

number produced by the female". Verrell (1984) also noted that the majority of females remain unresponsive to male courtship for 20 days after the first insemination. This study shows that 44% of non-inseminated females eagerly followed a courting male until the end of sexual sequences.

The prolonged receptiveness of females and the successive taking up of spermatophores might have both proximate, physiological and ultimate, adaptive reasons. When the tubules are filled with a great number of spermatozoa from several spermatophores (or from one large spermatophore) the functioning of the sperm distribution might be more efficient.

It seems that the amount of sperm reduces quickly in females which lay eggs each day, as some time after insemination the number of unfertilized eggs increases. This might explain the phenomenon, that the multiple inseminated females produce on average 11.9% unfertilized eggs, while once inseminated as much as 31.8%.

In this experiment some of the females after insemination with one spermatophore only produced a large number of eggs which is close to a measured value of the complete clutch size for a season (Hagström, 1980). A similar phenomenon was observed in *Ambystoma tigrinum* and *Desmognathus orhrophaeus* (Halliday and Verrell, 1984). The size of a spermatophore is highly variable and most probably depends on the level of male sexual activity. It might be that a large spermatophore may contain as many sperms as several smaller ones.

Multiple insemination can significantly increase genetic variation of the progeny produced by a female. This might be especially significant for a species which colonises transient environments and experiences sharp

reductions of a population size as is the case of many *Triturus* species.

#### ACKNOWLEDGEMENTS

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## EGG, CLUTCH AND MATERNAL SIZES IN LIZARDS: INTRA- AND INTERSPECIFIC RELATIONS IN NEAR-EASTERN AGAMIDAE AND LACERTIDAE

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#### ABSTRACT

We provide data on the fecundity of locally common Israeli reptiles, and use these data to examine current ideas on the reproductive ecology of lizards. Our methodology was selected in consideration of the acute problems of nature conservation in Israel. In the museum collections of the Hebrew University of Jerusalem and Tel Aviv University we used radiography to locate the shelled oviductal eggs of 164 female lizards, belonging to eleven species (Agamidae and Lacertidae). Each sample sums the species' variation over its range and over different years. Female body size, egg number and egg volume were determined. Specific clutch volumes, relative to maternal body lengths, resembled those reported in iguanid lizards from tropical America. Clutch size varied intraspecifically and, in most species, correlated to maternal size. In others, egg size was more influenced by maternal size. We argue that the latter species oviposit in more stable environments than do the majority.

## INTRODUCTION

The amount of energy available to an organism at any given time is finite; the amount expended may be partitioned into maintenance, growth and reproduction. In lizards the allocation of energy to reproduction has been reviewed by several investigators. The main areas of concern have been, first, whether and what differences in parental investment exist between species differing in body size, body shape, environment or behaviour, and how such differences may be explained.

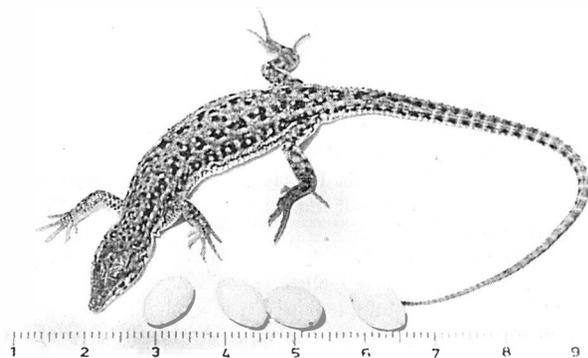


Fig. 1. A typical small desert lacertid lizard, *Mesalina guttulata*, and her freshly laid (modal) clutch of four eggs (female collected in the Judean Desert on 5.IV.1981, oviposited and photographed on 12.IV.81; from Kodachrome diapositive).

For example, species of lacertid lizards (Fig. 1) have been characterized by clutches which range from 14 to 40% of the pregnant female's weight. And second, how a female with limited energy available for reproduction reaches a compromise between emphasizing either egg number or energy content per egg. The latter value is roughly, though not precisely, paralleled by egg mass and size (Tinkle, 1969; Ballinger and Clark, 1973; Emlen, 1973; Ballinger, 1978; Vitt, 1978; Huey and Pianka, 1981; Vitt and Price, 1982; Fitch, 1985; Pianka, 1986).

Several factors affect the apportionment of energy in egg production, since natural selection should result in an energetic compromise that maximizes the parent's total (long-range) contribution to future generations. Larger eggs may be more resistant (especially to drought) during incubation (Ackerman, Seagrave, Dmi'el and Ar, 1985). They give rise to larger young (Ferguson, Brown and DeMarco, 1982; Werner, 1986a, 1988), which are able to utilize a broader range of food items, more able to withstand a shortage of food, and compete better in social encounters (Fitch, 1970; Ferguson et al., 1982; Rand, 1982). On the other hand, a low level of competition, or a high level of predation of a type not affected by juvenile size, may press for a strategy of producing many small eggs. The production of large numbers of small eggs may be adaptive also in coarse-grained patchy environments (Emlen, 1973) or in those changing in time. As the environment becomes less stable, selection favours greater fecundity rather than survivorship (Cody, 1966).

The aspect of reproductive ecology most commonly studied in reptiles is the number of eggs in a clutch (Turner, 1977; Fitch, 1985). From studies elsewhere this number is known to vary intraspecifically between populations (Kramer, 1946; Fitch, 1985). In some species, clutches are larger in warmer parts of the specific range; this results in part from the variation in female size, larger females producing larger clutches (Oliver, 1955; Fitch, 1970). But in a majority of wide-ranging new-world species clutches are larger in cold latitudes (and high altitudes), allegedly in compensation for the smaller number of clutches in the shorter season (Turner, 1977).

Nevertheless Vitt and Price (1982) listed several reports in which also the size of the eggs had been considered. These authors calculated the relation of clutch mass to parent mass, and concluded that this relation differs between ecological types and between families. The accuracy of some of the data and hence the validity of some of the conclusions have since been questioned by Werner (1988). Dunham, Miles and Reznick (1988) analyzed the relations among clutch size, relative clutch mass and foraging mode in reptiles and found that active foragers produce significantly smaller clutches than sit and wait foragers, with significantly smaller relative clutch mass. They also found a relation between clutch size and habitat: fossorial (burrowing) lizards produced the smallest clutches, arboreal and arenicolous (sand-dwelling) lizards produced larger clutches and terrestrial and saxicolous (rock-dwelling) lizards produced the largest clutches.

