EVOLUTION OF NESTING PATTERNS IN IGUANINE LIZARDS

FROM *IGUANAS OF THE WORLD* WITH PERMISSION OF THE AUTHOR,
THOMAS A. WIEWANDT

Introduction

The concept of reproductive effort, defined as the proportion of the total energy budget an organism invests in reproduction, is receiving increasing attention from biologists interested in population biology and life history evolution (Williams, 1966a, b; Tinkle, 1969; Gadgil & Bossert, 1970; Tinkle *et al.,* 1970; Schaffer, 1974; Wilbur et al., 1974; Tinkle & Hadley, 1975; Hirshfield & Tinkle, 1975; Pianka, 1976). Studies of reproductive effort have spawned theoretical models, predictions, new models, and more predictions, all aimed at formulating general theory on the evolution of life history types. Tinkle (1969) and Tinkle & Hadley (1973, 1975) attempted to relate various measures of reproductive effort in lizards to demographic parameters such as age at maturity, body size, clutch size, and nesting frequency. The outcome was not terribly encouraging (Hirshfield & Tinkle, 1975, p.2227):

> The difficulties in understanding the evolution of reproductive effort stem from the fact that predictions from theory are, in many cases, results of assumptions in the models which require careful examination before the predictions may be considered relevant to organisms in nature. Difficulties also arise because it is not clear what data constitute adequate measures of reproductive effort. It is impossible at present to decide whether failure of the data to be consistent with theory is due to inappropriate estimators or to inadequate theory.

In this study I examine social and ecological factors influencing reproductive effort in a small group of lizards, the Iguaninae, by taking a close look at the adaptive significance and evolution of nesting patterns. I hope to stimulate thinking about factors seldom considered in studies of lizard life history evolution. My approach is qualitative and somewhat speculative, because demographic data in iguanines are fragmentary (for a comprehensive, pre-1978 compilation, see Table 6 in Iverson, 1979), and there are few comparative data on social behavior and habitats. Following a generalized description of the "typical" reproductive pattern for iguanine lizards are five sections concerning different, though interrelated, aspects of an iguana's nesting strategy: (1) size and age at first nesting; (2) clutch, egg and hatchling sizes; (3) nesting phenology; (4) nest-site selection and migrations; and (5) origins and consequences of communal nesting.

Generalized Reproductive Pattern for Iguanine Lizards

Most small insectivorous lizards attain sexual maturity 1-2 years after birth or hatching (Fitch, 1970), but iguanas normally require at least 2-3 years and then reproduce regularly for three or more years thereafter, until death. All iguanines are oviparous. Typically breeding is annual and seasonal, with mating taking place in male territories 3-7 weeks before nesting.

Gravid females select nesting sites on the ground in sunlit areas and excavate burrows large enough to accommodate a female's entire body. Each burrow terminates in an egg chamber wide enough to permit the female to turn around inside. She lays only one clutch, and then blocks the passageway to the eggs by filling and packing, leaving a pocket of air over the eggs. Sites are vigorously defended against conspecifics during nest preparation.

Incubation commonly requires 10-14 weeks. Nest temperature remains nearly constant, with mean values of 28°-32°C for most species. Eggs from each clutch usually hatch in synchrony, and young dig to the surface without parental assistance. Hatchlings are highly vulnerable to predation and are cryptic. The young disperse from nest sites shortly after emerging.

This synthesis was drawn from a multitude of papers, which include the following key references: *Amblyrhynchus* (Carpenter, 1966; Boersma, 1979; Trillmich, 1979); *Conolophus* (Werner, 1982; Christian & Tracy, 1982); *Ctenosaura* (Fitch,1970; Fitch, 1973a; Fitch & Henderson, 1977a; Hackforth-Jones & Harker, MS.); *Cyclura* (Carey, 1975; Wiewandt, 1977, 1979; Iverson, 1979); *Dipsosaurus* (Norris, 1953; Mayhew, 1971); *Iguana* (Rand, 1968a; Muller, 1968, 1972; Fitch & Henderson, 1977b; Dugan, 1982); *Sauromalus* (Johnson, 1965; Nagy, 1973; Berry, 1974).

While there are few known exceptions to this generalized pattern among New World iguanines, Fiji iguanas, *Brachylophus* show several pronounced departures (see Gibbons and Watkins, 1982). Sexual activity appears to be relatively less seasonal (ca. 5 mos/yr) in *Brachylophus,* and females possibly lay more than one clutch annually. Mating takes place about six weeks before, and again about two weeks after, nesting. No air space is left over the egg clutch (this is sometimes also true for *I. iguana* – A.S. Rand, pers. comm.). Furthermore, incubation time is extremely long, ranging from 18 to 35+ weeks; intermediate incubation periods of 14-17 weeks have been noted for *Conolophus.*

Size and Age at First Nesting

At what point in an organism's lifetime should it first attempt reproduction? Theoretically, selection should favor individuals making the earliest possible investment in reproduction without sacrificing long-term reproductive success (see discussion by Pianka, 1976). For a long lived species, this might mean delaying the onset of breeding to permit growth to a larger and more advantageous body size. Among iguanine lizards, for example, young, inexperienced males are at a severe disadvantage in combat over breeding territories. To avoid injury and probable loss of long-term competitive ability, members of this size class must forego breeding or adopt an alternative and less profitable mating strategy (see Dugan & Wiewandt, 1982).

