

Ecology and Energetics of the Island Night Lizard, *Xantusia riversiana*, on San Clemente Island, California

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Abstract - A population of island night lizards, *Xantusia riversiana*, inhabiting a rocky maritime desert scrub habitat on San Clemente Island was studied during the years 1979-1986. Population density in this habitat was $1,458 \pm 103$ SE lizards per ha. Mean growth rate in the first year of life was 0.05 mm/day, and growth rate in the second year was 0.03 mm/day. Lizards recaptured at 6 mo intervals were found at the same rock shelter in 45% of samples; lizards that moved were recaptured at mean 3.0 m from the previous site. *Xantusia riversiana* had a field metabolic rate about one third that expected for a similar sized iguanid lizard. The life history of *X. riversiana* is characterized by extremes of slow growth, low reproductive potential, longevity and sedentary behavior. The high population density attained by *X. riversiana* is probably the result of: 1) low predation and abundant retreats in an island habitat with a mixture of rocks and thickets of shrubs and 2) the low energy requirements and sedentary behavior of these reclusive lizards.

Introduction

The island night lizard, *Xantusia riversiana*, is a distinctive reptile in numerous aspects of its biology. It is an island endemic confined to three of the California Islands: San Clemente Island, San Nicolas Island and Santa Barbara Island. Adults are 65-109 mm in snout vent length (Goldberg & Bezy 1974), and while moderate in size for lizards, *X. riversiana* is considerably larger than mainland *Xantusia* (i.e., *X. vigilis* and *X. henshawi*). In an analysis of morphology, karyology and protein electrophoretic differentiation, Bezy & co-authors

(1980) concluded that *X. riversiana* exhibited the greatest divergence from mainland relatives among extant California Island vertebrates. Such singularity has given this lizard recognition as a monotypic genus (*Klauberina*) by some authors (Savage 1957, 1963; Crother *et al.* 1986). Like other members of the family, Xantusiidae, *X. riversiana* is very secretive and confines activity to shelter in the form of dense vegetation and rocks (Regal 1968). Despite the common name, "night lizards", *Xantusia* species have circadian cycles of metabolic rate, locomotor activity and heat seeking behavior that indicate they are active primarily by day (Regal 1967; Lee 1974; Mautz & Case 1974; Mautz 1979), and live trap capture rate of *X. riversiana* on Santa Barbara Island is maximal at midday (Fellers & Drost, 1991). Standard metabolic rates of *X. riversiana* and other xantusiids are unusually low, being about half those of equivalent sized lizards in other families, and similar to those of salamanders (Feder 1976; Mautz 1979). In contrast to the largely carnivorous mainland *Xantusia*, *X. riversiana* consumes a variety of plant species which may amount to some 30% of the diet (Knowlton 1949; Schwenkmeyer 1949; Brattstrom 1952).

Studies of the life history characteristics of *Xantusia riversiana* (Goldberg & Bezy 1974; Bezy *et al.* 1980) and of mainland *X. vigilis* and *X. henshawi* (Miller 1951, 1954; Zweifel & Lowe 1966; Lee 1975) reveal an extreme pattern among lizards of slow growth, late maturation, low reproductive rate, long lifespan and low predation rate. Investigations of the reproductive biology of *X. riversiana* (Goldberg & Bezy 1974; Bezy *et al.* 1980) have shown that the sex ratio of neonates is 1:1. Males mature in the spring of their third year at a snout-vent

length of about 65 mm while females probably delay maturity to the fourth year at 75 mm body length. Breeding begins in March and broods of 2-7 (\bar{x} 4.4) young are born in September. Only half of the adult female population appears to breed in a given year, further reducing the reproductive potential of this xantusiid. A recent study (Fellers & Drost, 1991) of the Santa Barbara Island population of *X. riversiana* shows a similar pattern of reproductive characteristics.

The reproductive biology of *Xantusia riversiana* is indicative of a species potentially sensitive to ecological disturbance. That this lizard also is confined to a relatively small and insular geographic range reinforces this possibility; moreover, the island habitats have a recent history of damage by introductions of exotic plants and animals. In consequence, *X. riversiana* has been listed as a threatened species by the U. S. Fish & Wildlife Service. Demographic parameters such as growth, longevity, home range and population density are poorly known for *X. riversiana*. Because this information is important in understanding its population status, this study was initiated to measure density, growth and movements of a population of *X. riversiana* on San Clemente Island. A similar investigation on Santa Barbara Island (Fellers & Drost, 1991) provides a comparison of *X. riversiana* populations on the two islands.

