EVOLUTIONARY STRATEGIES IN LIZARD REPRODUCTION

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Several investigators have dealt in a theoretical way with the evolution of reproductive rates and attendant life history phenomena (Cole, 1954; Lack, 1954, 1966, 1968; Murphy, 1968; Svärdson, 1949; Williams, 1966a, 1966b). Tinkle (1969a) has applied evolutionary principles in an attempt to construct a general theory of the evolution of single-broodedness and iteroparity, of viviparity, and of clutch size and clutch number in lizards. Most of the data presented by him were qualitative.

In this paper we pose a series of questions concerning reproductive strategies which have evolved among one group of vertebrates (the lizards), and provide quantitative data to answer them. We further present comparable data from birds, the vertebrate group most thoroughly studied in this respect. Finally, we suggest the weaknesses in studies of reptilian reproduction in the hope of stimulating future workers to collect data that are essential to answer these specific questions.

NATURE OF THE PROBLEM

Lizards display variability in their reproductive habits. Some are evidently acyclic in reproduction, while others have restricted reproductive seasons. Among the latter group are species that reproduce once during each season and others that reproduce several times. There are also large differences in clutch size. A single egg may be laid (as in the sphaerodactylines) or two as in most other gekkonids; some iguanids produce more than 20 eggs per clutch and may do this several times in a single season. Finally, there are great differences in age at maturity, in the size attained by breeding adults and in the degree of parental care of the eggs.

Different reproductive strategies are followed by different species of lizards. Some lizards are early-maturing, short-lived and highly fecund; some mature later, live for several years as reproductive adults, lay fewer eggs per clutch and lay less often per season. Taxonomically unrelated species may have convergent strategies as would be expected of such highly adaptive traits. Each strategy may be dictated by a particular set of environmental circumstances such that it may be possible to specify the conditions under which one strategy or the other would prevail, as was attempted by Tinkle (1969a).

Our approach is to pose the following questions concerning reproductive strategies, their diversity, their components and selective values.

1) To what extent is clutch size correlated with body size, with age at first breeding, and with the number of clutches produced per season?
2) Do reproductive differences also exist between populations of the same species?
3) Do the reproductive strategies that we identify here differ in tropical versus temperate species, oviparous versus viviparous species, early-maturing and short-lived species versus late-maturing, longer-lived ones? Do strategies correspond with taxonomic groups?
4) How do the results obtained compare with those from birds?
5) With what factors should future studies of reptilian reproduction be concerned?

MATERIALS AND METHODS

The data for the present paper come from the literature except where noted in the text. For each species, we obtained the following information whenever possible: minimum size at sexual maturity, average size of breeding females, average clutch size, age at first reproduction, mode of reproduction (whether oviparous or viviparous), number of broods per year, and the climate (temperate versus tropical) in the area of the study (Table 1).

Age at first reproduction has been inexactly determined by most investigators. If papers stated that maturity occurs in the next summer following hatching, we used 12 months as the age at first breeding. Where an author stated that 2 to 3 years were required to reach maturity, we chose the higher figure as a necessary simplification. Broods-per-year is almost always unknown; most estimates were minimal ones. Therefore, we chose to state only that a species was single-brooded or multiple-brooded.

Season as used in this paper means reproductive season. A lizard generally hatches during one season and also grows, often to nearly adult size, during the same season. In spite of this, we use the statement "next season after hatching" as meaning approximately 1 year after hatching. A species that matures and reproduces in the next season after hatching or earlier is considered an early-maturing species; one that matures in a still later season is considered a delayed-maturing species.

To define reproductive strategies 37 species with fairly complete data were clustered in a Prim network (Prim, 1957). The reproductive characters used to compute the dissimilarity matrix were: body size at maturity, clutch size, age at maturity, mode of reproduction and number of broods per year. The distribution of each character was standardized to a distribution of mean 0 and standard deviation of 1 so that each character contributed equally to the dissimilarity matrix. The coefficient of dissimilarity was computed as:

$$d_{ij} = \sum_{i,k} (X_{ij} - X_{jk}),$$

where X_{ik} is the character state of the kth character of species i and X_{jk} is the character state of the kth character of species j. The prim network results from an algorithm which progressively links each species to the species with a life history strategy most similar to it. The resulting diagram (Fig. 2) is unidimensional so that only dimensions along the network are meaningful.

In a few instances we may have placed a particular species in the wrong strategy group simply because data for that species were inadequate, but these discrepancies should not have a significant effect on our generalizations. We have also excluded lizards of the family Gekkonidae from consideration because of the nearly constant clutch size in this group.

Data were incomplete for many species, precluding $2 \times 2 \times 2$ factorial analysis of variance to describe the statistical interactions of mode of reproduction (oviparous versus viviparous), broods per year (single versus multiple), and climate (temperate versus tropical), and to ascertain the effects of each of these factors on the form of the multiple regression of clutch size on age and size at maturity. Because of these inadequacies we grouped for comparison all species for which data were available on any two reproductive parameters (Table 2). For example, one such group contained all those species for which mean clutch size and size at maturity were known, and a simple product-moment correlation coefficient was computed between clutch size and size at maturity within the group. This correlation was assumed to be representative of the relationship between these two variables in lizards as a whole. Similarly, correlation coefficients were computed for all combinations of clutch size, body size and age at maturity. Student's "t" tests

TABLE 1. *Demographic and reproductive data on lizards.* s = *single-brooded*, m = *multiple-brooded*; o = *oviparous*, v = *viviparous*; tr = *tropical*, tm = *temperate*.