Little is known of the reproductive ecology of Israeli reptiles, as, with the exception of a few species, mostly venomous snakes and gekkonid lizards (Mendelssohn, 1963, 1965; Werner, 1965, 1966a, 1986a, 1988; Dmi'el, 1967; Orr, Shachak and Steinberger, 1979), knowledge is limited to the scanty information in local general texts (Margolin, 1959; Werner, 1966b, 1973; Arbel, 1984; Dor, 1987).

In this paper we examine the relationships among clutch size, egg volume, clutch volume and maternal size, in eleven common oviparous Israeli lizards in which clutch size is variable. Our aims are, first, to provide basic data about the fecundity of Israeli reptiles. Such information is necessary (though insufficient) for the planning of nature conservation. Second, to examine some of the currently prevailing generalizations (quoted above) concerning the reproductive ecology of lizards.

## MATERIALS AND METHODS

## SPECIES

Gravid females of eleven lizard species (agamids and lacertids) were examined. These are listed in Table 1, which details their full specific, and, where applicable, subspecific, names. Most of these species have been beautifully described and depicted in Anderson (1898). For the others (and some of the same) the reader is referred to Barash and Hoofien (1956), Başoğlu and Baran (1977), Arnold, Burton and Ovendon (1978) and Arbel (1984). The taxonomy of the Agamidae has been reviewed by Wermuth (1967) and that of the genus *Acanthodactylus* by Salvador (1982) and Arnold (1983).

Species and subspecies sampled	World Distribution of the species	Distribution in Israel	Annual rainfall (mm) (Isohyet ranges of drought year/wet year)	Average monthly August temperature (°C) (isotherm range)	Simplified summary of habitat
<b>Agamidae</b>					
<i>Agama pallida pallida</i> Reuss, 1833	E Egypt & SW Asia	Whole Negev	0-150/0-400	24-32	Desert and Steppe: except sand dunes
<i>Agama savignii</i> Duméril & Bibron, 1837	E Egypt, N Sinai & S Israel	N Negev	0-100/100-250	26-28	Semi-desert; sands
<i>Agama sinaita</i> Heyden, 1827	NE Africa & SW Asia	S Negev	0-100/0-250	28-34	Extreme desert: rocks
<i>Agama stellio</i> (Linnaeus, 1758) sspp.	SE Europe, N Egypt & SW Asia	Countrywide except most of S Negev	50-900/200-1400	20-28 (Isr)	Mediterranean and semi-deserts: rocks, tree trunks and buildings
<b>Lacertidae</b>					
<i>Acanthodactylus boskianus asper</i> (Audouin, 1829)	N Africa & SW Asia	Whole Negev	0-100/0-300	26-34	Desert and Steppe: sands, shingle etc
<i>Acanthodactylus pardalis</i> (Lichtenstein, 1823)	N Africa & S Israel	N Negev	0-150/150-400	26-28	Steppe; loess soils
<i>Acanthodactylus schreiberi syriacus</i> Boettger, 1879	S Turkey to N Israel	Mediterranean coastal plain	100-600/500-1000	24-28	Mediterranean; sands and light soils
<i>Acanthodactylus scutellatus scutellatus</i> (Audouin, 1829)	N Africa & SW Asia	N Negev & S Mediterranean coastal plain	0-300/250-800	26/28	Semi-desert and Mediterranean; sand dunes
<i>Lacerta laevis</i> Gray 1838	Turkey to N Israel	Countrywide N of Hebron	300-900/700-1400	20-28	Mediterranean; scrub, gardens etc
<i>Mesalina guttulata guttulata</i> (Lichtenstein, 1823)	N Africa & SW Asia	Whole Negev & S Jordan Valley	0-100/0-400	26-34	Desert and Steppe: except sand dunes
<i>Ophisops elegans</i> (Ménétriés, 1832) sspp.	SE Europe & W Asia	N Negev & northwards	50-900/200-1400	20-30	Mediterranean and Steppe; open habitats except sand dunes & sheer rocks

TABLE 1. Habitats of species studied (sources explained in the text).

We emphasize that our material of *A. boskianus* excludes the sibling species *A. ophiodurus* Arnold, 1980 (Werner, 1986b).

Specific distributional and environmental data are condensed in Table 1 from the following sources: World distribution — Flower (1933) and Werner (1966b), and, for *Agama pallida*, Haas and Werner (1969); Distribution in Israel — Werner (1966b) and, especially, Wahrman (1970) who presents approximate distribution maps for all the species except *Lacerta laevis*; Annual rainfall — relevant isohyet ranges between rainfall maps (Atlas of Israel 1970) for the drought year 1946/47 and the wet year 1944/45 (the potentially rainy season extends from September through May); and average monthly August temperatures — relevant isotherm ranges in an Atlas of Israel (1970) map averaging the ten years 1940-1949. Finally, the simplified summary of the habitats is based on Wahrman's (1970) classification of types of animal distribution in Israel and data in Werner (1966b) augmented by our personal knowledge.

#### SAMPLES

Lizard eggs are not truly cleidoic (closed to water flux). Depending on the conditions they may decrease or increase in mass and dimensions fairly rapidly after oviposition (Fitch and Fitch, 1967; Packard, Tracy and Roth, 1977). Therefore it is difficult to base a comparative study of egg size on laid eggs (although dry weights and caloric values could be substituted). We preferred to use eggs inside oviducts of females already preserved in collections, a policy which also appeared particularly desirable from the point of view of nature conservation, an acute problem in the small natural areas of Israel (Ashkenazi, 1987; Frankenberg, 1989).

Species	n	ra		N		V		RP
		$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV	
Agamidae								
<i>A. pallida</i>	17	78.8	8 67.5-85	9.4	34 1-12	0.63	30 0.36-1.06	II-VIII
<i>A. savignii</i>	2	70.5	15 63-78	4.0	35 3-5	0.86	5 0.89-1.01	?
<i>A. sinaita</i>	4	76.4	3 73-79	5.3	9 5-6	0.86	51 0.42-1.46	V-VIII
<i>A. stellio</i>	18	111.1	11 92-130	7.7	23 5-12	1.29	37 0.80-2.68	I-VII
Lacertidae								
<i>A. boskianus</i>	15	60.1	7 54.5-67	4.1	27 2-7	0.32	31 0.18-0.49	IV-VI
<i>A. pardalis</i>	23	66.0	7 59-74	4.8	25 3-7	0.36	25 0.20-0.53	III-VII
<i>A. schreiberi</i>	10	69.0	7 58-75	2.6	31 1-4	0.53	21 0.32-0.69	IV-IX
<i>A. scuellatus</i>	13	52.2	9 40-58	2.7	30 2-4	0.32	19 0.23-0.43	III-X
<i>L. laevis</i>	16	61.9	8 55.5-71	4.5	33 2-7	0.28	29 0.16-0.41	II-VII
<i>M. guttulata</i>	38	46.8	7 40-54.5	4.4	27 2-7	0.14	21 0.09-0.20	II-IV
<i>O. elegans</i>	8	48.1	6 45-52	4.0	53 2-8	0.09	33 0.05-0.11	V-VIII

TABLE 2. Basic reproductive data for eleven lizard species. Averages ( $\bar{x}$ ), coefficients of variation (CV) and (underneath) ranges, of body length (ra), number of oviductal shelled eggs (N) and egg volume in  $\text{cm}^3$  (V), for each of the species. RP, reproductive (oviposition) period of the species in months; and n is the number of females yielding data.