Materials and Methods

Field work was conducted on San Clemente Island during the years 1979 through 1986 in a rocky maritime desert scrub habitat. An initial survey of San Clemente Island indicated that this habitat supported the highest densities of *Xantusia riversiana* on the island. The community is dominated by low shrubs and cacti (*Lycium californicum*, *Berberocactus emoryi*, *Opuntia littoralis* and *O. prolifera*) and occupies the first old beach terrace bordering the southwest facing length of the island. The study site was located 1.7 km north of Eel

Point and consisted of a quadrat 190 m² in area which was extended after the first year to 500 m². The maritime desert scrub habitat on San Clemente Island bears scattered outcrops of rock with abundant loose boulders and smaller surface stones that provide retreats for *X. riversiana*. Lizards were sampled by systematically turning all rocks that might shelter the animals. Lizards were captured by hand and permanently marked by clipping toes. Snout-vent length and tail length were recorded to the nearest millimeter and body mass was measured to the nearest 0.1 g. Sex was determined by presence or absence of hemipenes in lizards in the third year or more of life. Capture position was plotted on a map of the rock shelters on the site.

A sampling interval of 6 mo was selected based on the sensitivity of the habitat to disturbance and the biology of xantusiid lizards. It was apparent in the beginning of the study that a thorough survey of accessible lizard retreats could not be repeated more often than semi-annually without visibly altering the habitat. The effects of repeated rock turning resulted in stones being perceptibly unsettled on the ground, and an adverse effect on vegetation of repeated walks on the plot also could be detected. Sampling period was then changed to 6 mo intervals. A low sampling frequency also was appropriate, because demographic studies of *Xantusia vigilis* (Miller 1951; Zweifel & Lowe 1966) and *X. henshawi* (Lee 1975) showed these lizards to be late maturing, long lived, sedentary, and by inference, sustaining low predation rates. *Xantusia riversiana* was likely to exhibit a similar life history and late maturation had been documented by Goldberg & Bezy (1974). The low sampling frequency was expected to permit mixing of marked and unmarked animals between examined and inaccessible retreats on the plot, but not introduce biases of mortality, immigration and emigration any more severe than in other studies of less sedentary and reclusive lizards sampled more frequently. During the 7 years of the study the site was

sampled in November-December, just after young of the year were born and in May-June, except in 1981 when no samples were made and in 1983 when only the winter sample was made.

Population density was estimated by chain capture-recapture analysis using the regression method (Schumacher & Eschmeyer 1943; Blower *et al.* 1981) as advocated by Turner (1977) for lizard demographic studies. Following the first year estimate based on 5 samples, subsequent estimates were based on 3 successive samples over each 1 yr period beginning and ending with winter samples and excluding new young of the year from consideration in the final sample.

Results

Xantusia riversiana is found in all major habitats on San Clemente Island except a stabilized sand dune habitat along the northwest coast which offers scant vegetative cover and no rock shelters. Presence of suitable cover clearly was important to the lizards, as both lizard abundance and shelter were highly variable in other habitats. Rocky *Lycium* maritime desert scrub supports particularly dense populations of *X. riversiana*. Cover for the lizards includes loose stones on the ground, crevices in low-lying outcrops of rocks, matlike thickets of vegetation (especially *Lycium*, *Atriplex* and clusters of *Opuntia* and *Berberocactus* cacti) and crevices in the soil. Rocky *Lycium* maritime desert scrub offers the full diversity of these retreats and the low (0.3 m) *Lycium californicum* shrubs form a mosaic thicket within which the lizards move with minimal exposure. Loose stones on the study site were abundant (approximately 1 in each 6 m²) and provided a means of sampling most of the available retreats. Although circadian rhythm studies indicate the lizards are diurnally active (Regal 1968; Mautz 1979), lizards were sighted abroad on only two occasions during the study. A total of 120 *X. riversiana* were marked and 70 of these individuals were recaptured one or more times. Among 57 adult lizards captured, 25 were males and 32 were

females, however the sample sex ratio was not significantly different from an expected value of 1:1 (Chi Square statistic = 0.86, $P < 0.35$).

The lizards are extremely sedentary as shown in a frequency distribution of recapture distances (Fig. 1). For recaptures over 6 mo intervals, 45% occurred at the same rock shelter. Lizards that changed shelters moved an average of only 3.0 m, and the longest distance recorded for any lizard over any time interval was an 18.5 m displacement in a 1 yr period. Six lizards were recaptured 4 - 9 times during the study. Areas of convex polygons enclosing capture sites and corrected for sample size bias (Jennrich & Turner, 1969) ranged from 1.0 - 204 m², $\bar{x} = 84$, SE = 33. These polygons covered movements between shelters occurring over periods of 3 - 6.5 yr, and while they are not good estimates of home range in the usual sense of an area that an animal traverses in daily activities (Burt 1943), the data illustrate the extraordinary sedentary behavior of *Xantusia riversiana*.

