Autecological Observations of *Acanthodactylus erythrurus* (Sauria: Lacertidae) in Southern Spain

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Abstract. Autecological aspects of *Acanthodactylus erythrurus* were examined at La Algaida, Cádiz Province, Spain. The male population is composed of 60 % adult and 40 % subadult individuals; male hatchlings increase in size at a rate of 0.06 mm/day from hatching ($\leq$ 31 mm snout-vent length) to sexual maturity (~ 61 mm); 50 % do not survive beyond 1.5 years, but those which reach adult size may live 1.9 years. Females grow from hatching (~ 28 mm) to sexual maturity ($\geq$ 57 mm) at a rate of 0.05 mm/day; less than half survive 1.4 years and the life span of some individuals is 2.1 years. Adult males outnumber adult females 1.4:1, but subadult ratios are 1:1. Adults and subadults associate with different plant species during their activity period, but each age class tends to avoid open sand patches. These 8.4—13 g lizards feed on a wide variety of insects and appreciable quantities of plant material. 49 % of all males and 82 % of all females actively consume *Halimium halimifolium*. We suspect this lizard species is wide ranging and non-territorial; only one agonistic encounter was recorded and it was interspecific (with *Psammodromus algirus*). The frequency of escape from predation is estimated at 26.8 %, based on tail-loss figures, and the incidence of cestode parasitism *(Oochoristica* cf. *tuberculata)* is 2.1 %. The population studied was highly resilient to 16 months of intense human predation.

Resúmen. Examinamos aspectos de la autoecología de *Acanthodactylus erythrurus* en La Algaida, provincia de Cádiz, España. La población de machos se compone de 60 % adultos y 40 % subadultos. Los individuos recién nacidos ($\leq$ 31 mm longitud cabeza + tronco) crecen a una velocidad de 0.06 mm/día hasta alcanzar la madurez (~ 61 mm); 50 % de ellos no sobrevive más allá de 1.5 años, pero aquéllos que alcanzan el tamaño adulto pueden llegar hasta 1.9 años de edad. Las hembras recién nacidas (~ 28 mm) crecen 0:05 mm/día hasta alcanzar la madurez ($\geq$ 57 mm); menos de la mitad sobrevive 1.4 años y la máxima longevidad es de alrededor 2.1 años. Los machos adultos exceden a las hembras adultas a razón de 1.4:1, pero esta tasa numérica es 1:1 en los subadultos. Adultos y subadultos se asocian a diferentes especies vegetales durante su período de actividad, pero ambas clases de edad coinciden en evitar espacios arenosos expuestos. Estas lagartijas se alimentan de una amplia variedad de insectos y consumen cantidades apreciables de vegetación pese a su pequeño tamaño (8.4—13 g); 49 % de los machos y 82 % de las hembras consumen *Halimium halimifolium* activamente. Sospechamos que no son territoriales; sólo una vez observamos un encuentro agresivo y fué interespecífico (con *Psammodromus algirus*). El 26.8 % de los individuos escapa intentos de predación a expensas de la cola y el 2.1 % está parasitado por cestodos *(Oochoristica* cf. *tuberculata).* La población estudiada es altamente resistente a la predación humana; no observamos mayores cambios poblacionales al cabo de 16 meses de continua remoción de individuos.

Introduction

Analyses of the activity, thermal environment, and metabolism of a single population of
Acanthodactylus erythrurus (SCHINZ 1833) at La Algaida, Cádiz Province, Spain are available (BUSACK, 1976; POUGH and BUSACK, 1978) and, in an effort to further describe the
ecology of this population, we now analyze the structure and dynamics of the population,
habitat use, diet, predation, parasitism, and effects of intense removal. These data, together with those concerning biogeographic history (BUSACK, 1977) and general biology
(SALVADOR, 1981), provide detailed knowledge of the life of one species of lacertid lizard in southern Spain.

Materials and methods

General

We collected and immediately preserved specimens of *A. erythrurus* from La Algaida
(25.5 km [AIR] NW of Jerez de la Frontera, Cádiz Province, Spain) between May 1970
and November 1971 (see BUSACK [1976] for a full description of the habitat).

At Rota, 25 km from La Algaida, freezing air temperatures are limited to November
through January and maximum temperatures rarely exceed 35 °C (June and July).
Rainfall occurs primarily between December and May. Comparisons with weather records available for the years 1959 through 1971 show that weather conditions from May,
1970 through November, 1971 were average for this area of southern Spain in all respects except rainfall. While precipitation was similar between years (513.9 vs
457.5 mm), each year was drier than normal (660.5 mm).

Prior to December 1970, we collected lizards with dust shot during visits to the same
one-hectare plot for periods of from < 1 to > 8 h. These visits, made without regard to
a schedule, frequently took place more than once monthly but we did not attempt to interdigitate collecting periods with the full daily range of lizard activity. After December
1970, scheduling became more rigorous and followed procedures outlined previously
(BUSACK, 1976). Combined samples totalling 300 males and 229 females, on deposit at
Carnegie Museum of Natural History (CM), provided the data for this report.

Specimens examined

CM 53245, 53282–53288, 53330, 53333, 53350, 53373, 53383, 53397, 53425, 53438, 53471, 53885–53886,
53888–53890, 53916, 54218–54220, 54223, 54225, 54256–54257, 54277, 54279, 54561, 54565, 54592, 54594,
54676, 54789, 54794, 54873, 55305–55328, 55337–55341, 55474, 55659, and 55699–55701.

Population structure and individual growth

We determined sexes of individual lizards by examination of the gonads; the snout-vent length (SVL) of each entire specimen (299 ♂♂, 227 ♀♀) was determined with dial calipers accurate to 0.1 mm. After all specimens had been sexed, measured, separated by
year of capture, and placed into 1.0 mm SVL categories, we analyzed the data in accor-

dance with instructions provided by HARDING (1949). We determined the line(s) of best fit to the resultant sigmoid curve by a Chi-square goodness-of-fit test and defined best fit as the line for which the value of χ^2 was lowest, and for which the $\underline{P}$ level was as close to 1.0 as possible.

There were two size classes present in the male population during 1970 and the point of division between them as 61 mm SVL (Fig. 1). We used specimens for which SVL was $\leq$ 61 mm as our markers for the growing class; presumably growth had slowed considerably in those male individuals > 61 mm SVL. The mean SVL of 299 males collected during both years was 57.6 mm and the mean of the 227 females was 53.8 mm. Since females attain, on average, 93 % of male SVL, we considered females to be members of the growing class if they were $\leq$ 57 mm SVL.