For a female, egg production may result in an appreciable drain on her energy reserves requiring growth to be slowed or suspended temporarily (e.g., Van Devender, 1978), and an abdominal cavity packed with eggs apparently limits food intake (Rand, 1968; Wiewandt, 1977). In some ecological settings, female iguanas have much to gain by trading-off an early reproductive effort for maximal growth. Fecundity typically increases with advancing age/size (e.g., Berry, 1974; Fitch & Henderson, 1977b; Iverson, 1979; Hackforth-Jones & Harker, MS.), and in a review of reptilian reproductive cycles, Fitch (1970) noted that larger females of the same species not only produce larger broods but also produce them with greater consistency or at shorter intervals. Susceptibility to predation may be significantly reduced (e.g., Van Devender, 1978; Harris, 1982) or completely eliminated in adults of large body size (Wiewandt, 1977; Werner, 1982). Where suitable nest sites are scarce (e.g., on Mona I., P.R.) a female's size affects her chances of successfully defending a site from intruding conspecifics (Wiewandt, 1977). Moreover, larger lizards are endowed with added resistance to dehydration and starvation in harsh, unpredictable environments. Such benefits may be particularly meaningful to iguanas due to their predominantly herbivorous habit (Pough, 1973; Iverson, 1982; Van Devender, 1982).

Just as reproduction and growth are inseparable phenomena, both are closely tied to an organism's food environment. Pianka (1976) emphasized that interactions and constraints between foraging and reproduction are vital to understanding an animal's time and energy budget and that these factors have barely begun to be considered jointly in empirical studies of either growth or reproductive effort. There have been few rigorously designed comparative investigations of growth and reproduction in lizards (Van Devender, 1978), and none are available for the Iguaninae (but Van Devender and Case, both in 1982). Unfortunately many iguana populations are now precariously small and can provide the large data base statistically desirable for such analyses only through unscrupulous sampling or a long-term commitment to studying marked individuals in the field. The latter approach is nicely

Table 1: Comparisons of Relative Size and Age at First Nesting and Relative Pre-Reproductive Growth Rates in Females from Ten Populations of Iguanine Lizards

Values in parentheses indicate odd samples, estimates taken from different populations; asterisks indicate data source.

Species	Location	Body Size (SVL in mm) • • • X̄ Hatchling A	Smallest Breeding Female B	X̄ Adult Female C	Percent Pre-Reproductive Growth Relative to Growth to Adult X̄ Female Size (B-A) (C-A) x 100	Approxi-mate Age at Maturity D	Growth/Year as Percent Female Size at Sexual Maturity (B-A)÷D÷B x 100	Sources (A, B, C, D) and Remarks
Dipsosaurus dorsalis	California	(49 *)	110	120	86	5-6 yr	9	Mayhew, 1971 * Parker, 1972
Sauromalus obesus	California	54	150	~170	83	4-7 yr	11	* * Berry, 1974
	California	(54 * *)	149	~163	87	–	–	Johnson, 1965
Cyclura carinata	Caicos Is.	80	190	225	76	6-7 yr	8	Iverson, 1979
Cyclura pinguis	Anegada, BVI	(~105)	~375	468	74	7-9 yr	9	Carey, 1975 small sample
Cyclura stejnegeri	Mona I., P.R.	119	~375	475	72	5-7 yr	11	Wiewandt, 1977 small sample
Ctenosaura similis	Nicaragua	57	200	276	65	21-33 mo	32	Fitch & Henderson, 1973 a
Iguana iguana	Costa Rica	57	212	335	56	21-33 mo	32	Fitch, 1973a
	Nicaragua	74	250	327	70	21-33 mo	31	Fitch & Henderson, 1977b
	N.E. Colombia	68	201	280	63	21-33 mo	29	Müller, 1968, 1972 See note 1 in text.

exemplified by Case's on-going integrative research on mainland and insular *Sauromalus* populations and should serve as a model for others to follow. In spite of the status quo, enough information is available on the ecology of some iguana populations to allow a few preliminary comparisons (Table 1).

Three species categories can be distinguished in Table 1 using broad ecological criteria: (1) desert dwellers of the Temperate Zone — *Dipsosaurus* and *Sauromalus;* (2) species of dry subtropical islands — *Cyclura;* and (3) mainland forms from moist subtropical or tropical environments — *Ctenosaura* and *Iguana.* The same three groups are evident in demographic data comparing species by the degree of pre-productive growth in females relative to growth normally achieved through adulthood. *Dipsosaurus dorsalis* and *Sauromalus obesus* do comparatively more of their growing before the onset of nesting, while *Ctenosaura similis* and *Iguana iguana* do the least; *Cyclura* are intermediate. Age at maturity is clearly independent of species body size, with *C. similis* and *I. iguana* being outstanding in their relatively early start at egg production. These two iguanas are also distinctive in showing unusually rapid overall growth rates during their pre-reproductive years; females grow approximately three times faster than any other species under consideration. A look, albeit superficially, at the ecological settings of each species appears to provide at least a partial evolutionary explanation for the above life history differences.

Iguanas from North American deserts have short activity seasons (ca. 6 mos.) limited by both low winter temperatures and unpredictable dry periods which reduce food quality and abundance (Norris, 1953; Nagy, 1973; Berry, 1974). Consequently, annual growth tends to be low and variable, and reproduction risky. For example, female *Sauromalus* grow slowly and do not produce clutches every year (Nagy, 1973; Berry, 1974). They apparently have lower survivorship than males, possibly due to the high energetic cost of reproduction in an uncertain environment (Berry, 1974). A spent female chuckawalla may have difficulty surviving through winter hibernation following a dry desert summer because suitable forage is typically gone when oviposition occurs. *Dipsosaurus dorsalis* probably experiences less severe limitations because it is well adapted for activity in extreme heat (Norris, 1953) and may be less susceptible to desiccation. Desert iguanas also appear to be better suited for utilizing subterranean refugia offering more favorable microclimates. All else being equal, however, smaller size is a physiological handicap under stressful conditions. That females of both species do not begin reproducing at smaller sizes seems to reflect a climactically imposed need to postpone reproduction and channel surplus energy resources into growth, until reaching a size that will lower the risks of starvation and dehydration.