Species	Minimum size at maturity (mm)	Mean size of mature females (mm)	Mean clutch size	Age at first breeding (months)[1]	Mode of reproduction	Broods per season	Climate	Study locality	Author(s)
IGUANIDAE									
1) *Amblyrhynchus cristatus*	—	—	2.0	late	o	s	tr	Galapagos	Carpenter (1966)
2) *Anolis carolinensis*	45	50	1.3	12	o	m	tm	Louisiana	Gordon (1956); Hamlett (1952)
3) *Anolis limifrons*	38	44	1.0	8	o	m	tr	Panama	Sexton et al. (1963)
4) *Basiliscus vittatus*	83	—	4.2	12	o	–	tr	Costa Rica	Hirth (1963)
5) *Corythophanes percarinatus*	—	—	7.1	24	v	s	tr	Guatemala	McCoy (1968)
6) *Crotaphytus collaris*	92	—	7.6	12	o	m	tm	Kansas	Fitch (1956)
7) *Crotaphytus wislizeni*	87	—	3.0	24	o	–	tm	California	Montanucci (1965, 1967)
8) *Crotaphytus wislizeni*	90	—	7.3	24	o	s	tm	Colorado	McCoy (1967)
9) *Holbrookia maculata*	45	54	6.1	12	o	m	tm	Texas	Tinkle and Walker (unpub.)
10) *Holbrookia texana*	55	—	5.3	12	o	–	tm	Texas	Cagle (1950)
11) *Holbrookia texana*	50	—	5.0	12	o	m	tm	Texas	Johnson (1960)
12) *Iguana iguana*	—	—	35.0	late	o	s	tr	Panama	Rand (1968)
13) *Liolaemus multiformis*	70	81	5.8	18	v	s	tm	Peru	Pearson (1954)
14) *Phrynosoma cornutum*	—	60	32.0	—	o	–	tm	Kansas	Givler (1922)
15) *Sauromalus obesus*	—	—	—	late	o	s	tm	California	Johnson (1965)
16) *Sceloporus cyanogenys*	88	106	13.0	late	v	s	tm	Texas	Hunsaker (1959)
17) *Sceloporus graciosus*	50	—	3.3	48	o	s	tm	California	Stebbins (1944, 1948); Stebbins and Robinson (1946)
18) *Sceloporus jarrovi*	—	79	10.0	—	v	s	tm	Arizona	Carpenter (1960a)
19) *Sceloporus merriami*	45	49	3.7	early	o	–	tm	Texas	Chaney and Gordon (1954)
20) *Sceloporus occidentalis*	62	—	8.0	24	o	–	tm	California	Davis (1967)
21) *Sceloporus occidentalis*	65	—	13.7	24	o	s	tm	Oregon and California	Fitch (1940)

[1] Early or late designate species for which we could state with fair assurance that a species matured in one year (early) or required 2 or more years to mature (late).

TABLE 1. (Continued)

Species	Minimum size at maturity (mm)	Mean size of mature females (mm)	Mean clutch size	Age at first breeding (months)[1]	Mode of reproduction	Broods per season	Climate	Study locality	Author(s)
22) *Sceloporus olivaceus*	80	—	15.0	12	o	m	tm	Texas	Blair (1960)
23) *Sceloporus orcutti*	87	92	9.2	36	o	–	tm	California	Mayhew (1963*a,b*)
24) *Sceloporus undulatus*	—	—	14.0	late	o	s	tm	Maryland	McCauley (1945)
25) *Sceloporus undulatus*	52	—	7.6	12	o	m	tm	Georgia	Crenshaw (1955)
26) *Sceloporus undulatus*	52	60	7.2	early	o	–	tm	Oklahoma	Carpenter (1960*b*)
27) *Tropidurus albemarlensis*	54	60	2.3	—	o	–	tr	Galapagos	Stebbins et al. (1967)
28) *Uma inornata*	70	81	2.5	24	o	m	tm	California	Mayhew (1965)
29) *Uma notata*	70	76	2.0	24	o	m	tm	California	Mayhew (1966*b*)
30) *Uma scoparia*	70	—	2.6	24	o	m	tm	California	Mayhew (1966*a*)
31) *Uta stansburiana*	37	—	3.2	12	o	m	tm	Colorado	Tinkle (1967)
32) *Uta stansburiana*	42	46	3.9	9	o	m	tm	Texas	Tinkle (1967)
AGAMIDAE									
33) *Agama agama*	70	85	6.0	12	o	m	tr	Liberia	Daniel (1960)
34) *Agama agama*	85	90	6.0	—	o	m	tr	Ghana	Chapman and Chapman (1964)
35) *Agama agama*	—	97	5.5	12	o	m	tr	Nigeria	Harris (1964)
36) *Agama cyanogaster*	—	—	11.0	12	o	m	tr	Tanganyika	Robertson et al. (1965)
37) *Amphibolurus caudicinctus*	60	—	—	9	o	m	tm	W. Australia	Storr (1967)
38) *Calotes rouxi*	57	60	6.0	—	o	–	tm	India	McCann (1940)
39) *Calotes versicolor*	100	—	15.0	12	o	m	tm	India	Asana (1931); McCann (1940)
40) *Draco melanopogon*	73	84	1.9	—	o	m	tr	Borneo	Inger and Greenberg (1966)
41) *Draco quinquefasciatus*	85	97	2.7	—	o	m	tr	Borneo	Inger and Greenberg (1966)
42) *Gonocephalus chamaeleontinus*	—	—	4.0	—	o	m	tr	Java	Kopstein (1938)
43) *Phrynocephalus helioscopus*	52	—	—	12	o	–	tm	USSR	Rustamov and Shammakov (1967)

TABLE 1. (Continued)