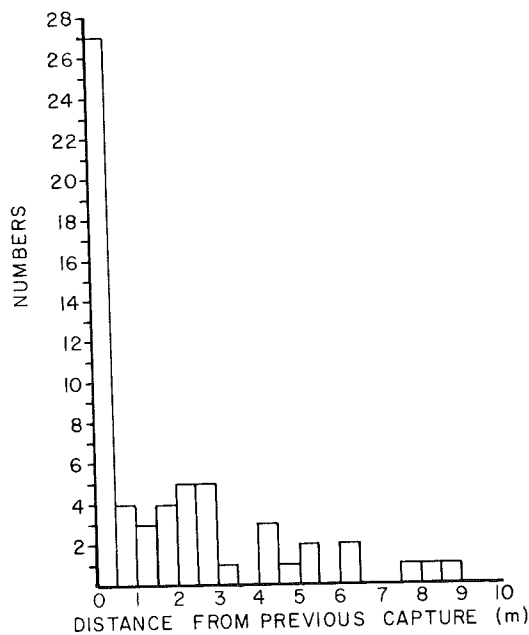


Figure 1. Distances moved by *Xantusia riversiana* recaptured at intervals of six months.

Figure 2 shows snout-vent length distributions for winter (November-December) samples, and a growth curve derived from recaptured lizards is shown in Figure 3. In winter, the neonate and yearling age classes are usually identifiable based on size alone. In 1983, however, conditions favored rapid growth, and the yearling age class in that winter's sample overlapped the range of lizards that were older in other years. The break point in the 1983 sample between these yearlings and individuals entering their third year was clearly established both by clustering of the distribution for that year and by recapture of marked individuals. Snout-vent length of adult female *Xantusia riversiana* exceeded that of males. Lengths of adult lizards at first capture over 1982-1986 (when the study plot was 500 m²) was 71.3 ± 1.7 mm SE for males ($n = 20$) and 76.9 ± 2.1 mm SE for females ($n = 23$). The difference is significant ($t = 2.1, P < 0.05$).

The growth curve in Figure 3 shows the snout-vent lengths of lizards of known age drawn from winter samples in all years of the study. Neonate and yearling age classes were identified by body size and the illustration includes all lizards, marked and unmarked, in winter samples of these age classes. Marked neonate lizards recaptured at the end of their first year grew at an average of 0.049 ± 0.004 SE mm/day ($n = 14$) and growth of yearlings over their second year averaged 0.034 ± 0.023 SE mm/day ($n = 12$). Data in Figure 3 for adult lizards of known age are based on recaptures of individuals marked as neonates or yearlings in previous years. Growth rate of adults continued to decline with age, however, lizards in their seventh and eighth years (age 6 and 7) were still some 10 mm short of maximum lengths observed in the general population, and other lizards initially captured as large adults of unknown age must have been considerably older. For instance, an individual female first captured in summer of 1980 at 92 mm snout-vent length was recaptured in 8 subsequent samples and showed no measurable growth from 1983 at

94 mm through her most recent capture in winter of 1986. Under the assumption that this individual was older than 7 yrs at first capture, her age at the most recent capture was greater than 13 yrs. Another female captured in a pitfall trap 0.8 km from the present study site was 68 mm in January 1976 and likely to have been in her fourth year (age 3). The lizard measured 88 mm when recaptured in August of 1980, and on the most recent recapture in December of 1983, she was 91 mm in snout-vent length. If the initial estimate of age was accurate, this lizard was entering her twelfth year when last recorded.

Estimates of population density of *Xantusia riversiana* on the study plot are given in Table 1. An average of 22 lizards were caught in each sample of the 502 m² plot and an average of 49% of lizards captured in a sample were recaptured in the next sample. Although the values of density show an increase between the two early and two most recent estimates, the increase is not statistically significant, and the values were averaged to yield an estimate of average density over the total time period sampled.

Discussion

The distinctive suite of life history traits reported for mainland *Xantusia* (Zweifel & Lowe 1966; Lee 1975) characterizes the insular *X. riversiana* as well. When compared to lizard species in other families, *Xantusia* species grow slowly, are late to mature, long lived and have an extraordinarily low reproductive potential (Goldberg & Bezy 1974).