To compute the relationship between the increase in size of the growing class and time, we examined members of the growing class collected between August, 1970 and August, 1971 and converted their dates of collection to Julian dates. The Julian date of our hypothesized date of hatching (15 August) was subtracted from each subsequent collection date to determine the number of days which had elapsed. Each of the 97 males and 77 females then became a single point for regression analysis with SVL as the ordinate and the number of days from hatching as the abscissa. We entered transformed data into linear, logarithmic, exponential, and power curve regression formulae and determined the curve of best fit by choosing that with the highest coefficient of determination (r^2).

Using previously calculated growth relationships to generate age classes we computed survival curves for the males and females of each year. If the size of the La Algaida population remained relatively constant over the period of our 1970 survey, and the age structure within our male and female samples paralleled the survival of individuals within a normal year, then our estimate of the survival curve for 1970 is representative of this population, and that for 1971 reflects the effect of severe predation. The most serious restriction of this technique is that the number of hatchlings must not vary between years; our data are not contrary to this restriction.

Habitat utilization

Field observations

We recorded the microhabitat in which the lizard was first observed; we did not record observations for lizards that changed position unless the lizard's original location could be accurately determined. Since lizards could not be visually separated by sex, but could be categorized as adult or subadult on the basis of size, we considered specimens of 60 mm SVL or larger as adults. We observed lizards either on open sand or beneath or close to shrubs and trees. Identification to the species level of the dominant vegetation allowed us to accurately assign each observation to a precise microhabitat category.

Basic procedures

We evaluated percent cover contributed by each plant species through a modification of the line-intercept method described by MUELLER-DOMBOIS and ELLENBERG (1974).

We constructed 11 transects across projected color transparencies; each transparency clearly illustrated a portion of the study site in which the species identification of plants was unambiguous. Except for *Pinus pinea,* our transects intercepted the canopy of each species. We computed percent cover for *P. pinea,* a fairly tall tree whose canopy generally begins well above ground level, using trunk diameter at the level of the transect. *Chamaerops humilis, Erica scoparia, Myrtus communis,* and *Pistacia lentiscus,* which do occur locally, were not recorded in our transects because of their low density. *Acanthodactylus erythrurus* was rarely associated with these plants and we do not feel that our evaluation of habitat use is seriously affected by this discrepancy.

We combined resulting habitat data into a single "type" description of plant cover on the study site. Plant nomenclature follows TUTIN et al. (1964 et seq.). We recorded use of the 10 microhabitat categories (9 plant species plus open sand) by adult and subadult lizards as a percentage of the total for winter (December–February), spring (March–May), summer (June–August), and fall (September–November).

Statistical procedures

We omitted from statistical analysis those plant species not detected in transects but used by lizards because an infinite number results from having an expected value of 0, and because lizards were very rarely associated with these particular species. We applied KRUSKAL-WALLIS one-way ANOVA (with correction for ties when necessary) to each data set to assess similarity of habitat use among seasons. Our use of a 2 x 10 contingency table allowed comparison of the yearly use of microhabitat categories between adults and subadults.

We used one-tailed procedures to evaluate the statistical significance of the results for these tests.

Diet

Taxonomic composition

We excised stomachs from all specimens and recorded the frequency of all food items. We identified invertebrates to order, vertebrates and plants to species, and used the ocular micrometer of a stereoscopic dissecting microscope to determine the total length of each intact invertebrate. We organized the data for each sex by season.

Quantitative procedures

We recorded and arranged by sex and season the number of prey items per individual stomach, the number of empty stomachs, those stomachs with ants, stomachs containing plant material, and those containing only plant material. Mean prey size (MPS) of invertebrate prey, as used below, is the grand mean obtained by multiplying the length of an individual prey item by the number of items of that length, summing these values over all prey lengths represented, and dividing by the total number of measurable items in the stomach.

We evaluated correlation between SVL and MPS, by sex and within season, with PEARSON's product-moment correlation coefficient, similarity in taxonomic composition of the diet between males and females with PIANKA's (1973) symmetric overlap measure, and trophic diversity per individual (sensu HURTUBIA, 1973) with BRILLOUIN's diversity index (PIELOU, 1969; BUSACK, 1980).

We tested for statistical significance the differences between male and female MPS, SVL, number of prey items per stomach, and trophic diversity using a STUDENT's two-sample t test in which one-tailed procedures identified the directionality of observed seasonal differences. We then collapsed seasonal P values into a single figure for the year by combining probabilities from each of the four independent tests (SOKAL and ROHLF, 1969: 623). We evaluated the statistical significance of differences between sexes in our data recording the frequency of empty stomachs, stomachs with ants, stomachs containing plant material, and stomachs containing only plant material, with the MANN-WHITNEY U-test. We performed two-tailed tests for these data after the lack of seasonal directionality in differences between males and females became obvious.

Predation and Parasitism

Basic procedures

We obtained our data on predation by enumerating those individuals in the population with either intact or regenerated tails. We disregarded specimens with broken tails showing no evidence of regeneration because we could not determine whether the tail had been broken by a predator, or by the collector. We deposited the parasites encountered in the U.S. National Helminthological Collection (USNM 74378) and with the Laboratoire de Zoologie (Vers), Muséum National d'Histoire Naturelle, Paris (MNHN 153 Hb − 164 Hb, Bocal C 91). We determined the frequency of parasitism for each sex, computed as a percentage of the total sample.

Statistical procedures

We compared predation frequency, tabulated by sex and season, between sexes and among seasons by means of 2 x 2 contingency tables incorporating YATES' correction, or with FISHER's exact test. We also tested the differences in the prevalence of parasites between males and females for significance with a 2 x 2 contingency table incorporating YATES' correction.

Results and Discussion

Population Structure and Individual Growth

In 1970, we removed 164 males measuring between 31.0 and 77.5 mm SVL from La Algaida. During 1971 we collected 135 males that ranged between 33.0 and 76.1 mm SVL. Females from 1970 (116) ranged between 28.3 and 69.1 mm SVL; those from 1971 (111)

measured between 30.6 and 68.7 mm SVL. There were no significant differences between the number of males collected in 1970 and those from 1971 ($Yc\chi^2 = 2.82$, $\underline{P} > 0.09$), or between the numbers of females collected ($Yc\chi^2 = 0.11$, $\underline{P} > 0.74$) in each of these two years.