Iguanas native to islands of the Bahamas and Greater Antilles *(Cyclura)* are larger than Temperate continental desert iguanines, require as long or longer to reach sexual maturity, and tend to grow at proportionally similar rates (Table 1). Furthermore, a greater proportion of the average cycluran female's growth occurs after maturity, assuredly related to the fact that adults of at least the larger forms are extremely long-lived (Wiewandt, 1977) and growth continues, though slowly, throughout life. Major ecological differences which have accompanied the evolution of these attributes are lessened climactic extremes, low predator diversity, and limited nest site availability.

Cyclura habitats are influenced by maritime climates with high humidity year-round and appreciable thermal stability, especially at Antillean latitudes. While rainfall exceeds that of the Temperate deserts by three- to eleven-fold, little of this moisture is plant-available and productivity is curtailed due to highly permeable limestone (karst) substrata with shallow surface soils (Lugo *et al.,* 1979). Unpredictable rainless periods and a pronounced annual dry season are also characteristic (see data for Mona I., P.R., in Wiewandt, 1977). Consequently, many, if not most, important iguana foods remain highly ephemeral in occurrence, and pre-reproductive growth rates are slow (Wiewandt, 1977; Iverson, 1979). The availability of seasonally transient foods of high nutritive value is, however, relatively more certain on these subtropical islands than in desert environments, allowing more consistent year-to-year production of offspring (Wiewandt, 1977; Iverson, 1979).

The smallest of the three cycluran iguanas represented in Table 1, *C. carinata,* lives on tiny islands with comparatively little structural and biotic diversity. Reduced feeding options may restrict growth significantly, and the small size of this species facilitates climbing and canopy-foraging (Auffenberg, 1982). Of added importance, *C. carinata* populations occur far enough north to experience sporadically cool and dry winter conditions unfavorable for activity year-round (Iverson, 1979).

Strongly skewed pressure from island predators and competitive interference between nesting females would select against early maturity in cycluran iguanas. Because the only iguana predators native to the Greater Antilles and Bahamas are birds, snakes (which tend to be small), conspecific iguanas, and possibly crabs (Carey, 1975; Wiewandt, 1977; Iverson, 1979), reaching a large size early in life confers an enormous adaptive advantage. Iguanas exceeding approximately 600 g in weight and 25 cm in snout-vent length surpass the expected size limits of prey for any of these predators (Wiewandt, 1977). Large females are also better equipped to defend their interests while nesting in a highly competitive social environment arising from a natural scarcity of suitable nesting areas (Communal Nesting, Origins & Consequences). Both factors favor attaining a large body size before being burdened with egg-carrying, laying, and nest-defense.

The subtropical/tropical mainland iguanines *Ctenosaura similis* and *Iguana iguana* exhibit the fastest growth, earliest maturity, and smallest proportion of growth between hatching and first-nesting relative to mean adult female size (Table 1). These attributes, taken together with data on clutch size and nesting behavior (discussed in upcoming sections), hatchling behavior (Burghardt *et al.,* 1977), and tail-break frequencies (Harris, pers. comm.), clearly indicate that predation is the key ecological force operating on the reproductive patterns of these populations. Apart from varying degrees of seasonality imposed by rainfall, climates are generally equable and favor year-round activity.

Of special interest is the relatively slow growth of *I. iguana* studied by Muller (1972). This atypical population represents a distinct ecological race of the semi-arid coastal region at Santa Marta in northeastern Columbia. Food is seasonally scarce, and iguana growth is stunted relative to that in other populations examined in Central and South America. Compared with the population studied by Harris (1982), Santa Marta juveniles grow only half as fast and females mature at a size approximately 25% smaller.[1] Where drought-induced stress on vegetation is greatest, productivity and availability of preferred food resources can be expected to be lowest (Pielou, 1975). Much drought-resistant vegetation is unpalatable and difficult to digest (Auffenberg, 1982). Iguanines characteristic of subtropical-dry and subtropical-moist mainland ecosystems, i.e., most *Ctenosaura,* probably experience similar limitations in drier parts of their ranges.

While information on longevity of other *I. iguana* populations is unavailable, Muller calculated that females in his study area survive for a maximum of only 5-8 reproductive seasons. This figure is, however, difficult to interpret from an evolutionary perspective since females are intensively hunted today by humans in NE Colombia, as elsewhere in Latin America. In contrast, reproductive life expectancy for tropical and subtropical insular iguanas and Temperate desert iguanines is believed to be at least twice as long: 10-15 years (Johnson, 1965; Berry, 1974; Iverson, 1979) and upwards (Wiewandt, 1977; Werner, 1982).