Species	Minimum size at maturity (mm)	Mean size of mature females (mm)	Mean clutch size	Age at first breeding (months)[1]	Mode of reproduction	Broods per season	Climate	Study locality	Author(s)
ANGUIDAE									
44) *Anguis fragilis*	120	—	9.0	36	v	s	tm	Europe	Smith (1951)
45) *Diploglossus costatus*	75	85	5.6	—	v	–	tr	Hispaniola	Greer (1967)
46) *Diploglossus crusculus*	56	62	3.4	—	v	–	tr	Jamaica	Greer (1967)
47) *Gerrhonotus coeruleus*	80	100	6.2	late	v	s	tm	California	Fitch (1935)
48) *Gerrhonotus multicarinatus*	112	—	11.6	late	o	s	tm	California	Fitch (1935)
LACERTIDAE									
49) *Lacerta agilis*	55	—	9.5	24	o	s	tm	England	Smith (1951)
50) *Lacerta vivipara*	—	—	6.5	36	v	s	tm	Europe	Rollinat (1934); Smith (1951)
51) *Takydromus tachydromoides*	40	53	3.6	12	o	m	tm	Japan	Ishihara (1964); Fukada (1965)
52) *Takydromus tachydromoides*	43	—	3.0	12	o	m	tm	Japan	Telford (1969)
TEIIDAE									
53) *Ameiva festiva*	77	—	2.4	12	o	m	tr	Costa Rica	Smith (1968)
54) *Ameiva quadrilineata*	64	—	2.1	12	o	m	tr	Costa Rica	Smith (1968)
55) *Ameiva quadrilineata*	48	—	2.0	12	o	m	tr	Costa Rica	Hirth (1963)
56) *Cnemidophorus exsanguis*	60	75	2.7	early	o	s	tm	New Mexico	Medica (1967)
57) *Cnemidophorus hyperythrus*	53	60	2.3	12	o	m	tm	Baja Calif.	Bostic (1966)
58) *Cnemidophorus inornatus*	50	57	2.2	early	o	m	tm	New Mexico	Medica (1967)
59) *Cnemidophorus neomexicanus*	60	65	1.6	early	o	m	tm	New Mexico	Medica (1967)
60) *Cnemidophorus sexlineatus*	54	61	2.3	12	o	m	tm	Kansas	Fitch (1958, 1967)
61) *Cnemidophorus sexlineatus*	55	65	2.5	12	o	–	tm	Oklahoma	Carpenter (1959, 1960*b*)
62) *Cnemidophorus sexlineatus*	53	—	3.1	early	o	–	tm	Texas	Hoddenbach (1966)
63) *Cnemidophorus tigris*	70	—	2.2	12	o	m	tm	Texas	Hoddenbach (unpubl.)
64) *Cnemidophorus tigris*	61	72	2.0	12	o	m	tm	New Mexico	Medica (1967)

TABLE 1. (Continued)

Species	Minimum size at maturity (mm)	Mean size of mature females (mm)	Mean clutch size	Age at first breeding (months)[1]	Mode of reproduction	Broods per season	Climate	Study locality	Author(s)
65) *Cnemidophorus tigris*	70	—	3.4	late	o	s	tm	Colorado	McCoy and Hoddenbach (1966)
66) *Cnemidophorus tigris*	75	—	3.0	24	o	s	tm	Nevada	Turner et al. (unpubl.)
CHAMAELEONIDAE									
67) *Chamaeleo bitaeniatus*	77	81	17.3	—	v	–	tr	Kenya	Bustard (1966)
68) *Chamaeleo hohneli*	74	80	10.0	—	v	–	tr	Kenya	Bustard (1965)
XANTUSIIDAE									
69) *Xantusia vigilis*	38	41	1.9	36	v	s	tm	California	Miller (1951, 1954); Zweifel and Lowe (1966)
SCINCIDAE									
70) *Emoia atrocostata*	—	80	2.0	9	o	m	tr	Philippines	Alcala and Brown (1967)
71) *Emoia cyanura*	—	—	2.0	early	o	m	tr	New Hebrides	Baker (1947)
72) *Emoia werneri*	—	—	2.0	early	o	m	tr	New Hebrides	Baker (1947)
73) *Eumeces egregius*	40	—	4.8	12	o	s	tm	Florida	Mount (1963)
74) *Eumeces fasciatus*	65	—	9.5	24	o	s	tm	Kansas	Fitch (1954)
75) *Eumeces obsoletus*	107	—	11.4	36	o	s	tm	Kansas	Fitch (1955, 1967)
76) *Eumeces septentrionalis*	65	—	8.8	36	o	s	tm	Minnesota	Breckenridge (1943)
77) *Eumeces skiltonianus*	58	64	4.4	30	o	s	tm	California and Utah	Tanner (1957); Rodgers and Memmler (1943)
78) *Leiolopisma aeneum*	45	—	2.2	—	v	–	tm	New Zealand	Barwick (1959)
79) *Leiolopisma fuscum*	—	58	2.0	—	o	m	tr	Australia	Wilhoft and Reiter (1965)
80) *Leiolopisma rhomboidalis*	—	48	2.0	—	o	m	tr	Australia	Wilhoft (1963)
81) *Leiolopisma zelandica*	54	—	5.1	24	v	s	tm	New Zealand	Barwick (1959)
82) *Lygosoma laterale*	35	—	2.5	9	o	m	tm	Florida	Brooks (1967)
83) *Lygosoma laterale*	40	—	3.3	12	o	m	tm	Louisiana	Johnson (1953)
84) *Lygosoma laterale*	38	47	3.8	12	o	m	tm	Kansas	Fitch and Greene (1965)

TABLE 1. (Continued)

Species	Minimum size at maturity (mm)	Mean size of mature females (mm)	Mean clutch size	Age at first breeding (months)[1]	Mode of reproduction	Broods per season	Climate	Study locality	Author(s)
85) *Mabuya multifasciata*	—	—	6.0	—	v	m	tr	Java	Kopstein (1938)
86) *Mabuya striata*	62	70	7.0	12	v	–	tr	Tanganyika	Robertson et al. (1965)
87) *Neoseps reynoldsi*	45	—	2.0	12	o	–	tm	Florida	Telford (1959)
88) *Sphenomorphus tanneri*	41	45	2.0	—	o	m	tr	S.E. Asia	Greer and Parker (1967)

of the differences of the means were computed for clutch size, body size and age at maturity between oviparous and viviparous, single-brooded and multiple-brooded, and temperate and tropical species. A Chi Square test of independence was used to test the degree of association between the mode of reproduction and the climate. Because of small sample sizes in the other comparisons, Fisher's Exact Probability Tests were used instead of Chi Square.

There were sufficient data to compute multiple regressions of clutch size on body size and age within single and multiple-brooded, oviparous, tropical and temperate lizards. For comparison with these subsamples, the same analysis was performed for all lizards for which there were data on clutch size and on age and size at maturity. The F-ratios of the regression mean squares to the error mean squares were used to test whether a significant amount of the variance in clutch size is accounted for by consideration of age and size at maturity.

Simple regression analyses of mean clutch size on snout-vent length at maturity were computed for the subsamples mentioned above (Fig. 1). The regressions

for single vs. multiple-brooded and oviparous versus viviparous species were compared by covariance analyses.