All the preserved lizards of relevant species in the National Collections (Hebrew University of Jerusalem and Tel-Aviv University) were inspected. These had been collected during many years and over all seasons. Females apparently gravid were radiographed for verification as explained below. The ensuing sample sizes (numbers of females yielding data) varied from 2 to 32 per species (total 164) and are given in Table 2. These individuals originated, in principle, from throughout the specific ranges in Israel and Sinai, with emphasis on the former. However, of three species material from neighbouring countries was available and included: *Agama pallida*, Syria; *L. laevis*, Lebanon (Bayrut only); *O. elegans*, Cyprus and Turkey.

#### DATA COLLECTION AND ANALYSIS

Our technique involved the calculation of egg volumes from linear measurements of preserved shelled eggs.

Various distorting effects of fixation and storage in formalin and alcohol on the relative weight of lizard eggs have been described (Martin, 1978; Vitt, Howland and Durham, 1985). Guillette, Rand, DeMarco and Etheridge (1988) even found that the weight of eggs preserved after removal from their mother by dissection, is reduced during fixation by a third as a stable factor.

Our material had been preserved fairly uniformly for all species (mothers fixed in 10% formalin, stored in 70% ethanol for periods usually >1 yr) and our study involved mainly the interspecific comparison of intraspecific traits; hence we deem the technique adequate. We observed no obvious collapse of the eggshells as noted by Rand (1982).

Each suspected gravid female was radiographed (Softex type E X-ray machine and Ilford Industrial G film) to find out whether it contained shelled (or other oviductal) eggs. We initially tested whether measurements of eggs on the X-ray plate were reliable, by comparing a sample to measurements of the same eggs after dissection. Fig. 2 shows that in the case of radiographs, considering the egg as representing an ellipsoid, as done hereinafter with the direct measurements of the eggs, would yield a somewhat poorer approximation than regarding the egg as an irregular sphere, with a diameter averaged between length (L) and width (W), using the equation  $V = 4/3 \pi [(L+W)/4]^3$ . Although approximations of egg sizes could be obtained radiographically in this way if dissection were precluded, we considered the inaccuracy excessive and employed only direct measurement of oviductal eggs in opened bodies.

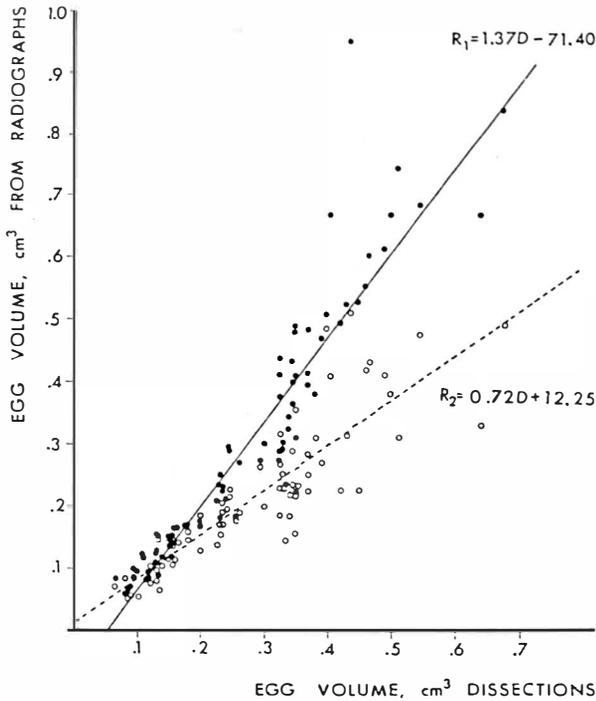


Fig. 2. The correlation of egg volumes (cm<sup>3</sup>) based on the measurement of radiographs (R) and calculated in either of two manners, to the volumes of the same eggs derived from measurements in dissections (D). In the first regression, R<sub>1</sub> is calculated from the formula for an irregular sphere,  $R_1 = 4/3\pi [(L+W)/4]^3 = 1.37D - 71.4$ ; in the second, R<sub>2</sub> is calculated from that of an ellipsoid,  $R_2 = 4/3\pi (LW^2/8) = 0.71D + 12.25$ . D is based on the latter for both regressions.

For each lizard the following data were noted: body length (ra = rostrum-anus = snout-vent, following Werner, 1971); number of eggs in each oviduct; whether these were shelled; length and width of all eggs in lizards carrying up to four, and of four eggs in lizards carrying a greater number; and the date and location of capture.

The volume of each egg was calculated by using the equation  $V = 4/3 \pi (LW^2/8)$ , where V is egg volume in mm<sup>3</sup>, L is egg length in mm, and W is egg width in mm. The average volume of all eggs measured of one female gave the characteristic egg volume for that particular specimen. These individual averages were then averaged for each species to yield the specific egg volume.

Linear and partial correlations and linear and multiple regressions (Steel and Torrie, 1960) between the three variables, body size (ra) in mm (Rand, 1982), egg number (N) and egg volume (V) (average per female) were calculated to test the relationships between them. In all these calculations only mature, shelled, eggs were used. The length of the reproductive period and the number of clutches were roughly estimated for each species by relating egg volumes to the dates of collection. For this purpose, immature oviductal eggs were measured as well.

RESULTS

The data obtained from the eleven species are summarized in Table 2. It will be remembered that in our samples, we pooled for each species, quite randomly, females collected from different areas of the range of distribution, in different years (including rainy ones and drought ones) and at different times during the year. Hence, for the time being, we ignored any geographical and temporal effects (Van Devender, 1982; Ballinger, 1983; Fitch, 1985), including those of enriched food supply through above-average rainfall in xeric habitats (Turner, Lannom, Medica and Hoddenbach, 1969). Rather, by combining all data, we derived the average characterizations of the specific clutch parameters, and approximate limits of their extreme variation in the area concerned (constrained, as ranges are, by sample size). Geographical variation remains to be treated.