Clutch, Egg, and Hatchling Sizes

Few measurements of lizard offspring have been systematically collected or reported. Reasonably complete records exist for only 11 New World species of iguanas (Table 2), half of which are data compiled from two or more sources. Interspecific diversity in sizes of adult females, clutches, eggs, and neonates is extreme. Adult females of the smallest species *(Dipsosaurus dorsalis)* are nearly identical in body length to hatchlings of the largest *(Cyclura stejnegeri)*[2]; their eggs approximate the size and shape of seedless grapes and goose eggs, respectively. In general, hatchling size increases with increasing species size. Larger species tend to lay larger clutches, but the correlation is not close across generic lines. The largest clutches, for example, ($\bar{X}$ = 43.4 in *Ctenosaura similis*) are produced by iguanas roughly half the adult weight of those with the smallest clutches ($\bar{X}$ = 2.3 in *Amblyrhynchus*).

How each female apportions her expenditure in progeny is, like growth vs. reproduction, a give-and-take proposition. The cost of larger hatchlings is a smaller clutch and that of a larger clutch is smaller hatchlings. This relationship is evident in iguanas if clutch size is compared with relative female investment in individual offspring, termed Expenditure Per Progeny or EPP by Pianka (1976) and others. EPP is frequently offered as a measure of reproductive effort, a synonymy that I believe is unsatisfactory and one that is not implied here.

The 11 species examined invest between 0.8 and 5.7% of their body weight in each hatchling. Iguanas investing the most live on subtropical islands or in temperate continental desert environments. All have small clutches. The five species laying an average of more than 15 eggs per clutch have uniformly low EPP values, near 1% (0.8-1.4%). They comprise an assortment of island and tropical/subtropical mainland forms.

Ecological factors that encourage a stepped-up investment in individual progeny are not often considered. They are undoubtedly diverse, varying with respect to both local conditions and the lizard's habits. One rather obvious benefit of large hatchling size in the marine iguana, *Amblyrhynchus,* is decreased vulnerability to physical dangers associated with life at the surf edge (Boersma, 1982). Large egg and hatchling size in Mona iguanas *(Cyclura stejnegeri)* probably offers several advantages, some of which may be shared by other iguanine lizards. First, by virtue of their lower surface-to-volume ratio, large eggs and hatchlings are less susceptible to desiccation than are small ones. Moreover, an iguana's soft-shelled eggs dehydrate much faster than hard-shelled crocodile and bird eggs (Rand, 1968b). In semi-arid habitats with uncertain rainfall, as on Mona, even a slight reduction in desiccation rate might be critical in some years. Second, large hatchlings are less likely to be trapped underground, for they are stronger and have metabolic advantages associated with larger body size. Assuming that all hatchlings carry an equivalent proportion of yolk per gram of body weight, those of larger body size would be capable of sustaining activity longer without additional food. Third, because juveniles, like adults, are predominantly herbivorous, smaller hatchlings would be at a physiological disadvantage in their ability to utilize plant foods (Pough, 1973; Wilson & Lee, 1974; Van Devender, 1982). Fourth, large hatchlings would have a greater variety of food types available. This is probably important on Mona because the fruits of several common trees are near the upper size limit for consumption by hatchlings. Finally, any increase in body size helps to shorten the interval during which juveniles are exposed to predation, particularly important on Mona since hatchlings are near the upper prey size limit for two species of snakes, the only known non-avian predators native to the island (Wiewandt, 1977). Clearly all such factors are interrelated. Perhaps the remarkable uniformity in body size (SVL) among Mona hatchlings (coefficient of variation = 4.2 for a sample taken from nine clutches) reflects the force with which smaller hatchlings are selected against in this environment.

Possibly the most peculiar reproductive pattern known for the subfamily is that of the marine iguana *(A. cristatus).* Its clutch size is consistently small, never exceeding three eggs (mode = 2), and each egg is relatively enormous. In contrast, young female Mona iguanas, which attain sexual maturity at a body size near the maximum recorded by Carpenter (1966) for adult female marine iguanas, lay five or six eggs, and older females lay as many as 18 or 19. Eggs of both species are similar in size (Table 2).

Why has selection not favored slightly larger adult female marine iguanas capable of (1) avoiding all risk of predation by Galapagos Hawks, (2) laying more, but not smaller, eggs, and (3) gaining a competitive edge during disputes over nest sites? A number of observations suggest that limits on clutch and body sizes are imposed by special problems associated with nesting in loose sand. Carpenter (1966) noted that stamping heavily on the sand above a known *Amblyrhynchus* nest had no effect on the underground air space in the egg

Table 2: Egg and Hatchling Data for the Eleven Best-Studied Species of New World Iguanine Lizards

Where known, sample sizes given in parentheses and ranges beneath sample means.

			• • • • • • Eggs • • • • • •		• • • Hatchlings • • •		
Species Location	**$\bar{X}$ Adult Female Weight (g)**	**$\bar{X}$ Clutch Size**	**$\bar{X}$ Weight (g)**	**Dimensions (mm)**	**$\bar{X}$ Weight (g)**	**$\bar{X}$ Body Size SVL in (mm)**	**Sources and Remarks**
Dipsosaurus dorsalis CA; AZ; NV	70	– 3-8	– –	24 x 17 (5) 22-76 x15-20	4* –	47 (9) 44-52	Norris, 1953; Mayhew, 1971; Parker, 1972.
Sauromalus obesus California	175 –	8.6 (27) 6-13	8 (1 clutch) –	20 x 15 –	8 –	54 –	Berry, 1974; Iverson, 1979; Case, this vol.
S. hispidus Angel de la Guarda I., Baja	900* –	22.0 (5) 14-29	10 (2 clutches) –	25 x 24 –	10 –	70 –	Case, this vol. (hatchling size estimated).
S. varius San Esteban I., Baja	1,200* –	23.4 (5) 16-32	18 (1 clutch) –	40 x 28 –	14 –	75 –	Case, this vol. (hatchling size estimated)
Ctenosaura similis NW Costa Rica; W. Nicaragua	651 (263) –	43.4 (69) 12-88	– –	28 x 19 (117) 20-31 x 16-28	5.1 (13) 4-8	58 (13) 54-60	Fitch & Henderson,1977a 1978; Hackforth-Jones & Harker, MS; Van Devender, pers.comm.
Iguana iguana Costa Rica; Nicaragua Colombia; Panama	1,195 (169) 400-2,150	35-43 14-76	– 9-14 (86)	39 x 26 (41) –	11.6 (23) 8-15	76 (23) 72-79	Fitch & Henderson,1977b; Harris, this vol.; Licht & Moberly, 1965; Müller, 1972; Van Devender, pers. comm.; Rand, pers. comm.