All of the above was concerned strictly with the interspecific comparisons. For intraspecific comparison of the body size–clutch size relationship, we chose *Uta stansburiana*, a species for which samples were available from many populations through much of the range of the species. Most of these samples were collected from May 8 to June 4, 1967. In each sample the clutch size was determined from counts of oviducal eggs or of yolked ovarian follicles. Tinkle (1961, 1967) has shown that the differences in clutch size estimated by these two methods are not significant.

Covariance analysis was used to compare the regressions of clutch size on snout-vent length for each population. The regressions were linear and the variances homogeneous for the lizard data. Tilley (1968), making similar comparisons between salamanders found that these conditions were not met, requiring transformation of the data.

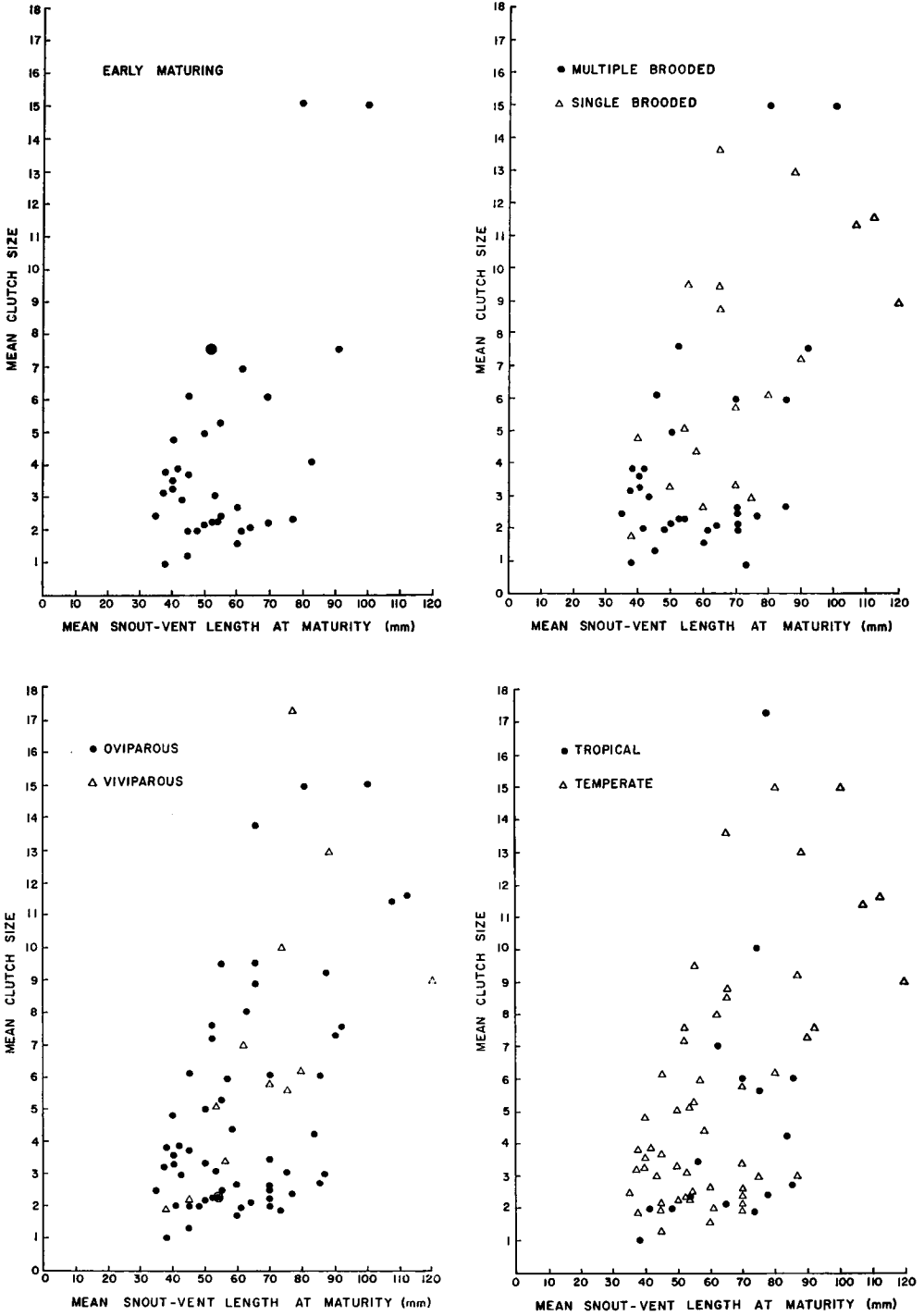The statistical terminology follows that of Steel and Torrie (1960) and Snedecor (1966).

FIG. 1. Regression of clutch size on body size for several different groups of lizards based upon their reproductive habits or climatic zone inhabited.

TABLE 2. *Two way variable comparisons for all available data on lizard species.*
[*, **, *** - .05, .01, .001 probability levels.]

VARIABLES	Product moment correlation coefficients	Sample size
Snout-vent length at maturity (mm) Mean length of reproductive females	0.593**	35
Snout-vent length at maturity (mm) Clutch size	0.547**	69
Snout-vent length at maturity (mm) Age at first reproduction (months)	0.379**	50
Snout-vent length adult females (mm) Clutch size	0.241	41
Snout-vent length adult females (mm) Age at first reproduction (months)	0.238	19
Clutch size Age at first reproduction (months)	0.31*	53

	Mean	Variance	Sample size	Student's t	Degrees of freedom
Snout-vent length at maturity					
oviparous	61.644	334.198	59		
viviparous	69.916	470.810	12	−1.234	69
single brood per year	71.526	533.374	19		
multiple broods per year	58.911	305.233	34	2.072*	51
tropical	66.375	230.516	16		
temperate	62.072	399.214	55	0.924	69
early maturing	55.297	244.436	37		
late maturing	74.260	401.381	23	−3.866**	58
Snout-vent length of adult females					
oviparous	65.483	254.923	31		
viviparous	77.800	340.400	10	−1.894	39
single brood per year	76.285	486.905	7		
multiple broods per year	65.909	310.753	22	1.134	27
tropical	72.875	319.050	16		
temperate	65.680	273.641	25	1.294	39
early maturing	62.368	201.023	19		
late maturing	80.125	430.695	8	1.294	39
Clutch size					•
oviparous	5.798	37.332	66		
viviparous	7.023	15.543	17	−1.006	81
single brooded	7.937	43.358[1]	27		
multiple brooded	3.987	10.890	40	2.883*	
tropical	5.589	46.079	28		
temperate	6.135	26.380	57	−0.375	83
early maturing	4.300	10.782[1]	40		
late maturing	7.814	42.536	28	2.628*	66

[1] Sample had unequal variances; means were compared by adjusted student's t (Cochran and Cox, 1957).