The body space a lizard can devote to carrying eggs is limited. Species-specific clutch volume (species-specific V x N from Table 2) was significantly correlated (interspecifically) to body size (Fig. 3). Viewing clutch volume as if it were packed in a sphere, its diameter maintained a quite constant proportion to specific body length:  $23.5 \pm 3.2$  perca (percents of ra — Werner, 1971) with no significant deviations from the mean (Chi square test) (Fig. 4). Therefore, on spatial grounds, any attempt by one of these species to increase egg volume would have to be compensated by a decrease in egg number (per clutch), and vice versa.

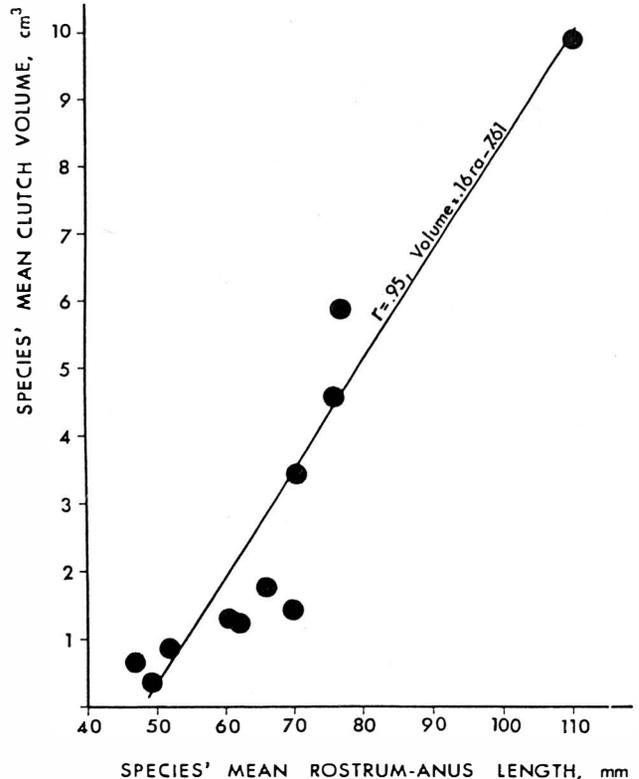


Fig. 3A. Mean clutch volume (cm<sup>3</sup>) as a function of mean body size (mm.ra) among eleven lizard species.

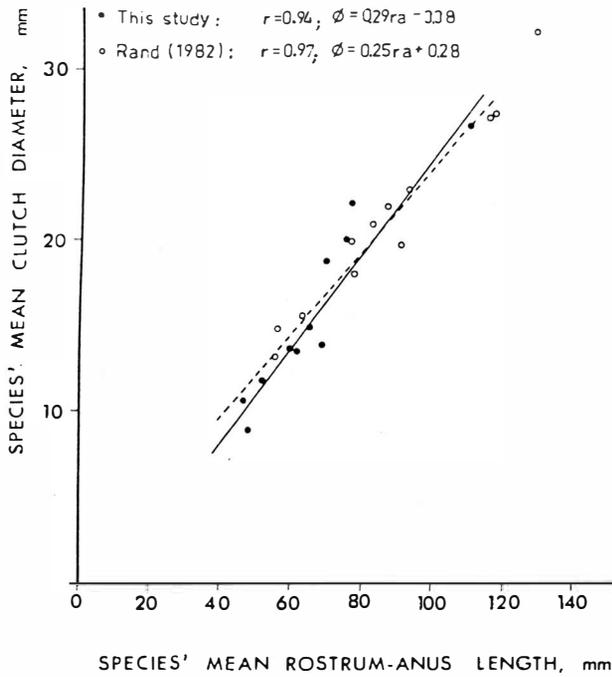
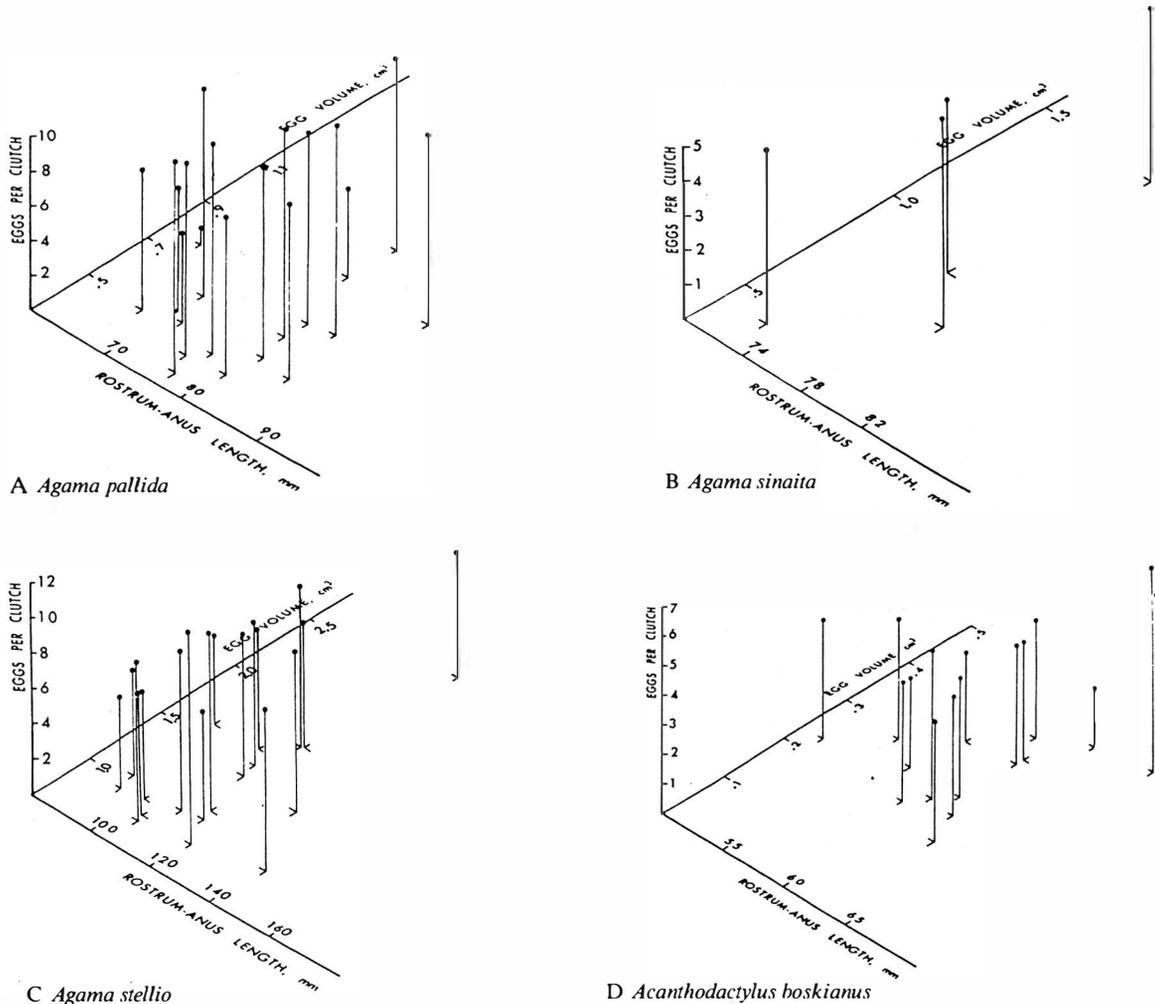