During 1970, male specimens ≥ 61 mm, and those < 61 mm, SVL formed two distinct size classes. A Chi-square test for goodness of fit ($\chi^2 = 12.20$, df $= 41$, $\underline{P} > 0.99$) indicates that 60 % of the 1970 male population (N $= 98$), with an estimated mean and standard deviation of 70.0 $\pm$ 3.35 mm, was ≥ 61 mm. The remaining 40 % measured < 61 mm SVL and the mean of these smaller specimens was estimated at 39.5 $\pm$ 9.25 mm. In 1971, however, we found no significant differences between classes and the line of best fit ($\chi^2 = 12.25$, df $= 39$, $\underline{P} > 0.99$) estimates the mean and standard deviation of 135 specimens at 55.1 $\pm$ 13.41 mm SVL (Fig. 1).

Females showed no size class differentiation within either year ($\chi^2 = 2.56$ [1970], 1.21 [1971]; df $= 33$ [1970], 32 [1971]; $\underline{P} > 0.99$) and the distribution of individuals among the size classes was not different between years ($\underline{F} = 2.04$; df $= 32,31$; $\underline{P} > 0.05$). When regression lines are compared, neither the slopes ($\underline{t} = 4.14$, df $= 63$, $\underline{P} < < 0.001$) nor the means they estimate ($\underline{t} = 1.21$, df $= 225$, $\underline{P} < < 0.001$), are different. The mean SVL of females from either year is estimated at 52.4 mm (see also Fig. 1).

We considered males ≤ 61 mm SVL to belong to the growing class; females, generally smaller than males, were considered to belong to this class if they were ≤ 57 mm SVL. Figure 2 summarizes the growth data; hatchlings entering the population account for the decreasing means between July and September. Our hypothesized growth curves (Fig. 3) suggest that male growth is best described by an exponential equation while female growth best fits a linear equation.

There are apparent between-year differences in sex ratios. During 1970, the adult male : female ratio (98 : 68) was significantly different from 1 : 1 ($Yc\chi^2 = 5.43$, $\underline{P} < 0.02$) while the subadult distribution (66 : 48) is not ($Yc\chi^2 = 2.85$, $\underline{P} > 0.09$). The sex ratio (49 : 58) in the 1971 adult population was not significantly different from 1 : 1 ($Yc\chi^2 = 0.77$, $\underline{P} > 0.38$), but the subadult ratio (86 : 53) was ($Yc\chi^2 = 7.84$, $\underline{P} < 0.01$). When examined on a month by month basis within each year, more males than females were present on the site in May ($Yc\chi^2 = 4.69$, $\underline{P} < 0.03$) and September 1970 ($Yc\chi^2 = 4.88$, $\underline{P} < 0.03$), and during March of 1971 ($Yc\,\chi^2 = 5.48$, $\underline{P} < 0.02$).

Table 1 presents life tables for each sex within 1970 and 1971. We estimate little difference in life spans between sexes; male maximum longevity is 1.9 years, female maximum longevity is 2.1 years.

Because of the removal technique, we feel that only the data for 1970 are instructive in categorizing the natural population structure. Subadults from late 1970 – early 1971 collections, however, provided growth rate data. Removal sampling decreased the probability of including older subadults that may have grown slowly. In essence, we feel that the growth data are best interpreted as estimates from a population in which intraspecific competition has been reduced, both by abnormally high mortality, and by the effect of prior years of high primary productivity.

