of production and energy turnover than do populations of small homeotherms. Such a situation has been demonstrated (Burton and Likens, 1975) in a temperate zone deciduous forest community in which the ectothermic vertebrates are salamanders, rather than lizards.

We are cognizant of the many difficulties associated with a study of this type. Many estimates may be open to errors, particularly those involving animal densities and the cost of field existence, and these may influence the magnitude of our results. We have attempted to use conservative estimates of these factors. This study was carried out for only one month, and there are undoubtedly seasonal and year-to-year fluctuations in animal abundance. However, the climate of the island is not highly seasonal, the larger animals appear to be fairly long-lived, and juveniles do not constitute a large proportion of the biomass measured or the metabolic costs estimated. In spite of the conservative nature of our estimates, our measurements indicate quite clearly the tremendous energetic impact of the lizards on this island community. We anticipate that further studies on the energetics of lizards on Caribbean islands will demonstrate even greater levels of energy turnover. We agree with the conclusion of Turner et al. (1976) that the significance of small lizards to the energetic dynamics of natural communities has not generally been appreciated and has been underestimated.

Acknowledgements. We thank Todd Gleeson for extensive field assistance during this study. Rudi Berkelhamer, Christine Fraizer, Robert Goodrich, and Sara Jones also assisted with data collection and we are grateful for their help. This research was supported by NSF grants PCM 75-10100 and PCM 77-24208 to AFB, and NSF Grant DEB 77-0359 to GCG.

References

- Andrews, R.: Evolution of life histories in island and mainland *Anolis*. *Breviora*, in press (1979)
- Andrews, R.M., Asato, T.: Energy utilization of a tropical lizard. *Comp. Biochem. Physiol.* **58A**, 57-62 (1977)
- Barbault, R.: Recherches écologiques dans la savane de Lamto (Côte d'Ivoire): Le cycle annuel de la biomasse des amphibiens et des reptiles. *La Terre et la Vie* **3**, 297-318 (1967)
- Bennett, A.F., Dawson, W.R.: Metabolism. In: *Biology of the Reptilia*, Vol. 5 (Physiology A) (C. Gans, W.R. Dawson, eds.), pp. 127-223. New York: Academic Press, 1976
- Bennett, A.F., Gleeson, T.T.: Activity metabolism in the lizard *Sceloporus occidentalis*. *Physiol. Zool.* **49**, 65-76 (1976)
- Bennett, A.F., Gleeson, T.T.: Metabolic expenditure and the cost of foraging in *Cnemidophorus murinus*. *Copeia* **1979**, In press (1979)
- Bennett, A.F., Nagy, K.A.: Energy expenditure in free-ranging lizards. *Ecology* **58**, 697-700 (1977)
- Burton, T.M., Likens, G.E.: Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experimental Forest, New Hampshire. *Ecology* **56**, 1068-1080 (1975)
- Cagle, F.R.: A lizard population on Tinian. *Copeia* **1946**, 4-9 (1946)
- Case, T.J.: Species numbers, density compensation, and colonizing ability of lizards on islands in the Gulf of California. *Ecology* **56**, 3-18 (1975)