Fig. 3B. Mean clutch diameter derived from a clutch volume assumed spherical, as a function of mean body size (mm, ra), among eleven lizard species studied herein (solid symbols) and among thirteen iguanid species studied by Rand (1982) (hollow symbols).

It is apparent from Table 2 that the species could be classified into two categories regarding egg number and egg size. Lizards with relatively large but few eggs were *Agama savignii*, *A. sinaita*, *Acanthodactylus schreiberi* and *A. scutellatus*; whereas all the others had relatively small and numerous eggs (Table 2).

The relation between the three variables, maternal body size, egg volume and the number of eggs, is presented three-dimensionally for each species in Fig. 4. (Excluded is *Agama savignii* of which the sample size was too small.) From these figures and from Table 3 it is apparent that in the terms of this relation each lizard belonged to one of four categories: (1) Lizards which, as stated above, basically have relatively numerous small eggs, and which in response to increased body size strictly increase the number of eggs; *Agama pallida*, *A. stellio*, *Acanthodactylus pardalis*, *L. laevis*, *M. guttulata*, and *O. elegans*. (2) A lizard which also basically has numerous eggs but which with increased maternal size increases egg size rather than egg number is *Acanthodactylus boskianus*. (3) *A. schreiberi*, which basically has few large eggs, further increases egg size with increasing maternal size. (4) Three other lizards which basically have large and few eggs are *Agama sinaita* which with increasing maternal size increases both egg number and egg size (as far as known), *Acanthodactylus scutellatus* which revealed no significant response to increasing maternal size, and *Agama savignii* where sample size enabled no conclusions.