During 1970, males clearly belonged to two size (i.e. age) classes, 60 % were 61 mm or larger (adult), and 40 % were smaller than 61 mm SVL (subadult). Females were more evenly distributed within size classes than males and this is apparent in the linear regression representative of the 1970 population. Females hatched on or about 15 August
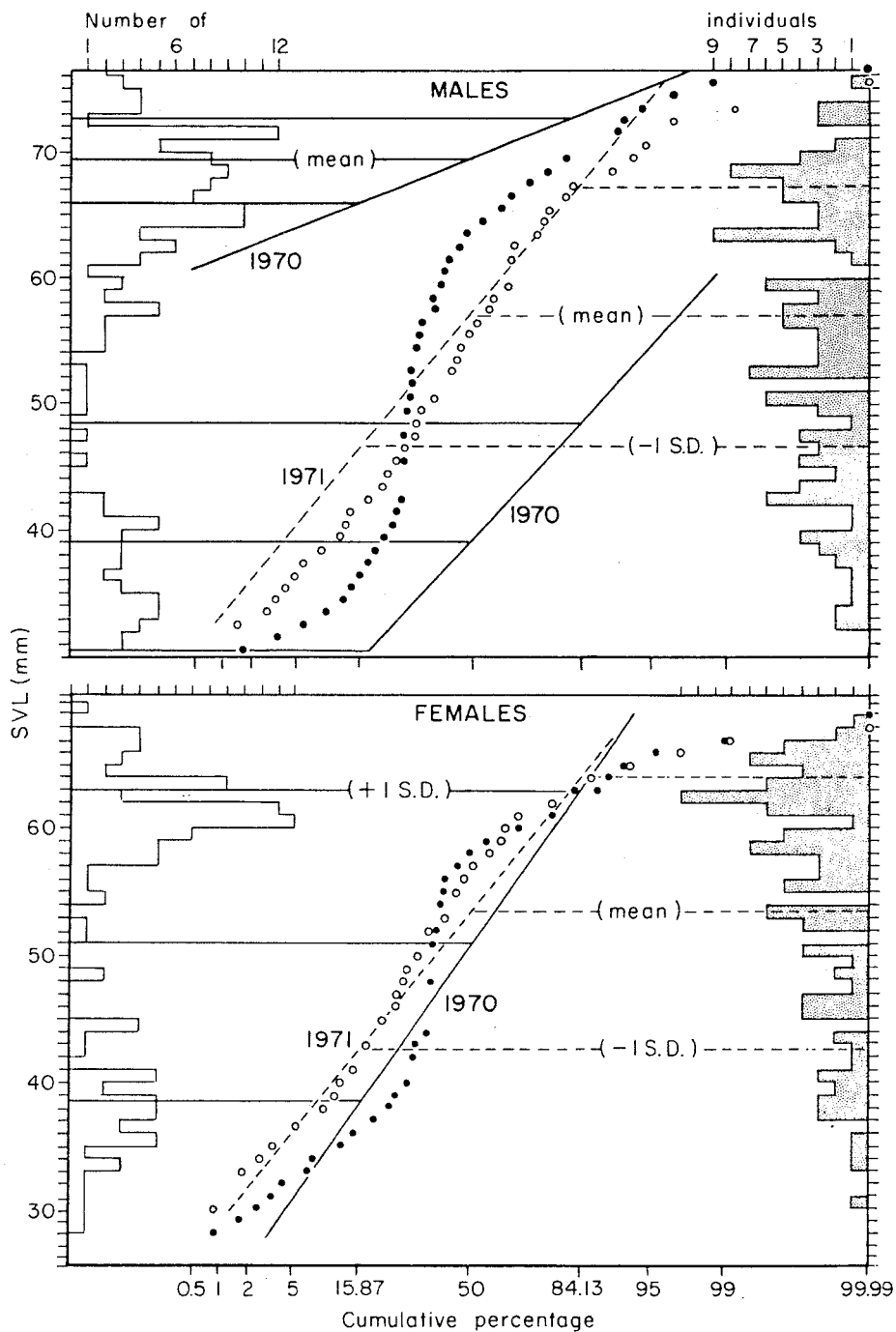
Fig. 1. Structure of 1970 (closed circles, solid lines, open histograms) and 1971 (open circles, dotted lines, closed histograms) male and female populations on La Algaida. Original data plotted on 90-division, Keuffel & Esser (No. 468003) probability paper.
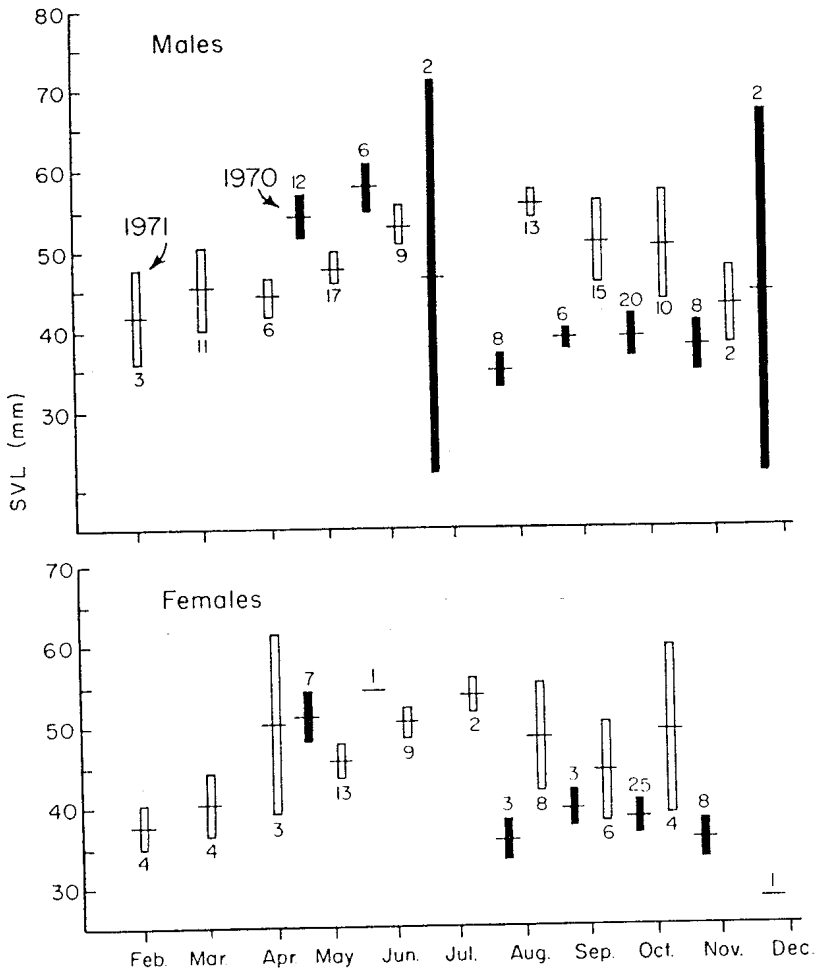
Fig. 2. Mean (± 2 SE) size of the growing class (♂ ≤ 61, ♀ ≤ 57 mm SVL). Sample sizes above data for 1970; below, 1971.

1970 would reach the adult category (≥ 57 mm SVL) by December, 1971, after a period of 1.3 years; males attain adult size (≥ 61 mm SVL) only slightly earlier (November, 1971). These calculations, based on estimates presented in Fig. 3, are not concordant with the three-year-to-maturity period in Morocco (BONS, 1969, 1972).

Males from hatching to 10 months of age (≤ 50 mm SVL) had a higher rate of survival in 1971 than in 1970; female survival from hatching to 14 months of age (≤ 54 mm SVL) was also increased between years (Table 1).

Habitat Utilization

There were no seasonal differences in the use of microhabitat categories by adults ($\underline{H} =$ 5.91, df = 3, $\underline{P}$ > 0.11) or subadults ($\underline{H}$ = 3.42, df = 3, $\underline{P}$ > 0.33; Table 2). While the two
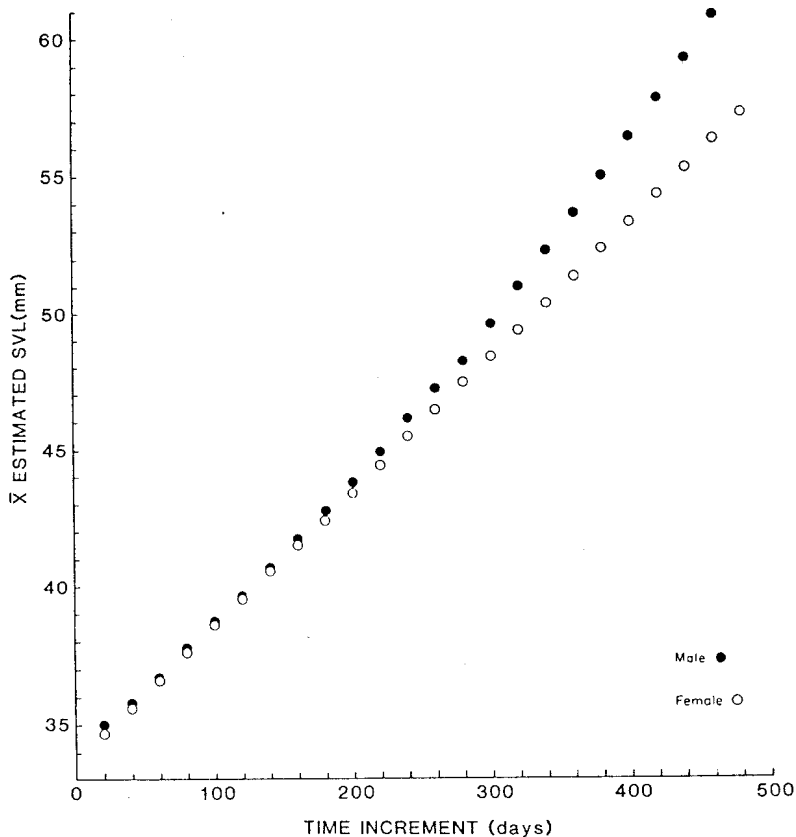
Fig. 3. Idealized growth curves based on August, 1970 through August, 1971 samples. Points illustrated are those estimated for each 20-day interval by the regression formula $Y = 34.07 (+ 0.71, - 0.70) {}_c0.0001 (\pm 8.99 \times 10^{-5}) \times (N = 97, r^2 = 0.67)$, which represents $\sigma\sigma$, or by $Y = 33.7 (\pm 1.01) + 0.05 (\pm 0.01) \times (N = 77, r^2 = 0.60)$, for $\varphi\varphi$; numbers in parentheses are standard errors.