TABLE 2. (Continued)

	Contingency Table	Probability	
	oviparous	viviparous	
Single brooded	16	9	P*** (more extreme < .001
Multiple brooded	41	1	distribution)
	oviparous	viviparous	
Tropical	21	7	$X^2 = 0.60$
Temperate	51	9	
	oviparous	viviparous	
Early maturing	42	1	P*** (more maturing = 0.001
Late maturing	18	8	distribution)
	tropical	temperate	
Single brooded	3	23	P*** (more extreme < 0.001
Multiple brooded	15	22	distribution)
	tropical	temperate	
Early maturing	12	31	P (more extreme = 0.09
Late maturing	3	23	distribution)

	early maturing	late maturing	
Single brooded	2	21	P*** (more extreme < 0.001
Multiple brooded	32	2	distribution)

RESULTS

Correlates of Clutch Size

There is a highly significant positive correlation ($r = 0.547$; $P < .01$) between snout-vent length at maturity and mean clutch size (Table 2). There is also a significant correlation ($r = 0.31$; $.05 > P > .01$) between clutch size and age at first reproduction; this is also shown by the significantly different clutch sizes of the groups of early and late maturing lizards ($t = 2.628$; $.05 > P > .01$).

Approximately 26% of the variance in clutch size among all species is accounted for by consideration of differences between these species in size and age at maturity. Size at maturity accounts for a significant amount of the variance in clutch size; an insignificant additional reduction of variance is gained from consideration of age at maturity ($F = 0.165$). In addition, there are some interesting correlations between clutch size and some other parameters. Mean clutch sizes and the mean body sizes do not differ significantly either

TABLE 3. *Results of regression analyses of mean clutch size on snout-vent length at maturity for various groups of lizards.*
[*, ** – .05, .01 probability levels.]

Grouping	N	Mean body size (mm)	Mean clutch size	b	a	r
Single-brooded	19	71.68	7.07	.090	.619	.558*
Multiple-brooded	32	58.69	3.96	.092	−1.440	.489**
Oviparous	57	61.84	4.85	.097	−1.148	.512**
Viviparous	12	69.92	7.21	.124	−1.460	.595*
Early-maturing	35	55.26	4.27	.114	−2.030	.563**
Late-maturing	22	72.55	6.48			.379
Temperate	53	62.30	5.42	.109	−1.371	.602**
Tropical	16	66.38	4.74			.409

between oviparous and viviparous or between tropical and temperate species. There is a significant ($t = 2.883$; $.05 > P > .01$) difference, almost two-fold, between the large mean clutch size of single-brooded and the small mean clutch size of multiple-brooded species. Single-brooded lizards have a larger mean body size than multiple-brooded species ($t = 2.072$; $.05 > P > .01$).

Simple regressions of mean clutch size on size at maturity (Fig. 1; Table 3) were appropriate because consideration of age at maturity contributed insignificantly to the variance around the regression. Furthermore, the sample sizes were increased by allowing us to use species for which age at maturity was not known.

Body size and clutch size are not significantly correlated in late-maturing or in tropical species (Table 3), a fact suggested by the multiple correlations discussed previously. The sample sizes in these two groups are larger than those for viviparous and for single-brooded species within which significant correlations were found.

Covariance analysis of the two comparisons in which clutch size and body size were significantly correlated (Table 4) indicate that data for oviparous and viviparous species lie on the same regression line. The points for single-brooded lizards lie on a regression line with the same slope as that for multiple-brooded species, but with a higher elevation. Therefore, single-brooded lizards at any given body size lay larger clutches than multiple-brooded lizards.

Intraspecific Comparisons

Differences in clutch size *between* species must arise through selection acting on variations in clutch size among individuals within populations of a species. In other words, it is the difference in selective regimes *within* species populations that ultimately produces differences between species. It is necessary to demonstrate that clutch sizes do indeed vary within and between populations of the

TABLE 4. *Results of covariance analyses comparing mean clutch size to mean snout-vent length at maturity regressions for various groupings of lizards.*

A) Single versus multiple-brooded species.

Source of variance	D.F.	b	Mean square
Within	47		9.308
Regression coefficient	1		.022
Common	48	.091	9.115
Adjusted means	1		40.556
Total	49	.104	9.756

$$F_{slope} = .002, P > .05$$
$$F_{elev} = 4.450, .05 > P > .01$$

B) Oviparous versus viviparous species.

Source of variance	D.F.	b	Mean square
Within	65		10.028
Regression coefficient	1		3.043
Common	66	.102	9.922
Adjusted means	1		22.597
Total	67	.107	10.112

$$F_{slope} = .303, P > .05$$
$$F_{elev} = 2.277, P > .05$$

same species, and further, that such differences can be inferred to have selective advantage in one or more populations. Tinkle (1967) has cited the numerous instances in which authors have noted increased clutch sizes in larger or older individuals within populations, and has demonstrated that differences in clutch size between at least two widely separated geographic populations of the lizard *Uta stansburiana* can be related to differences in the relative advantage of small body size versus large body size in these two populations (Tinkle, 1969*b*).

Table 5 summarizes the intrapopulation regressions of clutch size on snout-vent length for 23 populations of *Uta stansburiana*. The various populations differ considerably from one another in the degree to which these two variables are correlated. Geographic variation in the

TABLE 5. *Summaries of regression analyses of clutch size versus body size for populations of Uta stansburiana.*
[*, ** – .05, .01 probability levels.]