(continued)

Table 2: *(continued)*

Species Location	$\bar{X}$ Adult Female Weight (g)	$\bar{X}$ Clutch Size	Eggs		Hatchlings		Sources and Remarks
			$\bar{X}$ Weight (g)	Dimensions (mm)	$\bar{X}$ Weight (g)	$\bar{X}$ Body Size SVL in (mm)	
Cyclura carinata Caicos Is.	476 (32) 205-1,135	4.3 (11) 2-9	26 (20) 19-30	52 x 31 (32) 46-58 x 29-54	15 (9) 13-15	80 (20) 76-83	Iverson, 1979.
C. ricordi Dominican Republic	1,285 (8) 908-1,634	8.6 (5) 4-18	– –	– –	30 (11) 26-35	87 (11) 82-92	Castro & Duval, 1979 (zoo data); Carey, 1975; Wiewandt & Gicca, unpubl. zoo & field data.
C. cornuta Dominican Republic	3,519 (6) ** 2,951 - 4,767	15.3 (15) 8-24	– –	– –	51 (82) 38-68	105 (82) 96-112	Castro & Duval, 1979 (zoo data); Wiewandt, 1977 (zoo & field data); Wiewandt & Gicca, unpubl. notes.
C. stejnegeri Mona I., P.R.	4,750 (9) 3,400-5,400	12.0 (37) 5-19	104 (68) 82-159	80 x 51 (100) 70-95 x 45-61	74 (66) 60-92	119 (65) 105-127	Wiewandt, 1977.
Amblyrhynchus cristatus Narborough I. & Santa Cruz I., Galapagos Is.	1,370 (26) –	2.3 (18) 2-3	96 (38) 79-121	93 x 42 (38) 78-100 x 40-52	72.2 (6) –	– 105-130	Carpenter, 1966; Bartholomew et al., 1976; Boersma, 1982.

* Estimate made by author.

** Weights from three unhealthy captives and three healthy field animals.

chamber, vital for proper development and emergence of the young. This outcome is to be expected since sea-lions frequent the same beaches during nesting (Carpenter, 1966; Eibl-Eibesfeldt, 1966; Boersma, 1982). Clearly, the larger nest chambers required for larger clutch volumes are more likely to collapse under the weight of a heavy animal on the surface. Since the diameter of a nest tunnel should reflect the size of the iguana digging it, selection probably opposes large body size in female *Amblyrhynchus.* Carpenter and Boersma each found females fatally trapped in burrows that had collapsed around them, and wider burrows probably amplify such a risk. Nesting Mona iguanas select stabilized soil or sand deposits, the upper 20 cm of which are typically supported by a mat of plant roots. Consequently, burrows seldom collapse as females dig, but the weight of a person walking over a nest can readily destroy its air space. As no large mammals are native to Mona, nest-trampling by people and introduced mammals is a serious threat to the iguana's future (Wiewandt, 1977).

The two species laying the largest clutches by far and showing the lowest expenditure per progeny, *I. iguana* and *Ctenosaura similis,* both inhabit tropical and subtropical mainland environments where predation is assuredly most intense. High fecundity in these forms appears to be essential for keeping ahead of losses to predators, well supported by lines of evidence already presented. Noteworthy in this context is Fitch and Henderson's (1977b) observation that *I. iguana* nesting for their first time produce eggs that are only three-fourths the weights of those laid by large adults. Since these females often begin laying small clutches at the end of their second year, at a very small body size, possibly reproductive success at this age depends more upon offspring number than upon the size of each. I know of no other instance where egg size of iguanines varies between age or size classes. Unlike *I. iguana, Ctenosaura similis* exhibits an ontogenetic shift in diet (from insectivory to herbivory), enabling its numerous tiny hatchlings to experience accelerated early growth, thereby bypassing physiological handicaps associated with herbivory at extremely small sizes (Van Devender, 1982).

Iguanas making relatively low per progeny investments accompanied by moderately large clutch sizes are *Cyclura cornuta* and the two insular *Sauromalus* populations. Among West Indian ground iguanas, those populations on or near large islands produce the bigger clutches with smaller eggs, presumably a demographic response to relatively greater diversity and abundance of predators (Wiewandt, 1977; Iverson, 1977). Comparison of the species pair *Cyclura cornuta* and *Cyclura stejnegeri,* for example, shows that clutches laid by occupants of the Dominican Republic are 28% larger than those of Mona Island, and hatchlings are 31% smaller by weight; snout-vent lengths of adult females are similar in both (Wiewandt, pers. observ.). The two insular *Sauromalus* studied by Case (1982) occupy inhospitable desert environments and experience mass mortality of all age classes during prolonged rainless periods. By mainland standards (i.e., compared with *S. obesus*), recruitment is low in spite of their larger clutch sizes (accompanying larger body sizes) and lower susceptibility to predation. Reproduction in the insular populations is relatively infrequent and follows an "all-or-nothing" pattern (Case, 1982). Being able to produce young in quantity during years when food and moisture conditions are favorable is evidently critical to the fitness of these iguanas.