age classes do not seasonally vary their patterns of habitat utilization, they do use the available microhabitats differently. There is a significant difference in habitat use between adults and subadults when the comparison is based on yearly totals ($\chi^2 = 104.10$, df = 9, $\underline{P} < 0.001$; Table 2). The individual numerical contributions to Chi-square demonstrate that the main difference between age classes is that adults appear more frequently associated with *Juniperus phoenicea, Cistus crispus,* and *Halimium halimifolium* than subadults. Subadults are more frequent in *Corema album, Juncus acutus,* and open sand.

Neither adults nor subadults use the microhabitat categories in proportion to their availability on the study site ($\chi^2 = 201.81$ and 177.91, respectively; df = 6, $\underline{P} < 0.001$ in each case). The major discrepancy between on-site availability and the use of microhabitats by adults is the infrequent presence of adults in open sand patches, and in their higher than expected association with *Pinus pinea*. Subadults are disproportionately associated with *C. album* and also use open sand patches less frequently than predicted by their availability in the area.

Table 1. Life tables for *Acanthodactylus erythrurus* at La Algaida for the years 1970 and 1971.

Age Interval (Days)	Number dying during age interval				Number surviving at beginning of interval				Number surviving as a fraction of newborn			
	1970		1971		1970		1971		1970		1971	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
0— 30	15	9	4	3	164	116	135	111	1.000	1.000	1.000	1.000
31— 60	8	8	2	1	149	107	131	108	.909	.922	.970	.973
61— 90	2	5	1	3	141	99	129	107	.860	.853	.956	.964
91—120	6	7	5	5	139	94	128	104	.848	.810	.948	.937
121—150	3	5	4	3	133	87	123	99	.811	.750	.911	.892
151—180	7	0	2	1	130	82	119	96	.793	.707	.881	.865
181—210	2	2	6	3	123	82	117	95	.750	.707	.867	.856
211—240	0	4	6	0	121	80	111	92	.738	.690	.822	.829
241—270	1	0	7	8	121	76	105	92	.738	.655	.778	.829
271—300	1	0	5	1	120	76	98	84	.732	.655	.726	.757
301—330	2	2	9	3	119	76	93	83	.726	.655	.689	.748
331—360	2	0	7	4	117	74	84	80	.713	.638	.622	.721
361—390	2	2	6	4	115	74	77	76	.701	.638	.570	.685
391—420	4	0	8	6	113	72	71	72	.689	.621	.526	.649
421—450	7	3	8	5	109	72	63	66	.665	.621	.467	.595
451—480	9	1	7	3	102	69	55	61	.622	.595	.407	.550
481—510	10	10	11	10	93	68	48	58	.567	.586	.356	.523
511—540	27	7	11	5	83	58	37	48	.506	.500	.274	.432
541—570	17	25	13	7	56	51	26	43	.341	.440	.193	.387
571—600	25	3	6	11	39	26	13	36	.238	.224	.096	.324
601—630	9	9	6	6	14	23	7	25	.085	.198	.052	.225
631—660	5	5	1	11	5	14	1	19	.030	.121	.007	.171
661—690	0	4	0	5	0	9	0	8	.000	.078	.000	.072
691—720		5		3		5		3		.043		.027
721—750		0		0		0		0		.000		.000

Each recognized age class apparently makes a different use of the habitat. Adults seem to preferentially associate with plants different from those used by subadults and, while each age class seems to avoid open sand patches, the tendency to remain in vegetation is more pronounced in adults. Similar results to ours have been reported by Seva and Escarré (1980).

Diet

Taxonomic composition

Insects are numerically the most important prey of both sexes of *A. erythrurus* throughout the year; ants and coleopterans contribute the largest components to the insect portion of the diet (Table 3). Arachnids, represented by spiders, a few scorpions and mites, are conspicuous in stomach samples from all seasons but chilopods and diplopods, while present, are sporadic and rather rare in the diet of these lizards. The remains of an *A. erythrurus* in one of the stomachs indicates cannibalism.

Table 2. Microhabitat category availability and utilization. Figures are percentages; sample sizes appear in the final row.

Microhabitat Categories	Cover avail.	Adults					Subadults				
		Winter	Spring	Summer	Fall	Year	Winter	Spring	Summer	Fall	Year
Plant species											
Chamaerops humilis	*	–	–	–	0.6	0.1	–	–	–	–	0.0
Cistus crispus	2.2	–	1.1	5.8	2.3	4.0	–	0.8	0.5	0.4	0.5
Corema album	24.7	50.0	43.5	29.8	28.3	32.6	64.3	54.7	29.5	43.2	44.5
Halimium halimifolium	8.7	–	6.6	13.7	8.1	10.8	–	4.5	7.0	7.0	5.8
Juncus acutus	1.7	–	1.1	0.2	–	0.4	7.1	1.9	2.0	2.1	2.2
Juniperus phoenicea	17.0	–	22.5	22.7	22.5	22.6	14.3	7.5	11.0	13.2	10.6
Myrtus communis	*	–	–	0.7	0.6	0.5	–	–	1.0	–	0.3
Pinus pinea	0.3	–	1.6	2.2	0.6	1.7	–	0.8	0.5	1.2	0.8
Pistacia lentiscus	*	–	1.6	2.2	1.7	2.0	–	0.4	3.5	–	1.1
Open sand	45.4	50.0	22.0	22.7	35.3	25.3	14.3	29.4	45.0	32.9	34.2
Total by number	–	2	182	445	173	802	28	265	200	243	736

* Not detected in transects; occurs in low abundance and provides little cover.