Growth of *Xantusia riversiana* during the first year of life (0.049 mm/day) is lower than hatchling growth rates of 40 species of lizards representing 6 other families, and only *X. vigilis* at 0.020 mm/day and *X. benshawi* at 0.019 mm/day have lower growth rates (Zweifel & Lowe 1966; Lee 1975; Andrews 1982). In 1983, the relatively rapid growth rate of 0.053 mm/day observed in neonate *X. riversiana* over their first year (Fig. 2) was probably related to

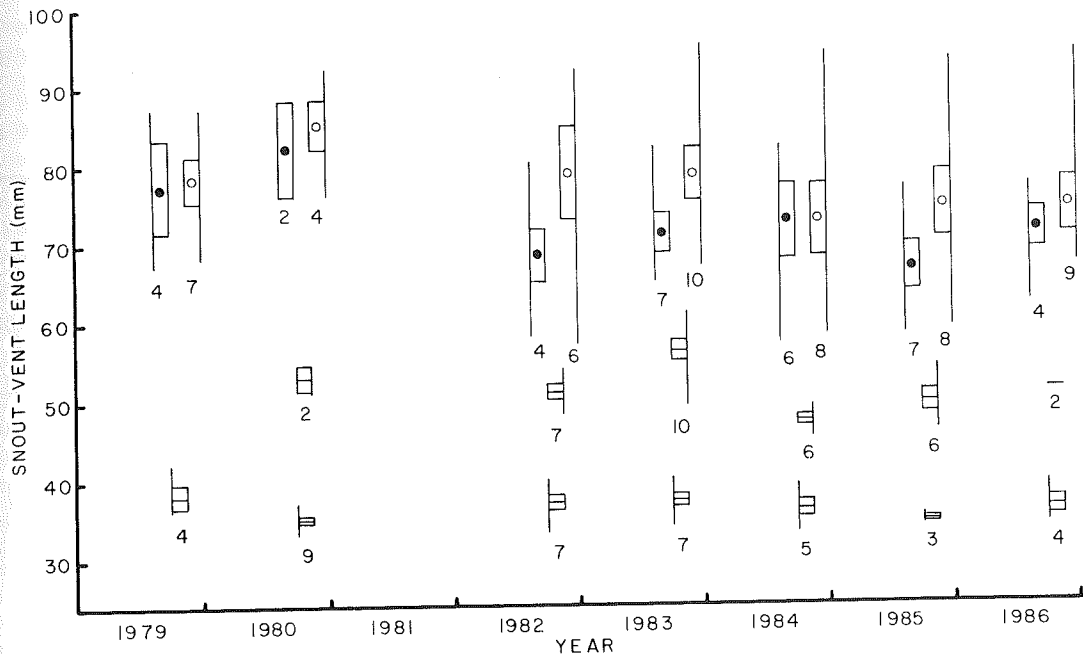


Figure 2. Snout-vent length distributions of *Xantusia riversiana*. Data were collected in November-December and are $\bar{x} \pm SE$ and range. Numbers are sample sizes and the adult age class is distinguished as males (solid circles) and females (open circles).