Frequency and Timing of Nesting

Most tropical or subtropical lizard species do not have short, well defined breeding and nesting seasons (Fitch, 1970), but iguanines tend to concentrate nesting activity into a 1-3 month period. Females lay single clutches each reproductive season, regardless of latitude. The tropical Fiji iguanas, *Brachylophus,* may be an exception (Gibbons, 1982).

Nesting phenology is broadly defined by abiotic forces, such as climate, which impose limits on the time and duration of a female's growing and reproductive season. Iguanines inhabiting North American deserts nest near the middle of their activity seasons, during or after peak abundance of high quality foods (Norris, 1953; Nagy, 1973). Since rainfall and plant foods vary from month to month and from year to year, earlier nesting might jeopardize a female's survival through the following winter, whereas later nesting would probably take a heavy toll on hatchlings (Parker, 1972). Whether reproduction is even possible in any given year appears to depend on the foraging conditions before the nesting season, and the availability of energy reserves stored from the previous year (Johnson, 1965; Nagy, 1973; Berry, 1974). The eggs of both *Dipsosaurus* and *Sauromalus* evidently require little moisture for successful incubation and hatching; and nesting normally occurs during the hot, dry summer months throughout the major portions of the ranges of these species.

Amblyrhynchus cristatus is another species whose reproductive phenology appears to be closely tied to seasonally fluctuating food resources. Boersma (1979) noted that the breeding cycle is coordinated with tidal rhythm. Females eat algae on exposed reefs. Egg laying occurs after the lowest tides of the year, when food is most accessible, and occurs first in the western, more productive, waters of the Galapagos archipelago.

Carpenter (1966) may also be correct in suggesting that the annual nesting season of the marine iguana is timed to avoid the cool and dry "garua" season which might inhibit hatching. Licht and Moberly (1965) showed that eggs of *I. iguana* have remarkably stringent thermal requirements, with high mortality at temperatures only a few degrees above and below 30°C; this might be true for *Amblyrhynchus* as well. Boersma (1979) discounts Carpenter's hypothesis on the grounds that occurrence of the garua season varies from year to year, and the iguanas show a rigid rather than a flexible breeding schedule. However, a female laying eggs in February or March cannot possibly forecast weather conditions two or three months later. I believe selection would favor females that lay during the period producing the best long-term results, a strategy that should result in a relatively fixed breeding schedule. The same line of reasoning can be applied to any situation in which female iguanas lack the cues needed to evaluate the fate of their progeny in an environment that is unpredictable from year to year.

Mainland species, *Iguana iguana*, and *Ctenosaura similis*, produce large numbers of eggs and hatchlings as a result of intense predation in their environments.

In most iguanine lizards, reproduction is timed to match seasonal conditions most favorable for survival of eggs and hatchlings. The tropical and subtropical iguanines *I. iguana* and *Ctenosaura similis* typically oviposit during the driest part of the year. This pattern provides insolation and thus high nest temperatures during incubation, minimizes the probability of nest flooding, and places hatching near the onset of the rainy season, when food is most plentiful. This permits emergent young to benefit from rapid early growth (Rand, 1968a; Fitch,1973a; Rand and Greene, 1982).

In drier, subtropical environments, such as *Cyclura* habitats, the pattern is similar, though somewhat different. Nesting begins after the spring dry season and hatching coincides with the late summer or fall wet season. This places incubation at a time when the eggs are not likely to desiccate, and hatching occurs during the best period for emerging and foraging on fruits and ephemeral herbs (Wiewandt, 1977; Iverson, 1979). *Conolophus pallidus* follows this pattern on Isla Sante Fe (Christian & Tracy, 1982). Such breeding cycles are probably cued by photoperiod; Wiewandt (1977) found extraordinary year-to-year precision in the timing of nesting by Mona iguanas, regardless of pronounced variations in rainfall.

Many species of iguanas place their eggs deep in the ground, which requires a concerted digging effort from hatchlings attempting to reach the surface. Consequently, emergence from the nest may typically be a team effort. In Mona iguanas, eggs of each clutch hatch in synchrony and the young dig to the surface as a group through packed sandy soil and a superficial mat of roots. Those last to hatch are sometimes buried alive by their siblings, accounting for about 1% of the in-nest mortality. Most emergence occurs after heavy rains. Without cooperative digging and periodic rain to soften the ground, many hatchlings would probably die underground. Presumably the large yolk reserves carried by each hatchling is an adaptation to ensure the animal's survival during this critical stage. Although hatchlings can apparently survive without food for at least 2-3 weeks underground, delayed emergence similar to that documented for some turtles (Gibbons and Nelson, 1978) is unknown for iguanine lizards.

Nest Sites and Migrations

Where an iguana nests is closely related to the physical structure of its habitat. Conditions permitting, the lizard's dwelling place may double as her nesting place. In *Dipsosaurus dorsalis* and *Cyclura carinata* females prepare their nests within sandy burrows normally used for shelter (Norris, 1953; Iverson, 1979). In other species, females must seek special places for nesting, and long-range movements may be necessary when suitable nest sites are scarce.