Date	Locality	N	Mean body size (mm)	Mean clutch size	b	a	r
Spring-summer 1959–60	Texas: Randall Co.	38	45.816	4.053	.129	–1.857	.356*
Spring-summer 1959–60	" Armstrong Co.	24	44.042	4.000			.300
Spring-summer 1959–60	" Ward Co.	52	45.865	3.500			.225
7 Jun 1963	" Kermit	20	48.850	4.400			.283
Jun–July 1965[1]	Colo: Colo. Nat. Monument	135	42.822	3.200	.106	–1.339	.428**
19 May 1968[1]	Ariz: Page	25	46.600	3.400	.147	–3.450	.470*
8–9 May 1967[1]	Calif: Victorville	27	43.815	3.037	.168	–4.324	.464*
15–16 May 1967	" Lone Pine	19	43.737	3.105			.049
16 May 1967[1]	" 5.4 mi N Bishop	24	45.750	3.875	.234	–6.831	.585**
11 May 1968	" 5.4 mi S Bishop	23	46.000	2.565			.203
31 March–1 Apr 1962	" Riverside Co.	17	45.000	3.588			.291
7–8 May 1968	" Shoshone	14	46.857	3.714			.026
24 May 1967[1]	Nev: Wendover	20	43.550	3.700	.168	–3.616	.619**
19 May 1967[1]	" Ely	16	46.750	4.750	.176	–3.478	.858**
21 May 1967[1]	" Eastgate	23	46.043	4.130	.224	–6.184	.789**
22–23 May 1967[1]	" Pyramid Lake	26	45.423	4.077	.191	–4.599	.680**
15 May 1967	" Daylight Pass	21	45.286	4.333	.326	–10.430	.576**
17 May 1967[1]	" Tonopah	21	45.762	4.476	.200	–4.676	.558**
18 May 1967	Nev: Caliente	16	45.438	4.000			.250
29 May–1 June 1967[1]	Utah: Grantsville	31	46.194	4.387	.288	–8.917	.713**
26–27 May 1967	" Hurricane	19	46.053	4.105			.426
28 May 1967	" Delta	21	46.095	3.619			.125
27 May 1967[1]	" Leeds	21	46.095	4.000	.245	–7.293	.670**
26 May 1967[1]	" Santa Clara	21	46.095	3.571	.127	–2.283	.439*

[1] Populations included in covariance analyses.

correlation between body size and clutch size indicates a cline from relatively high correlation in the north to relatively low correlation in the southwest (Table 5). In central Nevada, large body size is closely correlated with a large clutch, but in southern Nevada (Daylight Pass, Tonapah, Caliente), southwestern Utah (Delta, Leeds), and southern California body sizes are large but not accompanied by proportionately large clutches.

Even among those populations showing significant correlation of clutch size with body size there are differences in the variances around the regression lines (Table 5). These residual variances are unrelated to mean body sizes of the populations, making transformation of the data inappropriate. Thus, not all populations could be included in the covariance analysis, which assumes homogeneous variance around the regression being tested. The populations that were included are indicated in Table 5, the results of the covariance analyses in Table 6.

The F-test of the variance introduced by fitting a common slope to the data was significant ($F_{slope} = 1.927$; $.05 > P > .01$) indicating that not all of the regressions of body size on clutch size have the same slope. The Colorado population was excluded and the covariance analysis re-

TABLE 6. *Results of covariance analyses comparing clutch size—body size regressions for* Uta stansburiana *populations.* (A) *Comparison of all populations for which* r *is significant at the 95% level.* (B) *Comparison of the above populations excluding Colorado.*

A)

Source of variance	D.F.	b	Mean square
Within	366		.365
Regression coefficient	11		.703
Common	377	.170	.375

$$F_{slope} = 1.927, .05 > P > .01$$

B)

Source of variance	D.F.	b	Mean square
Within	233		.399
Regression coefficient	10		.294
Common	243	.198	.395
Adjusted means	10		4.204
Total	253	.205	.545

$$F_{slope} = .737, P > .05$$
$$F_{elev} = 10.650, P < .01$$

TABLE 7. *Comparison of simple regression analysis of clutch size on body size for all oviparous multiple-brooded species and 24 populations of* Uta stansburiana.
[*, ** − .05, .01 probability levels.]

	Oviparous-multiple brooded species	*Uta stansburiana* populations
Sample size	32	24
Mean body size	58.688	45.580
Mean clutch size	3.959	3.816
Correlation coefficient	0.489**	0.443*
Regression slope	0.092	0.179
y-intercept	−1.418	−4.343
Variance analysis		
Total mean square	11.376	0.267
Regression mean square	84.233	1.212
Error mean square	8.947	0.224
F regression/error	9.414	5.410*

peated. The slopes of the remaining populations did not differ significantly. If the sample sizes from populations other than Colorado had been as large as that for Colorado, other slope differences might have been detectable.

The absence of slope differences among the remaining populations made it possible to test for differences in the elevations of the regression lines which are significant between populations (F_{elev} = 10.650; $P < .01$). The Y-intercepts for different geographic samples suggest a gradient from higher intercepts in the north to lower ones in the south (Table 5).

The regression of clutch size on body size for all *Uta stansburiana* populations was compared with that for all oviparous, multiple-brooded species of lizards. This group was chosen for comparison because utas are oviparous and multiple-brooded. The results of these analyses are compared in Table 7. Size and fecundity are significantly correlated within the multiple-brooded species and within *Uta stansburiana*. The residual variance is higher for the interspecific regression (8.947 versus 0.224), indicating that the higher significance level is due to a greater spread of snout-vent lengths rather than to a tighter clustering of points around the regression line. This heterogeneity of the residual variances precludes comparison of the regression lines by covariance analysis; the two slope estimates (.092 ± .182 for the multiple-brooded oviparous species and .179 ± .159 for *Uta stansburiana*) do not differ significantly ($P > .05$).