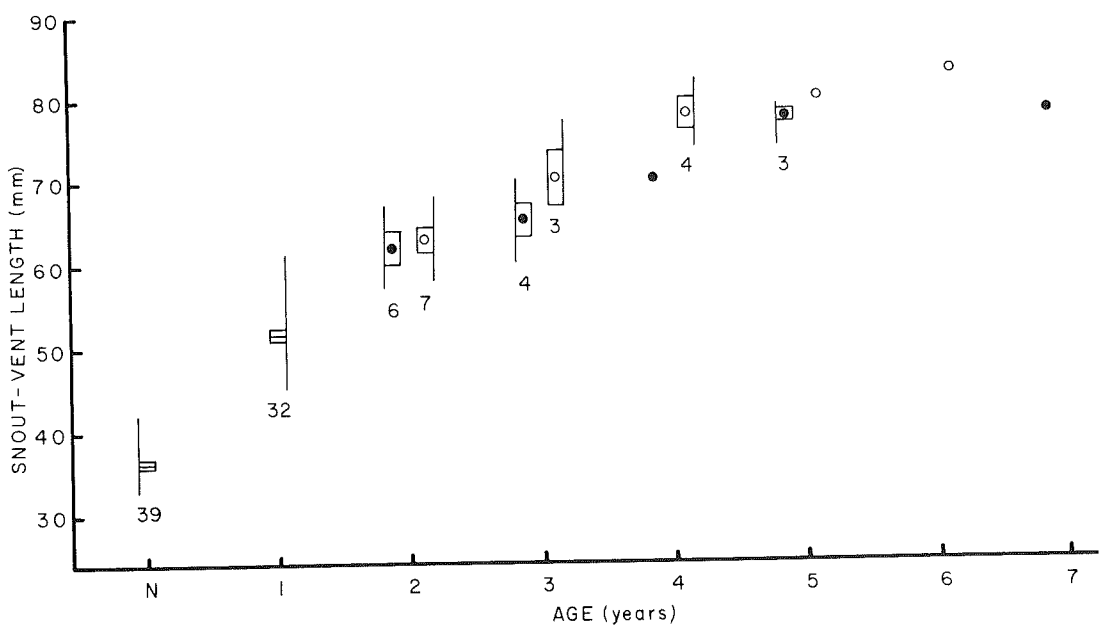


Figure 3. Snout-vent length of *Xantusia riversiana* of known age. Data are $\bar{x} \pm SE$ and range. Numbers are sample sizes, solid circles are males and open circles are females.

exceptionally wet conditions in southern California early in 1983. Rainfall records were not available for San Clemente Island, however, annual rainfall averaged for the three nearest weather stations (Avalon on Santa Catalina Island, Long Beach and San Diego) was 145% greater than normal in 1983 (U.S. Weather Service, Climatological Data). In all other years of the study the average departure from normal annual rainfall at these sites ranged from -31% to +75%. The increased rain in 1983 was concentrated in a series of storms in February, March and April, and these months accounted for 57% of the total annual precipitation at the three stations in 1983. The large size of the 1 yr old lizards measured the following winter probably is related to the relatively wet conditions prevailing the previous spring.

Frequency distributions of body length revealed distinct age classes in the first and second year of life (Fig. 2), but lengths of older animals have overlapping distributions. Goldberg & Bezy (1974) established body length at maturation of *Xantusia riversiana* at 65 mm for males and 75 mm for females, and estimated age at maturity as spring of the third year (males) and fourth year (females). Body lengths of adult *X. riversiana* of known age (Fig. 3) confirm these estimates. Males entering their third year in winter were 62 mm, and females entering their fourth year were 70 mm. By the following winter, the average length of each sex and age class had exceeded Goldberg & Bezy's (1974) estimated maturation length.

The long lifespan of *Xantusia riversiana* is evidenced by the fact that lizards at age 5 yr had reached only 80% of maximum adult body length and individual large adults were recaptured that were at least 12 and 13 yr old. Recapture data are insufficient to construct a vertical life table for adult *X. riversiana*, however, the structure of the young age classes (Fig. 2) indicates a population with a low annual turnover rate. In combined winter samples the neonate age class accounts for only 25% of the lizards, which is similar to the 22%

Table 1. Population density of *Xantusia riversiana* in *Lycium* maritime desert scrub habitat on San Clemente Island. Estimates were based on successive mark-recapture samples (Schumacher & Eschmeyer, 1943) over the designated year. The sample plot was 190 m² in 1980 and 502 m² in subsequent years.

Year	Number of Samples	Total Lizards Caught in Annual Set of Samples	Population Density (lizards/ha)
1980	5	47	1337
1984	3	65	1230
1985	3	76	1632
1986	3	60	1633
			\bar{x} 1456 ± 206 SD

proportion observed for *X. vigilis* (Zweifel & Lowe 1966). The yearling age class of *X. riversiana* numbered 85% of neonate numbers, again similar to an estimated 88% 1 yr survivorship of *X. vigilis* neonates (Zweifel & Lowe 1966). Mature *X. riversiana* (males at least 65 mm and females at least 75 mm) comprised 60% of the combined summer samples ($n = 65$ lizards). The population structure of *X. riversiana* consists of a large proportion of mature lizards with a low reproductive rate and a long lifespan. *Xantusia* species occupy very different habitats ranging from desert through chaparral to the more mesic climatic conditions on San Clemente Island. That the species exhibit such a consistent pattern of life history characters is a strong specific case in support of the idea that phylogenetic constraints are important determinants of life history traits at the familial or lower level (Dunham & Miles, 1985).

The sexual size dimorphism observed in adult *Xantusia riversiana* has been reported for the Santa Barbara Island population (Fellers & Drost 1991), and for the other species of *Xantusia* (Miller 1951; Zweifel & Lowe 1966; Lee 1975). Whether females achieve larger size because they grow faster or because they live longer is an open question. The first possibility would be revealed by the size of recaptured lizards of known age and sex and the second by a skewed sex ratio in the adult population.