Karst terrain, the principal habitat type of cycluran iguanas, has little surface soil (LeGrand, 1973) suitable for nesting. On Mona Island, less than 1% of the island's surface area provides conditions that nesting *Cyclura stejnegeri* prefer, and gravid females must migrate distances up to 6.5 km to reach nesting areas (Wiewandt, 1977). Apparently three other West Indian iguanas, *Cyclura collei* of Jamaica, *Cyclura nubila lewisi* of Grand Cayman, and *Cyclura n. caymanensis* of Cayman Brac and Little Cayman, face similar problems (Lewis, 1944, p. 97):

> This early French naturalist (deTertre) related that *Cyclura* come down from the mountains during May to lay 13 to 25 eggs in a heap in the sand on the seashore. *C. caymanensis* was found to conform to those observations.... On Grand Cayman, *Cyclura macleayi lewisi* (= *C. nubila lewisi*) is said to have been common in former years along the north coast...where there is a wide sandy coastal shelf. The people hunted the species for food, and in one way or another the population has been greatly reduced. According to the evidence of our searches in 1938, the species no longer frequents the coast, – not even during the breeding season – but digs nests in the earth (red phosphatic clay) in the more or less secure uninhabited east central portion of Grand Cayman.

Lewis also stated that the only evidence of past nesting by *C. collei* on Great Goat Island was found in the "red earth" near the island's coastal mangrove swamp. How many, if any, of the iguanas surviving in the rugged interiors of these islands continue to nest successfully is unknown.

***Why did the iguana cross the road?* Because it's his job!** IIS member Joe Wasilewski, of Natural Selections in Miami sent us this photograph of his Cuban iguana, *Cyclura nubila*, taken during a photo shoot on a somewhat deserted road in Kendall, Florida. *Photography: Steve Lipson*

[Recently, in the soil-rich sinkhole depressions of Jamaica's Hellshire Hills, nine *C. collei* nests were discovered in 1993 (Vogel, pers. comm.).]

Migration in itself indicates the important role that soil-rich coastal areas have played in the evolutionary history of these West Indian populations. Females on Mona commonly attempt nests in soil-filled potholes on the plateau, but most of those efforts are abandoned. The only completed nest I uncovered in this type of a situation suffered total mortality apparently from overheating or desiccation. On a portion of Andros I., Bahamas, where iguanas (*C. cychlura*) have no soil available, eggs are laid in large termite nests (Auffenberg, pers. comm.).

In the Pacific Ocean, on the island of Fernandina, Galapagos land iguanas (*Conolophus subcristatus*) sometimes migrate 15 kilometers or more to reach suitable nesting areas (Werner, 1982). An unusual combination of lava terrain and little sunshine over much of Fernandina during the nesting season evidently precludes nesting everywhere except within the island's volcanic cone. Nesting and incubation coincide with the cool season. Gravid females climb 1400 m to the crater rim and then descend to the crater floor in search of soil deposits. The sky normally remains clear over the crater, and nest holes are dug in places warmed by direct sunlight and/or fumaroles (Werner; 1982). Why these iguanas favor the cool, wet season for nesting is unclear.

Apart from the data on the Mona Iguana and Galapagos land iguanas (including *Conolophus pallidus* – Christian & Tracy, 1982), the only other well documented evidence of long-distance nesting migration in lizards is for the green iguana, *Iguana iguana,* on Barro Colorado Island, Panama. Montgomery *et al.* (1973) followed the postnesting movements of four *I. iguana* that swam to nest on Slothia, an islet adjacent to Barro Colorado, and found that upon returning to Barro Colorado, the four females traveled 300 m, 950 m, 2.2 km and 3.0 km into the depths of the rainforest. Here the availability of favorable nest sites appears limited by the presence of nest predators native to Barro Colorado and by "shading-out" from the dense tropical understory and canopy vegetation (Rand, 1968a). Even on Mona, where the canopy is comparatively thin, otherwise acceptable sites that receive shade much of the day are not used for nesting.

How and when do female iguanas learn where suitable nest sites are located? During the nesting season, there is conspicuous and widespread trial-and-error digging on Mona's plateau, suggesting that females acquire a migration pattern through experience. Once a female has encountered an appropriate site, the best strategy to adopt would be to return to that spot the next year and continue doing so as long as conditions remain favorable there. This interpretation appears to hold for the iguanas of Barro Colorado Island, for although Slothia is a young islet created within the past 50 years, it is now a major nesting area. If such finds occur largely by chance, a female would not necessarily encounter equally attractive sites nearer to her normal activity area. My observations agree with those of Montgomery *et al.* (1973) who were puzzled that some females travel considerably greater distances to nest than appeared necessary, assuming each had a single home area. We cannot assume that female iguanas know all parts of their home islands, and choice of a migration route is probably limited by individual experience. The possibility that neonates learn through imprinting to return to nest at their birthplace merits investigation.

A recent study of the migratory movements of the snake *Coluber constrictor* to and from winter hibernacula revealed that a formative period may exist during which dispersal distance and direction, as well as the home range occupied, become "fixed" behavioral attributes in many members of the population (Brown and Parker, 1976). I suspect that such an ontogenetic process may operate in iguanas. Extended radio-telemetry work on the movements of newly matured females would shed light on this point.