- Chew, R.M., Chew, A.E.: Energy relationships of the mammals of a desert shrub (*Larrea tridentata*) community. *Ecol. Monogr.* **40**, 1–21 (1970)
- Darevskij, I.S., Terentev, P.V.: Estimation of energy flow through amphibian and reptile populations. In: *Secondary Productivity of Terrestrial Ecosystems*, Vol. 1 (K. Petruszewicz, ed.), pp. 181–197. Warsaw: Państwowe Wydawnictwo Naukowe 1967
- Depocas, F., Hart, J.S.: Use of the Pauling oxygen analyzer for measurement of oxygen consumption of animals in open-circuit systems and in short-lag, closed circuit apparatus. *J. appl. Physiol.* **10**, 388–392 (1957)
- Englemann, M.D.: Energetics, terrestrial field studies, and animal productivity. In: *Advances in Ecological Research*, Vol. 3 (J.B. Cragg, ed.), pp. 73–115. New York: Academic Press 1966
- Golley, F.B.: Energy dynamics of a food chain of an old-field community. *Ecol. Monogr.* **30**, 187–206 (1960)
- Golley, F.B.: Secondary productivity in terrestrial communities. *Am. Zool.* **8**, 53–59 (1968)
- Gorman, G.C., Harwood, R.: Notes on population density, vagility, and activity patterns of the Puerto Rican grass lizard, *Anolis pulchellus* (Reptilia, Lacertilia, Iguanidae). *J. Herpetol.* **1**, 363–368 (1977)
- Grodziński, W.: Energy flow through populations of small mammals in the Alaskan taiga forest. *Acta Theriol.* **16**, 231–275 (1971)
- Grodziński, W., Görecki, A., Janas, K., Migula, P.: Effect of rodents on the primary productivity of alpine meadows in Bieszczady Mountains. *Acta Theriol.* **11**, 419–431 (1966)
- Heatwole, H., Sexton, O.J.: Herpetofaunal comparisons between two climatic zones of Panama. *Am. Midl. Nat.* **75**, 45–60 (1966)
- Hummelink, P.W.: A survey of the mammals, lizards, and mollusks. *Stud. Fauna Curaçao, Aruba, Bonaire and Venezuelan Islands* **1**, 59–108 (1940)
- Hummelink, P.W.: Landfauna. In: *Field Guide to National Park Washington*, No. 9, pp. 37–43. Netherlands Antilles National Parks Foundation 1975
- Janzen, D.H.: Sweep samples of tropical foliage insects: Effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* **54**, 687–708 (1973)
- McManus, J.J., Nellis, D.W.: Temperature and metabolism of a tropical lizard, *Anolis acutus*. *Comp. Biochem. Physiol.* **45A**, 403–410 (1973)
- McNeill, S., Lawton, J.H.: Annual production and respiration in animal populations. *Nature* **225**, 472–474 (1970)
- Mueller, C.F.: Energy utilization in the lizards *Sceloporus graciosus* and *S. occidentalis*. *J. Herpetol.* **4**, 131–134 (1970)
- Mullen, R.K.: Respiratory metabolism and body water turnover rates of *Perognathus formosus* in its natural environment. *Comp. Biochem. Physiol.* **32**, 259–265 (1970)
- Mullen R.K.: Energy metabolism and body water turnover rates of two species of free-living kangaroo rats. *Dipodomys merriami* and *Dipodomys microps*. *Comp. Biochem. Physiol.* **39A**, 379–390 (1971)
- Nagy, K.A.: Seasonal metabolism of water, energy and electrolytes in a field population of desert lizards, *Sauromalus obesus*. Ph. D. thesis, Univ. of California, Riverside 1971
- Nagy, K.A., Shoemaker, V.H.: Energy and nitrogen budgets of the free-living desert lizard *Sauromalus obesus*. *Physiol. Zool.* **48**, 252–262 (1975)
- Odum, E.P., Connell, C.E., Davenport, L.B.: Population energy flow of three primary consumer components of old-field ecosystems. *Ecology* **43**, 88–96 (1962)
- Pough, F.H.: Lizard energetics and diet. *Ecology* **54**, 837–944 (1973)
- Schall, J.J.: Relations among three macroteiid lizards on Aruba Island. *J. Herpetol.* **7**, 289–295 (1973)
- Schall, J.J.: Factors influencing the distribution of the Aruban whiptail lizard, *Cnemidophorus arubensis*. *Stud. Fauna Curaçao and Car. Isl.* **46**, 94–108 (1975)
- Scott, N.J., Jr: The abundance and diversity of the herpetofaunas of tropical forest litter. *Biotropica* **8**, 41–58 (1976)
- Soulé, M.: Trends in the insular radiation of a lizard. *Am. Nat.* **100**, 47–64 (1966)
- Stoffers, A.L.: The vegetation of the Netherlands Antilles. *Stud. Flora Curaçao, Aruba, Bonaire, and other Caribbean Islands* **1**, 1–142 (1956)

- Turner, F.B.: The dynamics of populations of squamates, crocodylians and rhynchocephalians. In: *Biology of the Reptilia*, Vol. 7 (C. Gans and D.W. Tinkle, eds.), pp. 157-264. New York: Academic Press, 1977a
- Turner, F.B.: Rock Valley validation site report. US/IBP Desert Biome Res. Memo. 77-2 (1977b)
- Turner, F.B., Medica, P.A., Kowalewsky, B.W.: Energy utilization by a desert lizard (*Uta stansburiana*). US/IBP Desert Biome. Monogr. 1 (1976)
- Utter, J.M., LeFebvre, E.A.: Energy expenditure for free flight by the Purple Martin (*Progne subis*). *Comp. Biochem. Physiol.* **35**, 713-719 (1970)
- Western, D.: The distribution, density and biomass density of lizards in a semi-arid environment of northern Kenya. *E. Afr. Wildl. J.* **12**, 49-62 (1974)
- Wright, S.J.: Interclass density compensation: The *Anolis* lizards and insectivorous birds of the West Indies. *Am. Nat.*, in press (1979)

Received April 1, 1979