Zweifel & Lowe (1966) favored the first hypothesis based on growth rate data from multiple recaptures of *X. vigilis*, but sex designation was presumed and not definitive. Snout-vent lengths of *X. riversiana* of known age (Fig. 3) show a trend toward size dimorphism after age 2, but the data are too few to be conclusive. The sex ratio for neonates is 1:1 (Goldberg & Bezy, 1974), and the sex ratio of adults does not differ significantly from 1:1 (Fellers & Drost 1991; this study). However, sex ratio data accumulated from lizards at first adult capture in a long term mark-recapture study emphasize young animals newly recruited to maturity, and may not adequately reflect differential survival of old adults. Goldberg & Bezy (1974) reported that females were more common than males in monthly capture-removal samples, and females are more abundant than males in the annual samples shown in Figure 2. Combined data from all winter samples (Fig. 2) and the summer samples include 82 females and 54 males, and the sex ratio of females to males = 1.5, (Chi Square = 5.8, $P < 0.03$, $n = 136$). While this data set is not biased toward young adults, it contains multiple entries for recaptured adult individuals. The evidence for either explanation of size dimorphism is equivocal; a large independent sample of lizard sexes and age-size data will be required to resolve this question.

The extreme sedentary behavior and high population density of *Xantusia riversiana* were two surprising discoveries of this study. The fact that such a large proportion of recaptures occurred at the same rock shelter as the previous capture suggests that *X. riversiana* may occupy a single retreat for an extended period and may move to a new shelter when displaced by relatively infrequent events. Four of the 6 lizards recaptured 4 - 9 times over periods of 3.5 - 6 yr exhibited strings of captures at one shelter among movements to new shelters. The home range associated with daily activity has been studied in the Santa Barbara Island population (Fellers & Drost 1991) and averages

17 m², a considerably smaller area than the 84 m² area in the present study based on polygons enclosing long term displacements.

The estimate of population density for *Xantusia riversiana* in *Lycium* maritime desert scrub habitat on San Clemente Island (Table 1) is high among lizard species, and Fellers & Drost (1991) also report high densities on Santa Barbara Island ranging up to 3,200 lizards/ha in *Lycium* scrub habitat. The higher densities reported from Santa Barbara Island are likely due to differences in vegetative cover in this habitat. Fellers & Drost (1991) sampled patches of *Lycium* for their estimates of lizard density. *Lycium* maritime desert scrub on San Clemente Island is more open and the quadrat sampled for the present study contained a mosaic of shrubs and open ground with grasses and herbaceous vegetation. Population densities of *X. riversiana* exceed density estimates for most mainland lizards (Turner 1977), but populations of many island species of lizards are equally or more dense than those of *X. riversiana* (Andrews 1979; Bennett & Gorman 1979; Schoener & Schoener 1980; Barbault & Mou 1988; Hasegawa 1990). While available retreats may limit the population size of *X. riversiana*, as is likely for mainland *Xantusia* (Zweifel & Lowe 1966; Lee 1975), the large numbers of *X. riversiana* observed in maritime desert scrub raises the question of how this semiarid habitat can foster such high densities of lizards. A combination of island ecological factors and the physiological characteristics of xantusiids appear to contribute to the maintenance of high population densities in a habitat apparently undistinguished by high productivity. The islands occupied by *X. riversiana* have 1 or no other lizard species and only 2 - 4 small rodents as potential food competitors (Savage 1967; von Bloeker 1967). It is possible that *X. riversiana* is able to utilize a greater proportion of community productivity than mainland lizard members of more diverse vertebrate assemblages. Furthermore, the omnivorous diet, including about 30% plant material

(Knowlton 1949; Schwenkmeyer 1949; Brattstrom 1952), gives *X. riversiana* a direct link to primary production that is largely unavailable to other species of similar sized lizards (Pough 1973, 1983). Such access to lower trophic levels provides a broad resource base in support of higher population densities. The population structure is indicative of low predation and significant predators likely are limited to small raptorial birds and feral cats. Secretive behavior reduces exploitation of high lizard densities by predators that cannot penetrate *X. riversiana* retreats. The unique metabolism of xantusiid lizards provides an additional and direct explanation for the capacity of the maritime desert scrub habitat to support high population densities. Standard metabolic rates of xantusiid lizards are about half those of equivalent sized lizards in other families (Mautz 1979). Sedentary behavior and selection of relatively low body temperatures by xantusiids (Brattstrom 1965) further increases the difference in the metabolic energy cost of life between xantusiids and other lizard species. The potentially high energy requirements of a dense population may thus be compensated by low metabolic energy requirements of individual *X. riversiana*.