The Identification of Reproductive Strategies

Lizards are clearly divided into two strategies: early-maturing, multiple-brooded vs. late-maturing, single-brooded (Fig. 2). Viviparity is just one form of the latter strategy inasmuch as almost all viviparous species produce one litter per year and have a significantly ($t = 5.585; P < .001$) later age at first reproduction. As can be
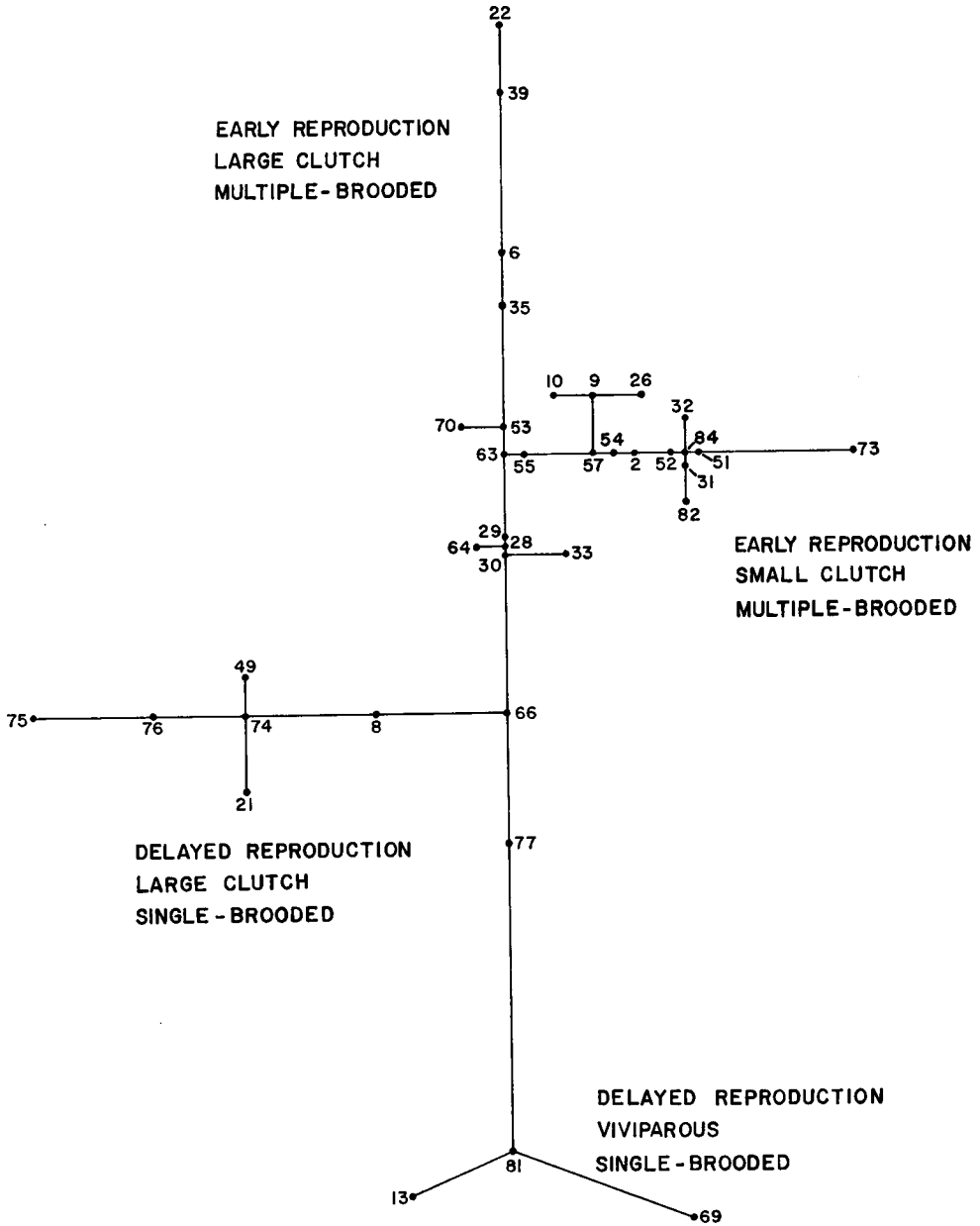
FIG. 2. Prim network of 37 species of lizards based upon reproductive strategies. Numerals refer to the number of species in Table 1.

seen from the Prim network (Fig. 2), these strategies cut across taxonomic lines.

We can state that in the early-maturing group as opposed to the late-maturing group: (1) oviparity is almost the universal type of reproduction (Table 2); (2) they are nearly all multiple-brooded; (3) the mean clutch size is significantly smaller ($t = 2.628$; $P < .01$); (4) more of the variance (41% versus 27%) in clutch

size between species is accounted for by consideration of size and of age at first breeding; (5) they are smaller-bodied at maturity ($t = 3.866$; $P < .01$) (Table 2); (6) they tend to be tropical and temperate in distribution as opposed to primarily temperate for the single-brooded, delayed maturity group.

DISCUSSION

The distinct strategies which we have deduced imply that each strategy is a coevolved complex of adaptations in morphology and ecology, as well as in reproductive physiology. Lizards which mature early have shorter adult life expectancies (Tinkle, 1969a), are almost always multiple-brooded and produce relatively small clutches. Lizards with delayed maturity must have greater survivorship, and are usually single-brooded and have larger clutches.

Because late-maturing lizards have lower per-season fecundities than early-maturing ones, it follows that in the evolution of a late-maturing species from an early-maturing one there must have been compensations for the loss of fecundity. One of these compensations is a greater body size at first breeding which allows for a larger clutch than would be possible in a smaller-bodied lizard. It may be true that species with delayed maturity are producing larger eggs than early-maturing ones, although our data do not support this (Fig. 1); in fact, we predict that this is the case and that this type of parental care results in greater survivorship among the young from these large eggs. The virtual restriction of postdepositional parental care and viviparity to late-maturing species indicates that these particular aspects of the strategy of this group also contribute to greater egg and juvenile survivorship.

The relatively larger body sizes of adults of late-maturing species may remove them from some predation, thereby increasing their adult longevity. The re-duced intensity of their reproductive effort also may feed back positively on their adult life expectancy, ultimately providing more opportunities for reproduction.