Table 3. Taxonomic composition of the animal portion of the diet of *A. erythrurus*; plant material is discussed in the text. Figures are percentages by number; subtotals for each class appear in parentheses. Diet similarity is measured with Pianka's overlap formula; (A) = adult, (L) = larva.

Prey categories	Winter ♂♂	Winter ♀♀	Spring ♂♂	Spring ♀♀	Summer ♂♂	Summer ♀♀	Fall ♂♂	Fall ♀♀	Yearly ♂♂	Yearly ♀♀
Arachnida	(.222)	(.128)	(.050)	(.097)	(.046)	(.029)	(.012)	(.023)	(.033)	(.040)
Acarina	—	—	.002	—	—	—	.001	—	.001	.001
Araneae	.222	.107	.046	.088	.033	.020	.010	.019	.026	.033
Scorpionida	—	.021	.002	.009	.013	.009	.001	.004	.006	.007
Chilopoda	(.111)	(.000)	(.006)	(.000)	(.000)	(.001)	(.000)	(.000)	(.002)	(.001)
Diplopoda	(.000)	(.000)	(.000)	(.000)	(.000)	(.000)	(.001)	(.003)	(.001)	(.001)
Insecta	(.667)	(.872)	(.944)	(.903)	(.954)	(.970)	(.987)	(.973)	(.964)	(.957)
Coleoptera(A)	.111	.234	.226	.299	.202	.190	.082	.052	.157	.153
Coleoptera(L)	.111	.064	.065	.050	.029	.016	.004	.003	.027	.018
Diptera(A)	—	.021	.004	.009	.001	.006	.004	.003	.003	.006
Diptera(L)	—	—	—	—	—	.015	.002	—	.001	.006
Hemiptera	—	.043	.024	.050	.009	.022	.020	.043	.017	.036
Homoptera	—	.043	.022	.022	.012	.012	.019	.009	.017	.013
Hymenoptera*	.445	.106	.049	.084	.034	.018	.030	.057	.037	.049
Formicidae	—	.276	.467	.298	.637	.664	.813	.794	.667	.641
Lepidoptera(A)	—	—	—	.003	—	—	.001	—	.007	.003
Lepidoptera(L)	—	—	.022	.003	.004	.007	—	—	.001	—
Neuroptera(A)	—	—	.002	—	.001	—	—	—	.001	—
Neuroptera(L)	—	.021	.030	.069	.012	.015	—	.003	.012	.020
Odonata	—	—	—	—	—	—	.002	.001	.001	.001
Orthoptera	—	.064	.022	.016	.013	.004	.010	.008	.014	.009
Unidentified(L)	—	—	.011	—	—	.001	—	—	.003	.001
Reptilia	(.000)	(.000)	(.000)	(.000)	(.000)	(.000)	(.000)	(.001)	(.000)	(.001)
A. erythrurus	—	—	—	—	—	—	—	.001	—	.001
Total by number	9	47	465	321	678	668	841	752	1993	1788
Diet similarity	.478		.929		.998		.998		.999	

* Formicidae excluded

The taxonomic composition of the diet of males and females is almost identical on both a yearly basis (Pianka's overlap = 0.999, Table 3), and in all seasonal samples except winter. Our small sample size for winter, however, precludes our obtaining a reliable estimate of overlap for this season.

Quantitative description

Mean prey size (MPS, examined seasonally) peaks in spring for both males and females. Since males are consistently larger than females throughout the year, it is not surprising that they consistently take larger prey (Table 4). On a yearly basis, SVL is significantly correlated with MPS for males ($r = 0.471$, df = 224, $P < 0.001$) and females ($r = 0.402$, df = 189, $P < 0.001$). Because the mean SVL of both male and female populations varies seasonally with differences in size class composition, each size class contributes a

Table 4. Seasonal characterizations of the diet-ecology of *A. erythrurus*. Figures are $\bar{x} \pm$ SD, sample sizes appear in parentheses, and $\underline{P}$ values are for one-tailed tests.

	Males	Females	t	$\underline{P}$
A. Mean prey size (mm)				
Winter	7.2 ± 3.7 (3)	4.0 ± 2.1 (6)	1.703	0.066
Spring	7.8 ± 5.3 (74)	6.0 ± 4.2 (60)	2.141	0.017
Summer	6.9 ± 4.4 (86)	5.9 ± 3.5 (69)	1.537	0.063
Fall	5.5 ± 4.4 (65)	4.8 ± 3.1 (57)	1.002	0.159
Combined probabilities: $\chi^2 = 22.792$ (df = 8)				0.001
B. Snout-vent length (mm)				
Winter	42.7 ± 8.9 (5)	35.8 ± 4.8 (5)	1.526	0.083
Spring	59.2 ± 11.9 (94)	56.6 ± 8.6 (72)	1.566	0.060
Summer	61.8 ± 10.7 (108)	58.1 ± 7.9 (80)	2.610	0.005
Fall	51.9 ± 14.3 (92)	47.3 ± 11.8 (70)	2.179	0.015
Combined probabilities: $\chi^2 = 28.928$ (df = 8)				0.001
C. Prey items per stomach				
Winter	3.0 ± 2.0 (3)	3.8 ± 5.9 (6)	0.222	0.415
Spring	5.3 ± 5.8 (90)	4.4 ± 3.1 (70)	1.174	0.121
Summer	6.7 ± 14.1 (103)	8.4 ± 16.4 (77)	0.746	0.229
Fall	10.2 ± 17.2 (84)	11.9 ± 21.9 (63)	0.527	0.300
Combined probabilities: $\chi^2 = 11.339$ (df = 8)				0.183
D. Trophic diversity				
Winter	0.395 ± 0.410 (3)	0.772 ± 0.359 (6)	1.424	0.099
Spring	0.421 ± 0.321 (90)	0.418 ± 0.311 (69)	0.059	0.477
Summer	0.324 ± 0.314 (103)	0.387 ± 0.259 (76)	1.425	0.078
Fall	0.296 ± 0.275 (84)	0.369 ± 0.284 (64)	1.574	0.059
Combined probabilities: $\chi^2 = 16.868$ (df = 8)				0.032

MPS to the overall figure for the seasonal sample. Therefore, when juveniles are well represented, the MPS appears smaller for the entire population.