Daily metabolic energy expenditure of free living *Xantusia riversiana* has been measured during autumn-winter and spring- summer

seasons using the doubly labeled water technique (Mautz & Nagy unpubl.). Energy expenditures for *X. riversiana* with average body masses of the age classes distinguished in Figure 2 are listed in Table 2. These rates for individual lizards are about one third the field energy expenditures of equivalent sized iguanid lizards (Nagy, 1982). An estimate of population energy expenditure is derived in Table 2 assuming a stable age structure and population density. Relative proportions of identified age groups in the *X. riversiana* population were estimated from average relative numbers in winter (Fig. 2) and in summer samples. Densities of separate age groups were estimated from these proportions and from population density (Table 1) which were in turn used to estimate biomass and population daily energy expenditure per unit area. Population daily energy expenditure finally was combined for the two seasons to estimate annual population energy expenditure by *X. riversiana*. Biomass of *X. riversiana* greatly exceeds estimates for the temperate and mainland habitat lizards, *Cnemidophorus tigris*, *Uta stansburiana* and *Gambelia wislizenii* (range 0.05-0.16 kg/ha; Turner *et al.* 1976), and higher values (15 - 81 kg/ha) are found only for the tropical and island habitat teiid, *Cnemidophorus murinus* (Bennett & Gorman 1979) and the large tropical and island habitat land iguana, *Conolophus* (Snell & Christian 1985).

Table 2. Estimates of biomass and annual energy expenditure of *Xantusia riversiana* in maritime desert scrub habitat on San Clemente Island.

Season	Age Class	Relative Proportion in Population	Body Mass (g)	Estimated Density (lizards/ha)	Energy Expenditure (kj/day/lizard)	Biomass (kg/ha)	Population Energy Expenditure (kj/ha/day)
Winter (Sept-Feb)	Neonates	0.25	1.2	364	0.090	0.44	32.9
	Yearlings	0.21	4.1	306	0.232	1.25	71.0
	Adults	0.54	11.6	787	0.521	9.14	410.0
Total				1458		10.83	514.0
Summer (Mar-Aug)	Neonates	0.19	2.7	277	0.168	0.75	46.7
	Yearlings	0.17	6.0	248	0.313	1.49	77.6
	Adults	0.64	14.8	933	0.630	13.91	587.0
Total				1458		16.04	711.0
Total Annual Energy Expenditure (Mj/ha/yr)							224.0

Analyses of energy expenditure of whole populations of lizards are few (Table 3), are derived from a variety of ecological settings and must be interpreted cautiously. All the tropical species in Table 3 except *Cnemidophorus hyperythrus* represent island as well as low latitude populations. Some of the estimates considered only adult lizards. Juvenile age classes may make a relatively small contribution to biomass, but due to greater mass specific metabolic rates of small animals, the impact of juveniles on total population energy expenditure is large. For example, the September energy expenditure rate of a *Uta stansburiana* population (Table 3) was more than double the annual mean and occurred when a preponderance of juveniles reduced mean body mass and led to a greater density of individuals without changing lizard biomass. In

spite of these sources of variability in the available studies of lizards, the *Xantusia riversiana* population on San Clemente Island is prominent with an energy expenditure an order of magnitude greater than other temperate zone lizards. A *Sauromalus obesus* population approached this high rate during the spring; however, this desert herbivore has a strongly seasonal activity pattern, and on an annual basis, energy expenditure of the population is an order of magnitude lower than for *X. riversiana*. Other temperate zone species with measurements available only for the active season also should have lower annual average rates of energy expenditure. In spite of the relatively low energy expenditure of individual *X. riversiana* in comparison to similar sized iguanid species, population energy expenditure of the xantusiid is still very high. This stems

Table 3. Biomass and population energy expenditure of lizards. Data include juvenile age classes except where noted.

Species	Period Sampled	Mean Body Mass (g)	Population Density (lizards/ha)	Biomass (kg/ha)	Energy Expenditure (kj/ha/day)	Reference
Temperate Habitats						
<i>Cnemidophorus tigris</i> (Adults)	March-July	17.3	9.4	0.16	44 ²	Anderson & Karasov 1981, 1988
<i>Sauromalus obesus</i> (Adults)	May Annual Mean	167 167	10 10	1.67 1.67	178 ² 61.3 ²	Nagy & Shoemaker 1975
<i>Sceloporus graciosus</i>	July	3.5	114	0.40	62 ²	Congdon & Tinkle 1982
<i>Uta stansburiana</i>	Maximum Mo. (Sept) Annual Mean Annual Mean	0.81 1.43	185 109	0.15 0.16	59.9 ¹ 25.9 ² 32.9 ²	Turner <i>et al.</i> 1976 Nagy 1983
<i>Xantusia riversiana</i>	Annual Mean	9.2	1458	13.4	613 ²	This Study
Tropical Habitats						
<i>Anolis bonairensis</i>	June	3.2	1318	4.2	693 ¹	Bennett & Gorman 1979
<i>Cnemidophorus hyperythrus</i> (Adults)	August-September	4.4	115	0.51	145 ²	Karasov & Anderson 1984
<i>Cnemidophorus murinus</i>	June	27.4	561	15.4	2510 ¹	Bennett & Gorman 1979
<i>Conolophus pallidus</i>	January-May	4610	3.3	15.0	615 ¹	Snell & Christian 1985
<i>Conolophus subcristatus</i>	January-May	1458	55.5	80.9	3496 ¹	Snell & Christian 1985
<i>Gonatodes antillensis</i>	June	0.8	4200	3.5	379 ¹	Bennett & Gorman 1979

¹Based on laboratory measurements of metabolic rates.