Delayed maturity appears to be more frequent in temperate than in tropical environments. By temperate we will not necessarily restrict ourselves to a latitudinal connotation. Perhaps we should substitute "equable" for tropical and "seasonal" for temperate. The tropical lizards are a subset of the strategy of early-maturity. The major difference between this subset and the rest of the group is the absence of a significant correlation between clutch size and size at maturity compared to a highly significant ($r = 0.602$; $P < .01$) one in temperate lizards (Table 3). This must imply that clutch size in tropical species is adjusted in different ways than in temperate ones. The more intense intraspecific competition that results in tropical populations that are presumed always to be near the carrying capacity of their environment may produce selection for improved survivorship rather than for large clutches. If this is the case, then we would expect egg sizes to be larger in tropical species and clutch sizes to be smaller than in other early-maturing species, as our data suggest. An alternate suggestion for explaining small clutch sizes in tropical species was advanced by Inger and Greenberg (1966) who argued that the competition for food precluded much fat storage, storage which has been shown to be important for reproduction in at least one temperate species (Hahn and Tinkle, 1964). The lack of a stored fat reserve reduces the number of eggs that could be produced. However, if further research demonstrates that tropical species are producing much larger, but fewer eggs, then the explanation must be sought in selection rather than in physiological limitations.

The intraspecific data on body size–clutch size relationships of utas indicates the variability to be expected within a

single wide-ranging species. The regressions for various populations of *Uta* differ primarily in elevation. This indicates that the number of eggs added to a clutch for each increment of body size varies little from population to population, a constancy previously noted by Tilley (1968) for salamanders of the genus *Desmognathus*. A more thorough study of these regressions within species might reveal differences in slopes, provided large samples are examined.

The apparent decrease in the Y-intercepts with latitude (Table 5) may result from the fact that late season clutches in *Uta stansburiana* are generally smaller than early season ones (Tinkle, 1967; Hoddenbach and Turner, 1968). Because almost all of the samples we used were collected in early summer, those lizards from the southwestern populations may have been at a later stage in their reproductive season than northern lizards. Greater variances in clutch size in late season clutches in southwestern populations may be responsible for the lower correlation of clutch size with body size. Future workers are advised to consider seasonal variation and differences in egg size when investigating latitudinal trends in clutch size.

The regression of body size and clutch size in *Uta stansburiana* is difficult to compare with that of the multiple-brooded lizards because the variances around the two regressions are not homogeneous (Table 7). The slopes of the regression lines are the same. In addition to sampling error, the greater residual variance about the regression line for interspecific comparisons may reflect differential evolutionary adjustment between species of clutch size independent of body size. That such adjustments have occurred seems likely from our discussion of clutch size in tropical lizards. Larger lizards apparently do not lay clutches containing either more or fewer eggs than would be predicted from the intraspecific regression shown for *Uta*

stansburiana. Evidently, within lizards of a given strategy there is a fundamental relationship between body size and clutch size that has been subject to little evolutionary adjustment.

More detailed intraspecific studies of reproductive parameters are necessary to understand selective processes within species populations and to strengthen any hypotheses about the origin of reproductive strategies.

A Comparison With Birds

Lack (1966, 1968) has reviewed the reproductive adaptations of birds. The reproductive strategies are similar in a general way to those of lizards; differences between the classes arise from the great diversity in birds of specializations such as hole-nesting, colony formation, brood parasitism and cooperative rearing of the young. The abundance of life history information and of experimental studies of bird reproduction makes the selective bases for the observed adaptations clearer than for lizards.

In birds there is no apparent intraspecific correlation between body size and clutch size; this is due in part to their determinate growth. Some iteroparous species of birds such as gulls produce smaller broods in their first year of breeding. There is likewise no correlation between clutch size and body size between species; clutches of one or two eggs are characteristic of small swifts and hummingbirds, but also of the large raptors and albatrosses. Large clutches are observed in small tits as well as some large ducks. Clutch sizes in birds are positively correlated with high latitudes, hole-nesting, nidifugous young, early maturity and with savannah as opposed to forest habitats.

Birds, like the lizards, may be divided into two groups on the basis of their age at first reproduction. Early-maturing birds (most nidicolous land birds and the nidifugous aquatic birds) generally

lay large clutches (in contrast to lizards), have short developmental periods and a low annual survivorship. Their nesting sites are relatively accessible to predators. The rapid developmental period from laying to fledging permits replacement of lost broods and, in many species, allows two or more reproductions per season. The larger clutch sizes of early-maturing birds compared to lizards is probably attributable to parental care of the young in birds.

The second group of birds (including large raptors, swifts and some colonial sea birds) is characterized by delayed reproduction, small clutches, single broods per season, high annual adult survivorship and long developmental periods. These birds nest in sites inaccessible to most predators so that the long incubation and fledging periods are not a great risk. This prolonged developmental period is considered an adaptation to the irregular feeding schedule imposed by an unpredictable food supply. The delayed maturity is thought to be imposed by the necessity of a period of learning by a young bird; premature reproduction is a risk to future reproductive success and hence is selected against.

Whatever environmental circumstances are responsible for the evolution of delayed maturity in birds and in lizards, in neither group is there evidence that delayed maturity is due simply to physiological inability to mature in a shorter period of time. Stable populations can result only when delayed maturity is accompanied by adjustment of other life history parameters such as degree of parental care, adult life expectancy, clutch size and the frequency of clutches (Cole, 1954). Late-maturing lizards have three adaptations to counter the cost in fitness imposed by delayed maturity. One adaptation is the production of larger clutches, achieved in part by growth to a larger size before maturity. The other is by increasing parental care and viviparity. The last is a longer reproductive life expectancy. Although birds have not evolved viviparity,

the large raptors and sea birds have increased the period of parental care for their one or two chicks to the point that the high probability of the young surviving to maturity coupled with a long breeding life expectancy of the adult balances the reproductive cost of delayed maturity.

Suggestions for Future Study

Data on tropical species, particularly those in constant environments, are badly needed as are more intraspecific population studies. Critical items of information needed are exact ages at first breeding, number of clutches actually produced in a single season, absolute size of eggs, egg size relative to weight of female, the reproductive life expectancy of adults, their age-specific fecundities and mortalities, and the survivorship of hatchling animals to sexual maturity. These items have been neglected in part because their significance has not been generally appreciated and in part because these are the items most difficult to study. As Turner (1968) has pointed out in review of Tinkle (1967), some items of information collected in life history studies constitute field bookkeeping and often are not collected with the view of answering particular questions. It is our judgment that the amount of time invested in any life history study could be better spent if concentrated on answering some specific questions.

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