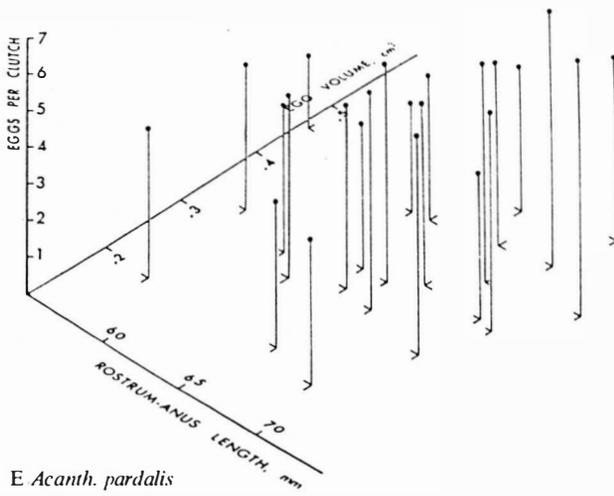


A *Agama pallida*

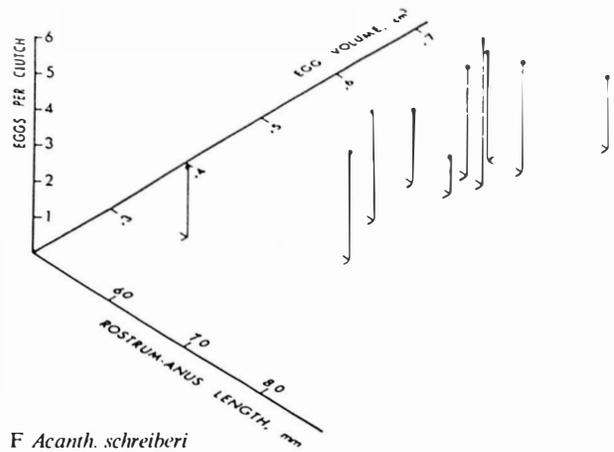
B *Agama sinaita*

C *Agama stellio*

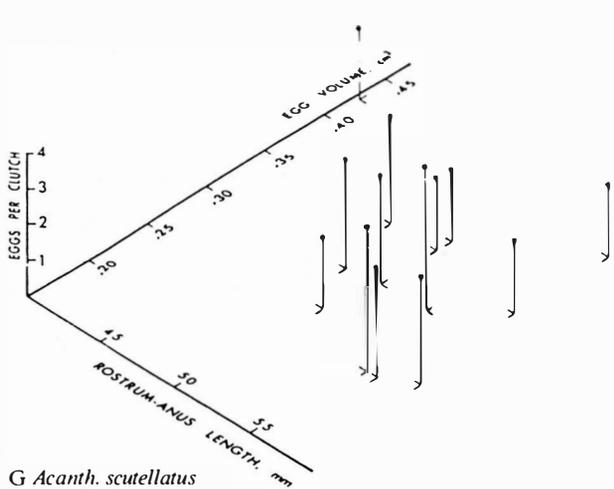
D *Acanthodactylus boskianus*



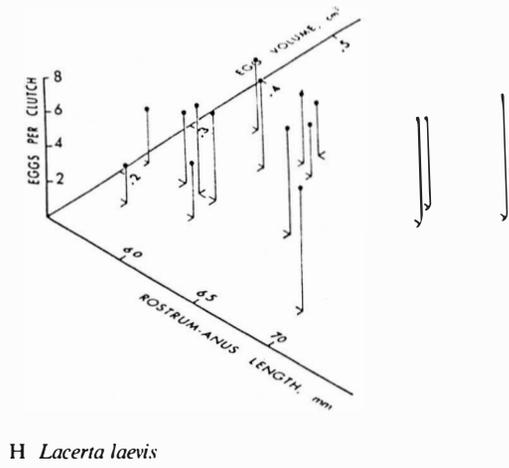
E *Acanth. pardalis*



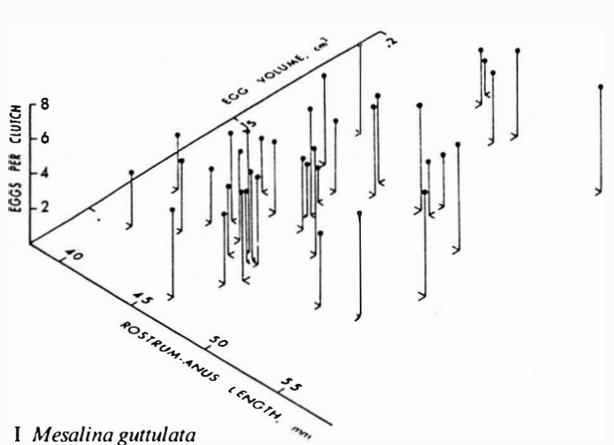
F *Acanth. schreiberi*



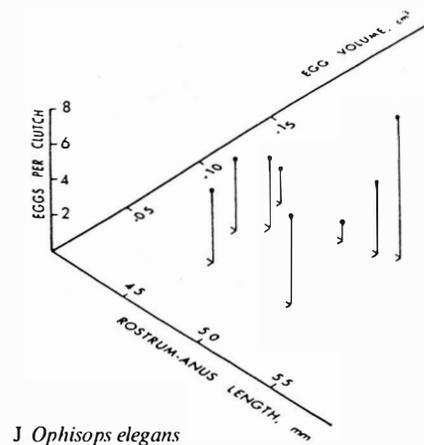
G *Acanth. scutellatus*



H *Lacerta laevis*



I *Mesalina guttulata*



J *Ophisops elegans*

Fig. 4A-J. Number of eggs (N) as a multiple function of maternal body size (ra) in mm and mean egg volume (V) in cm<sup>3</sup>, for each of ten species. Each vertical bar represents the clutch of one female. The top of each bar represents the multiple function; the base of each bar, the relation between egg volume and maternal body length. The multiple regression function for these graphs, expressing the number of eggs in a clutch (N) as a function of maternal body size (ra) and egg volume (V), is respectively: A.  $N = 0.32ra - 4.65V - 12.6$ ; B.  $N = 0.22ra - 0.92V - 10.38$ ; C.  $N = 0.09ra - 0.83V - 1.34$ ; D.  $N = 0.52ra - 31.75V - 17.27$ ; E.  $N = 0.19ra - 1.31V - 7.03$ ; F.  $N = 0.05ra - 0.87 - 0.39$ ; G.  $N = 4.92ra - 6.76V - 0.002$ ; H.  $N = 0.26ra - 2.72V - 10.84$ ; I.  $N = 0.18ra - 10.13V - 2.67$ ; J.  $N = 0.4ra - 16.3V - 15.2$ .

Species	<i>r</i>			<i>R</i>		
	ra-N	ra-V	N-V	ra-N(V)	ra-V(N)	N-V(ra)
Agamidae						
<i>A. pallida</i>	0.60**	0.17	-0.16	0.65*	0.34	-0.95
<i>A. sinaita</i>	0.68	0.52	-0.24	0.97	0.96	-0.31
<i>A. stellio</i>	0.62**	0.09	-0.19	0.65*	0.27	-0.31
Lacertidae						
<i>A. boskianus</i>	0.42	0.52*	0.20	0.37	0.50	-0.03
<i>A. pardalis</i>	0.71***	0.19	0.04	0.72**	0.23	-0.14
<i>A. schreiberi</i>	0.18	0.76**	0.09	0.18	0.76**	-0.07
<i>A. scutellatus</i>	0.26	-0.44	-0.61*	-0.01	-0.37	-0.57
<i>L. laevis</i>	0.76***	0.40	0.19	0.76**	0.39	-0.19
<i>M. guttulata</i>	0.46**	0.23	-0.12	0.51**	0.32	-0.26
<i>O. elegans</i>	0.52	0.26	-0.06	0.55	0.34	-0.23

TABLE 3. Correlations between reproductive data in each of ten lizard species. Coefficients of correlation, *r*; and of partial correlations, *R*; between the three variables N, ra and V, explained and reduced in Table 2. In the partial correlations the variable in parantheses is the one held constant. Significance levels indicated thus: \*, *P*<0.05; \*\*, *P*<0.01; \*\*\*, *P*<0.001; otherwise, the correlation is not significant.

The averages of all the species are plotted together along the three variables (ra, N and V) in Fig. 5, which demonstrates that their mathematical interspecific relation in Israeli agamid and lacertid lizards, as a group, is as follows. Any additional reproductive effort enabled through an (interspecific) increase in body size,

is directed so that it is invested in enlarging the egg rather than increasing the number of eggs per clutch (ra-V(N) = 0.92). This accords with the widespread observation, that larger species produce larger offspring. Table 2 also indicates the reproductive months (when females contained shelled oviductal eggs) per species.