²Based on field measurements with doubly labeled water.

from the fact that *X. riversiana* are moderate in body size and are maintained at very high population densities. Energy expenditure of a hypothetical iguanid lizard population with similar body size, age structure and density is estimated by data in Table 2 and by the iguanid lizard energy expenditure equation of Nagy (1982) to be 1870 kJ/ha/day (about three times higher than the value for the *X. riversiana* population). When considered in terms of population energy expenditure, the high densities of *X. riversiana* are explained partially by the low metabolic rates characteristic of individual xantusiid lizards. Other ecological factors including low competition and low predation in the island habitat and access to an herbivore trophic level also contribute to the high population density.

Xantusia riversiana is considered a threatened species, because: 1) its distribution is restricted to 3 islands; 2) it has an extremely low reproductive rate and 3) the island habitats have been disturbed by populations of feral animals. The presence of *X. riversiana* at a high population density and with a stable age distribution in the *Lycium* maritime desert scrub habitat suggests that this lizard presently is not declining on San Clemente Island, but these data alone do not ensure that the species is not threatened. Population biology of island species of lizards is not well known, but many insular lizards have very dense populations (Case 1975; Andrews 1979; Bennett & Gorman 1979; Schoener & Schoener 1980; Barbault & Mou 1988; Hasegawa 1990), and the status of an island lizard may be more properly evaluated in comparison to other insular species rather than to mainland species. The high density populations of *X. riversiana* on both San Clemente and Santa Barbara Islands are associated particularly with the *Lycium* maritime desert scrub habitats. *Lycium* maritime desert scrub on San Clemente Island is present on the first old beach terrace along the southwest facing length of the island, a narrow band amounting to about 10% of the island's 145 km² area. On Santa Barbara Island, *Lycium* scrub occupies only about 1.7% of the

2.6 km² area of the entire island (Fellers & Drost 1991). Although *X. riversiana* also is found in habitats other than *Lycium* maritime desert scrub on San Clemente Island, it is not clear whether the long term survival of peripheral populations is dependent on the presence of the high density population along the southwest coast.

The special biological characteristics of *Xantusia riversiana* make it highly vulnerable to habitat disturbance. The slow growth rate, late maturation and low reproductive rate are characteristics of a population that cannot tolerate high rates of predation or habitat disturbance, and San Clemente Island habitats have been severely degraded by exotic plants and animals. It is not known precisely when feral mammals were first introduced to the island. Goats may have occupied San Clemente Island for 150 years (Raven 1963), while cats and pigs probably arrived within the last 60 years (J. Larson pers. comm.). Feral goats in large numbers have had a major adverse impact on the vegetation structure of San Clemente Island (Raven 1963), although the *Lycium* maritime desert scrub does not appear to have been as severely altered as have the other island habitats. Feral pigs are much less numerous than goats, but they disturb the habitat by rooting through the soil and vegetation and by turning over stones and possibly preying on *X. riversiana*. If pig populations grow large, they could have a severe impact on the lizard habitat. The fact that the *X. riversiana* population is particularly dense will make it attractive prey to any new predator species that can access the lizards' retreats. Savage (1963) noted that there were no snake species on the 3 islands inhabited by *X. riversiana*, and isolation from snake predators that could penetrate deep recesses sheltering *X. riversiana* may be highly significant to the lizard population. *Lycium* maritime desert scrub is sensitive to physical disturbance. The low spreading shrubs are easily broken by foot or motor traffic, and recovery is slow. Single vehicle tracks over this habitat have been in evidence for at least a

decade and human activities to census the lizards for this study had to be performed with care and at semi-annual frequency to avoid an adverse impact on the vegetation.

The *Lycium* maritime desert scrub of San Clemente Island presently supports a dense population of *Xantusia riversiana* but this habitat has a highly restricted geographic range. To ensure that this unique reptile continues to thrive on the island, *X. riversiana* habitats should be protected from physical disturbance and the degrading influence of exotic plants and animals on the island habitats should be arrested.

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