Prey items per stomach increase throughout the year from winter to fall in both sexes and this increase is associated with a greater incidence of ants in the diet (Tables 3 and 4). Males and females do not differ significantly in the seasonal trend toward higher numbers of prey items per stomach. Trophic diversity is, however, significantly higher for females throughout the year (Table 4). Since the number of prey categories varies little between sexes, females apparently consume the different available categories more evenly than do males.

Stomachs containing ants, while fairly constant in number throughout the year, tend to demonstrate a slight increase during summer and fall for both males and females; the absence of ants in our male sample for winter is probably due to the small number of stomachs available (Table 5). There is no significant difference in the incidence of ants in the diet between males and females.

Vegetation is most frequently found in stomachs taken during the spring and summer months, and males do not differ significantly from females in the consumption of vegetation. Flowers and leaves of *Halimium halimifolium* (Cistaceae) were intentionally

Table 5. Indices used to characterize the diet-ecology of *A. erythrurus*. All figures (except stomach totals) are percentages of the seasonal sample; $\underline{P}$ values are for two-tailed tests.

	Winter	Spring	Summer	Fall	$\underline{U}$	$\underline{P}$
A. Total of stomachs						
Males	5	94	108	92	–	–
Females	6	72	80	71		
B. Empty stomachs						
Males	40.0	3.2	1.9	5.4	5.0	0.486
Females	0.0	0.0	3.8	7.0		
C. Stomachs with ants						
Males	0.0	41.5	45.4	45.7	3.0	0.200
Females	50.0	38.9	51.3	56.3		
D. Stomachs with vegetation						
Males	0.0	67.0	63.9	16.3	6.5	0.786
Females	0.0	84.7	70.0	9.9		
E. Stomachs with only vegetation						
Males	0.0	2.1	2.8	3.3	6.5	0.786
Females	0.0	2.8	1.3	2.8		

consumed by individuals on 28 and 30 May 1971 (BUSACK, field notes) and several stomachs collected during spring, summer and fall contain nothing but plant material (Table 5). Except for our winter samples, plant material is fairly constant in the diet throughout the year.

The relatively low incidence of empty stomachs appears to vary more in males than it does in females, but this seasonal difference is not significant (Table 5).

Our results closely parallel those reported from sandy localities contiguous to the sea of Almería (Almería Province, Spain), by VALVERDE (1967). He found the diet to consist mainly of ants and coleopterans and noted the remains of *Psammodromus algirus* in one of the 49 stomachs examined. We found the remains of a conspecific in one stomach but this observation might suggest either an especially aggressive encounter or a predatory habit. Perhaps of greater interest, however, is the herbivorous habit of the La Algaida population. While VALVERDE (1967: 38) reported that he found no vegetation in the diet of the Almería sample, the frequency of occurrence of flowers and leaves of *Halimium halimifolium* (Cistaceae) in our sample varied seasonally between 16 and 67 % in males, and between 10 and 85 % in females. Field observations confirm that this rather high incidence of vegetation is not coincidental with the lizards' having taken insects and accidentally included parts of leaves or flowers; 3 % of males and 2 % of females contained only vegetation.

POUGH (1973) examined the relationship between diet and energetics in five non-lacertid lizard families. He concluded that a species with mass < 100 g would most probably be carnivorous because, while readily available and requiring little energy expenditure for ingestion, plant material has a lower energy content, is more difficult to digest, and cannot provide as much energy per gram as animal matter. The smallest her-

bivorous lizard referenced (*Dipsosaurus dorsalis* at a range between 25–76 g) has an unusual tolerance for excessive heat (> 40 °C) which allows it to be active while few predators, competing lizards, and insects can. In this case, the increased energetic cost of being herbivorous is compensated by freedom from predation and competition.

One *A. erythrurus* tested at 13.5 °C maintained a metabolic rate between 0.18 and 0.23 ml O_2/g·h for seven hours and this impressive ability to be active at low temperatures (POUGH and BUSACK, 1978) may serve to free this small omnivore from potential reptilian predators and competitors. At 30 °C, 8.4–13.0 g *A. erythrurus* (POUGH, 1977) should be consuming 0.17–0.16 ml O_2/g·h. The actual rate of consumption is 0.24 in this population (POUGH and BUSACK, 1978). TROMP and AVERY (1977), who calculated metabolic rates in 1.8–2.2 g *Lacerta vivipara*, also reported a value (≈ 0.34) greater than the 0.22–0.21 ml O_2/g·h predicted by the relationship between mass and oxygen consumption cited by BENNETT and DAWSON (1976: 140). While these data hardly suggest that lacertids may be preadapted to survive on foods of lower caloric content, the omnivorous diet of *A. erythrurus* is certainly noteworthy. In years following those of above normal rainfall, at least, feeding on readily available *Halimium halimifolium* as a supplement to insect prey may be energetically more efficient than feeding on insects alone. The energy content of the leaves and flowers of this plant warrant investigation.

Predation and Parasitism

There were no significant differences in regenerated-tail frequency between males and females for both seasonal and yearly comparisons. The yearly frequency for combined sexes was 26.8% regenerated tails (Table 6). Winter sample sizes were small but regenerated tails apparently increase in the male sample as the seasons progress from spring to fall; this seasonality was not obvious for the females. If the number of predation encounters were constant, or increased through the year, and if lizards with regenerating tails were not handicapped in escaping a predator during a subsequent encounter, then greater numbers of regenerated tails would be expected as the activity season progresses.

Table 6. Frequency of regenerated tails. Figures are percentages, sample sizes in parentheses; P values are for one-tailed tests, * indicates use of Fisher's exact test after the addition of 1 to each cell.

Regenerated tails	Males	Females	X^2	P
Winter .	0.0 (2)	0.0 (5)	*	0.891
Spring	26.1 (88)	24.2 (62)	0.116	0.733
Summer	30.9 (97)	22.2 (63)	1.505	0.220
Fall	35.3 (68)	25.8 (62)	1.435	0.231
Yearly	30.2 (255)	23.4 (192)	2.553	0.110

The frequency of regenerated tails in a lizard population, while providing a rough index to the frequency of predator encounters, is more likely to reflect the escape success of the lizards (JAKSIĆ and NÚÑEZ, 1979; SCHOENER, 1979; JAKSIĆ and FUENTES, 1980; SCHOENER and SCHOENER, 1980). *Lacerta lepida, Coronella girondica, Malpolon mon-*

spessulanus, Vipera latasti, Ardeola ralloides (Ciconiiformes: Ardeidae) and *Tyto alba* (Strigiformes: Tytonidae) are listed as predators of *A. erythrurus* by VALVERDE (1967: 39). *Lacerta lepida, Elaphe scalaris, M. monspessulanus* and *Buteo buteo* (Falconiformes: Accipitridae) may be predators of *A. erythrurus* at La Algaida.