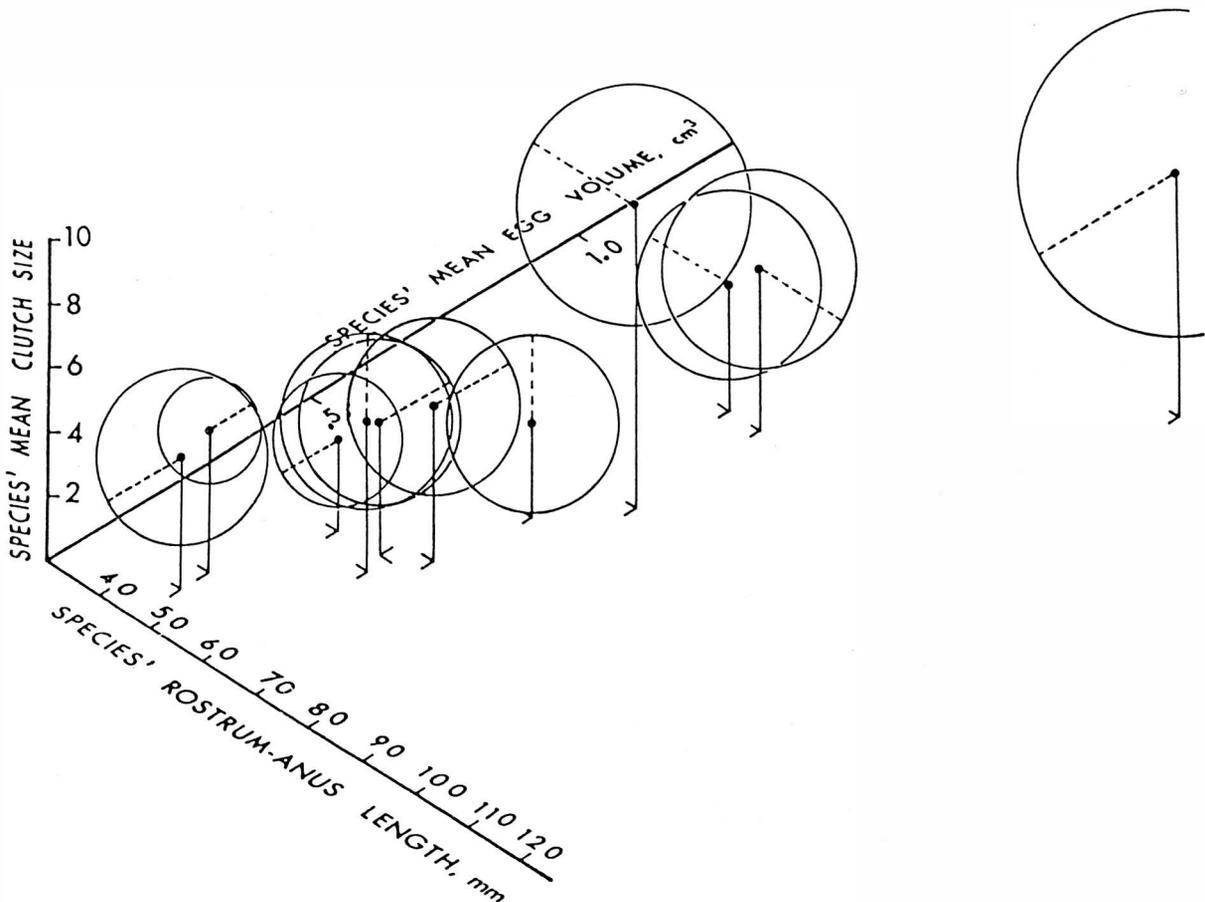


Fig. 5. Mean number of eggs in each species, as a multiple function of specific (mean) body length and of specific (mean) egg volume (as in Fig. 4). The circles represent for each species an average SD, calculated from the mean CV values of the three variables.

## DISCUSSION

In order to reproduce, each species of lizard has evolved so as to devote a certain proportion of the female mass (or energy) to produce eggs, and so as to divide this biomass into either many or few eggs (Smith and Fretwell, 1974). These two aspects represent different selection pressures, the first primarily affecting the survival of the mother and by this, of the eggs she carries; the second, only the survival of her offspring, since there is no parental care (Pianka, 1986). Both contribute to increasing the fitness (long-term reproduction success) of each individual in the species.

## PARENTAL INVESTMENT

The clutch mass of an individual female represents a compromise between several selection forces. Increased reproductive effort by investing in, and carrying, a larger clutch mass may lead to increased probability of the mother falling victim to predation (Shine, 1980). Vitt and Congdon (1978) demonstrated that in lizards the specific clutch mass is related to body shape and habitual mode of escape from predators. Nevertheless, it seems that lizards have attained optimization regarding the proportion of clutch mass to mother mass, values which we represent, respectively, by their correlates, clutch volume and body length. Rand (1982) furnished comparable data for 13 species of iguanid lizards in tropical America. We calculate from his data a strong interspecific correlation of clutch volume to body length ( $r = 0.94$ ,  $P < 0.001$ ), with a regression slope of 0.22, not significantly different from ours (Fig. 3). Calculation of the diameters of the average specific clutches found by Rand (from total clutch masses conceived of as sphere-shaped) yields a mean diameter of  $25.0 \pm 1.7$  perca, again not significantly different from our result of  $23.5 \pm 3.2$  perca ( $t$ -test) (Fig. 4). Thus, clutch diameter observes a fairly constant proportion of body length in these lizard groups. Interestingly, Vitt and Price (1982) too have found that the mean relative clutch mass of lizards of the families Agamidae, Iguanidae, and Lacertidae (also Scincidae) is of a uniform order of magnitude, about 25%. Lizard species apparently invest a certain amount in each clutch, regardless of how many clutches are produced during the year. This conclusion accords with those of Vitt and Congdon (1978) and Rand (1982). On the other hand, Barbault (1975) suggested that lizards in a fairly stable but predation-heavy environment are selected to increase fecundity, with an increased clutch volume, even at the expense of parental survivorship.

The reproductive investment per clutch seems to be uniform (by one yardstick) for Mediterranean, desert, subtropical and tropical lizards. A clutch diameter of about 25 perca represents a widespread value for Agamidae, Iguanidae and Lacertidae, presumably as an optimal compromise between retaining maternal survival and increasing reproductive success. In view of the near-uniform relative clutch volume, the number of clutches during a year seems to depend on the length of the available reproductive season rather than on the investment already made by the lizard at a given time. The longer the reproductive season, the more clutches are produced. In tropical zones with faint seasonality, lizards produce numerous clutches during the year (Barbault, 1975).

The reproductive period of the Israeli lizards considered here is restricted to spring and early summer, due to the pronounced climatic difference between winter and summer. It has often been suggested, that starting the breeding season relatively early in the year enables lizards to produce an additional clutch (thus Goldberg, 1975, 1977). But in our observations lizard species which are geographically (and climatically) sympatric nevertheless begin their breeding at different specific times in the season. Moreover, the number of reproductive months (when oviducts contain shelled eggs) is not affected by the seasonal timing of the onset of reproduction in itself (Table 2): *M. guttulata* which begins to oviposit early in the year had only 4 reproductive months, the same as *O. elegans* and *Agama sinaita* which begin to reproduce later in spring. *Agama stellio*, *Agama pallida* and *L. laevis*, which are early-season reproducers had 7, 6 and 6 months, respectively, whereas the late-season reproducers *Acanthodactylus schreiberi* and *Acanthodactylus scutellatus*, have an even longer reproductive season of 8 months each. Despite its long reproductive season, Lehman (1980) found in the latter only 1-4 clutches per year, with 2-6 eggs per clutch. No sacrifice at the expense of the first clutch occurs in favour of increasing the chance of reproducing a later clutch. Constraints and perhaps uncertainties concerning the length of the reproductive period lead to a maximization of each clutch; a smaller clutch mass (volume) seems not to be compensated for by the production of more clutches. By the same token, in a lizard population reproducing biennially (e.g., *Anguis fragilis* — Patterson, 1983), a female would not be expected to carry a clutch mass double that which accords with her survival. Thus when we deal with the relationships between the number of eggs in a clutch and the volume of each egg, each clutch may be regarded independently of others produced by the lizard.