On a yearly basis, 26.8 % of the population at La Algaida is successful in escaping encounters with predators. While a slightly smaller percentage (22.5 %) is reported for *A. dumerili* inhabiting an area of similar habitat characteristics in Senegal (CISSÉ and KARNS, 1977), the sand-dwelling *Liolaemus platei* in comparable habitats of central Chile presents a regenerated tail frequency of 40.5 % (JAKSIĆ and FUENTES, 1980). In an analysis of the incidence of lizards as prey in mediterranean ecosystems of Chile and Spain, JAKSIĆ et al. (1982) found that *A. erythrurus* represents 11.5 % of the total reptile prey taken by 19 predator species in southern Spain. The incidence of five *Liolaemus* species in the diet of 11 Chilean predator species is only 8.4 %. These data indicate that the correlation between regenerated tail frequency in a lizard species and its incidence as prey in local predator species may not be strong and, in some cases, may even be negative.

Agonistic encounters may likewise account for some tail breakages in *A. erythrurus*. During mid-morning on 1 August 1971 such an encounter was observed between *Psammodromus algirus* and *A. erythrurus*. When disturbed by the observer, an adult *A. erythrurus* ran into a stand of *Corema album* from which it was later chased by an adult *P. algirus*. Whether a bite was attempted or delivered to the fleeing lizard was not known, but there was no doubt that this encounter served as one example of agonistic behavior.

The only parasite, found in the coelomic cavity medial to the testis, and in the stomach of these lizards, was a cestode, *Oochoristica* cf. *tuberculata* (Cyclophyllidea, Davaineidae), which has been previously recorded from *A. erythrurus* in Morocco (DOLLFUS, 1958). Parasites were found in eight males and three females, representing an apparently low rate of parasitism (2.7 and 1.3 % for males and females, respectively). Two of the parasitized females, and three of the males, were collected during May; the remaining female was collected in June and the balance of parasitized males were collected during June (2), July (1), August (1), and October (1).

Effect of the Removal Method

We were somewhat surprised to find no significant differences between the numbers of males (Ycχ² = 2.82, $\underline{P} > 0.09$), or between the numbers of females (Ycχ² = 0.11, $\underline{P} > 0.74$), collected in either year. There was little reduction in the maximum size of individuals of either sex (77.5 vs. 76.1 for males, 69.1 vs. 68.7 mm SVL for females), and the mean SVL for neither sex was significantly reduced ($\underline{t}$ = 1.53 [♂], 1.21 [♀]; $\underline{P} > 0.10$ [♂], $\underline{P} > 0.20$ [♀]).

If we consider the size class distribution of 1970 to represent the normal unmolested population, and use the numbers of individuals in size classes between 31–40, 41–50, 51–60, 61–70, and 71–80 mm SVL to generate the expected numbers of individuals in these classes during 1971, then we can test for a significant departure from expected values in both male and female samples. Males between 41–60 mm SVL were more abundant in 1971, but fewer individuals between 31–40 and between 61–80 mm SVL were present; these differences were significantly different from expected values (Ycχ² va-

lues between 4.85 and 39.52, all with $\underline{P} < 0.05$). These data, along with those presented in Fig. 1, indicate a complete alteration of the structure of the male population. The female population, when examined as above, exhibited significant departure from expected values only for size classes 31–40, where fewer than expected numbers were found, and 41–50, which contained more individuals in 1971 than in 1970 ($Yc\chi^2 = 9.22$ and 17.60, respectively, $\underline{P} < 0.05$ in each case).

When the numbers of males and females collected between May and October, 1970, are compared with those from the same period in 1971, males from 1970 represent 59 % of the population while 56 % of the 1971 population is male. In 1970, the abundance of males contributes to a sex ratio significantly different from 1 : 1; in 1971 the sex ratio is not different from 1 : 1 ($Yc\chi^2 = 6.56$ [1970], 2.42 [1971]; $\underline{P} < 0.01$ [1970], > 0.12 [1971]). When examined on a month-by-month basis, males are most prevalent in May (67 %) and September (72 %), 1970, and during March of 1971 (71 %). When examined on a month-by-month basis between years, a difference in the distribution of sexes appears first in October of 1971. During 1970, males taken during October represented 44 % of the population, in 1971 this proportion increased to 68 %, an increase which represents a significant departure from the previous year for the first time after 17 months of the removal survey.

The ability of a population to resist disturbance can only be directly measured by implementation of a procedure which causes disturbance. Removal studies of birds have shown that, while the habitat controls the distribution of most species, the carrying capacity of the habitat is variable. When breeding males were removed from a Spruce-Fir forest community during one sampling period, over twice as many replacements entered the area (STEWART and ALDRICH, 1951); a second removal period allowed 2.25 as many replacements to enter and settle the area (HENSLEY and COPE, 1951).

Monthly removal at La Algaida demonstrated no such trend. When we controlled for months delimiting seasonal changes (such as between October and November), and for the August increase due to hatchlings, month by month comparisons of numbers of males were statistically uniform between all months except May and June. We attribute the increased numbers during May to the breeding season, which is probably a time of increased activity. Females respond as males, except that their numbers increase appreciably during April, a month before those of males. There were no significant differences between the numbers collected in 1970, and those collected in 1971, however.

The maximum size of neither sex was appreciably affected, nor was the mean SVL appreciably reduced between years as a result of the removal method. Figure 1 demonstrates, however, that the structure of the male population was altered. This alteration was apparently sufficient to reduce the sex ratio in the population to 1 : 1 by 1971, the second year of removal. While adult males outnumbered adult females 1.4 : 1 during 1970, the subadult ratio was 1 : 1. In 1971, after the adult sex ratio had been reduced to 1 : 1, the subadult sex ratio increased to 1.6 : 1. No significant sex ratio alteration occurred in the population, however, until after 17 months of removal had passed.

Males from hatching to 10 months of age ($\leq$ 50 mm SVL) had a higher rate of survival in 1971 than 1970; female survival from hatching to 14 months of age ($\leq$ 54 mm SVL) was also increased between years (Table 1). These data suggest that *A. erythrurus* is highly resilient to perturbation.

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