## NUMBER VERSUS SIZE OF EGGS

Since parental investment (per clutch) in all lizards considered here is similar (proportional to maternal body size), selective forces on reproductive success operate along one dimension — increasing either egg volume or egg number, each at the expense of the other. (This phenomenon is significant in our sample of *Acanthodactylus scutellatus*, as shown in Table 3.) The relative importance of each trend for offspring survival determines the relationship between egg volume and number within a clutch. Optimization is reached by a combination of maximizing both the number of eggs and the probability of each offspring to survive to maturity, which is believed to significantly depend on egg size (Ferguson et al., 1982; Vitt and Price, 1982).

Dunham and Miles (1985) reported a significant interspecific correlation of clutch size to maternal body length but did not consider egg size or clutch volume.

In tropical forests (and on islands — Fitch, 1985) larger young are selected for. In other environments a relatively greater nonselective mortality presses more strongly for large clutches (Tinkle, Wilbur and Tilley, 1970; Barbault, 1975; Rand, 1982). It is generally contended, though not proven, that tropical forests are stable over time, and that this characteristic accounts for the particular apportionment of clutch mass in this environment.

We may summarize the ecological and reproductive adaptations in the lizard species studied here. Whereas both Mediterranean and desert species mostly have relatively numerous eggs, most species which deviate and have large eggs live on sand. The only exception is *Agama sinaita* which has few, large eggs and lives on rocks in extreme desert. Initially this seems hard to reconcile with the prevalent theory: Both the Mediterranean and desert habitats in Israel are unstable and unpredictable, as may be seen in Table 1, and as indicated by the extreme fluctuations in rainfall and in the average temperatures of the warmest month between drought and wet years (Atlas of Israel, 1970). Such environments, as suggested by Rand (1982), impose nonselective mortality of eggs and young, with a selection pressure towards increasing the number of eggs per clutch.

Sands, however, seem to have a contrary effect on eggs. The lizards which live on sands bury their eggs in the ground. Due to the special character of the soil, arenicolous lizards are better able to dig, for oviposition, down to a level of appropriate moisture. Thus they secure for the eggs a stable environment (Ackerman, in press; Ratterman and Ackerman, 1989) conducive to high hatching success, enabling the evolution of fewer and larger eggs.

The large eggs of *Agama sinaita* may also be explicable by the predictable stability of the conditions in which they develop. Of all the species investigated here, this rupicolous desert lizard is the one whose occurrence is most strictly restricted to the extreme desert. Conceivably the correct oviposition sites may be relatively dry, or rare and hard to locate, or both, but, once located and employed, the conditions there remain stable.

#### EFFECT OF MATERNAL SIZE

In three Australian agamids of the genus *Amphibolurus*, both clutch size and the number of clutches per year increase with the age of the female (Bradshaw, 1981). Certainly, lizard species which are selected for a relatively large number of eggs in their clutch, would be expected to further increase clutch size with increasing maternal body size; indeed so do six of the species described here. These include *Agama stellio*, for which the same phenomenon has been verified in a Greek population (Loumbourdis, 1987). *Acanthodactylus boskianus* is an exception: This species retains the character of laying relatively numerous eggs in its clutch, although it lives also on sands; perhaps because sand is not its sole habitat. But with increasing body size it tends to increase egg volume, perhaps as an adaptation to its partial occupation of sandy habitats.

*Acanthodactylus scutellatus* which is an extreme sand-dweller, would seem to have reached optimum egg volume and clutch size, showing no increase in egg volume with the increase of body size. It is an individual forager, unlike *Acanthodactylus schreiberi* which is more territorial and has a rigid social structure (Avital, 1981). For this latter species, selection may be stronger for egg size, not merely to improve survival but also for attaining better social status. Young of lizards have been observed to establish social hierarchies depending on size (Fox and Rostker, 1982).

*Agama sinaita*, which lives in extreme arid southern Israel (Hertz and Nevo, 1981) exhibits strong individual territoriality (Arbel, 1981). In such a case of extreme environmental conditions and strong intraspecific competition, selection seems to be compromising, both egg number and egg volume increasing with body size.

#### CONCLUSIONS

The lizards treated here, as a group, basically tend to maximize the number of eggs, presumably because nonselective or random mortality favour an increased number of eggs. On the other hand, selection may favour large eggs when the conditions for their development are stable and when a larger offspring has a better chance to survive (Congdon, Vitt and Hadley 1978; Rand, 1982). Desert and Mediterranean environments seem to be alike in being unpredictable and unstable, selecting for an increase in clutch size, whereas extreme deserts and sandy environments appear to be predictable, though harsh, habitats, selecting for large eggs.

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## SODIUM CHLORIDE AND POTASSIUM CHLORIDE TOLERANCE OF DIFFERENT STAGES OF THE FROG, *MICROHYLA ORNATA*

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### ABSTRACT

Short term effects of different concentrations of NaCl and KCl on embryos and tadpoles of the frog *Microhyla ornata* were studied. Both NaCl and KCl caused significant reduction in swelling of the perivitelline space (PVS), an effect very similar to that reported for acidic pH. Tadpoles were observed to be somewhat more resistant to both NaCl as well as KCl, as compared to the embryos. KCl was found to be more toxic than NaCl. A typical teratogenic effect was observed in KCl treated embryos which showed swollen head coelom, whereas NaCl caused incomplete closure of the neural tube.

### INTRODUCTION

Amphibian embryos may be exposed to different salinities during the period of their embryonic development. Later the tadpoles also have to face varying environmental conditions. The reasons for variation in salinity are many. Intermittent rainfall often leads to drying of temporary rain-water pools thereby increasing the salinity (Munsey, 1972). It is also likely that the breeding sites on the coastline may be affected by tidal inundation. Thus, the salinity of the medium is an important factor in the developmental ecology of amphibians.

Some work has been done regarding the effects of salinity on breeding and development of a few amphibians (Ely, 1944; Ruibal, 1959; Beebee, 1985). Considerable work has been done on salt tolerance of the embryos, tadpoles and adults of the Indonesian frog *Rana cancrivora* (Gordan et al., 1961; Gordan and Tucker, 1965; Dunson, 1977). This frog is known to tolerate high salt levels in the ambient medium. However, no information is available regarding any of the Indian species of frog. In this study we estimated both the NaCl and the KCl tolerance limits at different stages of development of the frog *Microhyla ornata*.