Communal Nesting, Origins and Consequences

Origins of Communal Nesting: The natural scarcity of suitable nest sites on Mona has been a selective force of paramount importance to that iguana population. Presumably seasonal migrations and communal nesting were once a necessiforced to compete for limited available nest space (Wiewandt, 1977). Similarly, in the Galapagos, competition for nest sites is intense because accumulations of soil are sparse (Carpenter, 1966; Eibl-Eibesfeldt, 1966; Christian & Tracy, 1982), a problem compounded in one case by a shortage of thermally favorable areas resulting from great intra-island differences in climate (Werner, 1982). Iguana nesting aggregations found in the wet tropical lowlands of Central America occur where well drained sites warmed by sunlight are in short supply (Rand, 1968a; Fitch, 1973).

Natural selection may favor communal nesting for other reasons as well. A female choosing a site already worked by other iguanas will find digging easier, may be able to usurp another female's hole, or may lower the risk of predation to herself or her emerging hatchlings by nesting in synchrony with others. On the other hand, costs associated with aggressive interactions and the risk of losing a clutch to iguanas nesting later may be considerable. An assemblage of nests might also be more attractive to potential egg-predators than a solitary nest. In Guanacaste Province, Costa Rica, *Ctenosaura similis* utilize a network of subterranean passages for nesting. Several females oviposit in the same connecting burrow system, but individual clutches are laid in separate chambers (Hackforth-Jones and Harker, MS). In this case there was no evidence of a shortage of potential nest sites, so communal nesting probably evolved in response to other selective pressures, such as predation or energy constraints (Hackforth-Jones and Harker, MS) Whether *Ctenosaura* utilize the same sites in successive years in unknown.

Traditional use of the same localities year after year may actually improve conditions for nesting, enhancing the attractiveness of such sites. Rand (1968a) noted that group nest-digging by *I. iguana* over the years effectively maintained a clearing in the forest. While excavating nests in a study area on Mona, I discovered that approximately half of the nest tunnels were forked, one passage leading to the fresh clutch from that season and the other going to an old clutch of empty shells. Such old passages, though sand-filled, were still identifiable by their looser soil. With the low density of iguanas on Mona today, many apparently favorable nesting sites on the island's southwestern coastal plain are not used and a locally clumped nesting pattern predominates. Gravid females exploring for suitable sites at the onset of nesting are strongly attracted to shallow depressions left from the previous season (Wiewandt, 1977).

Nest Guarding: Guarding behavior (against conspecifics) after nest covering has been reported for eight iguana populations: *I. iguana* in Chiapas, Mexico (Alvarez del Toro, 1972); *Cyclura stejnegeri* on Mona I. (Wiewandt, 1977, 1979); *C. carinata* on Pine Cay, Caicos Is. (Iverson, 1979); *Amblyrhynchus cristatus* on Hood I. (Eibl-Eibesfeldt, 1966), on Fernandina I. (Trillmich, 1979), and on Caamano Islet (Trillmich, 1979), all in the Galapagos Is.; *Conolophus pallidus* on Sante Fe I. (Christian & Tracy, 1982); and *C. subcristatus* on Fernandina I. (Werner, 1982). Observations in Gibbons and Watkins (1982) suggest that guarding completed nests may also occur in the two South Pacific iguanines (*Brachylophus*). The absence of such behavior has been specifically reported in *A. cristatus* on Fernandina I. (Carpenter, 1966; Eibl-Eibesfeldt, 1966) While female *I. iguana* studied in a Panamanian nesting aggregation may return to add surface fill to nests for up to 4 days after laying (Rand, pers. comm.), parental care is not exhibited to the degree found by Alvarez del Toro. Some Mexican females visit their nests daily for 15 days to pile on more sand and debris, making repairs if for some reason they appear open or disarranged. These iguanas apparently were not assembled in aggregations and may have nested within their usual activity areas. No mention was made of the duration of such visits or where the females passed intervening hours.

The fact that the Panamanian *Iguana* depart from the nesting area soon after laying and presumably migrate back to their normal home ranges (Montgomery *et al.*, 1973; Rand, 1968a) suggests not that they would have little to gain by tending their nest sites for a few extra days, but rather that they cannot afford the additional energy expenditures. During nesting, *I. iguana* typically have shrunken muscle masses at the base of the tail and the animals' pelvic bones show, suggesting that they have metabolized both fat and protein (Rand

Announcing “Iguanidae”

A signed and numbered print by herp artist, Marty Capron. The print measures 22.5 inches by 17.5 inches overall and is printed on top quality heavy, white stock. This exquisitely detailed pen & ink drawing has been issued as only 100 signed and numbered prints, sure to become collectors items. Priced at $40.00 plus $5 for shipping and handling. Make check or money order payable to: Marty Capron RT 1, Box 59, Oxford, KS 67119. *Please mention IIS with order.*

and Rand, 1976). In contrast, shrunken tail musculature was seen in only four females nesting on Mona (Wiewandt, 1977) and has not been observed in *C. carinata* (Iverson, pers. comm.).

Owing to the geological and ecological similarities in *Cyclura* habitats throughout the range of this group, I would expect nest-tending behaviors to be common to most, if not all, West Indian ground iguanas. Mona iguanas, *Cyclura stejnegeri,* nest communally, away from normal activity areas. Spent females normally guard their covered nests for 1-10 days, a significant portion of the two-week nesting season. Even so, roughly 10-15% of egg-filled nests are dug into by intruding gravid females. Holes left by feral pigs that have rooted up and plundered iguana nests are diligently refilled the following day by nest-tending females. Iguanas do not attempt to challenge a hungry pig and are evidently unaware of their egg losses (Wiewandt, 1977).

Caicos Island iguanas, *Cyclura carinata,* defend completed nests for several days to a month or more after oviposition (Iverson, 1979). Because eggs are laid in a terminal portion of burrows normally used as retreats, they need protection not only from other females seeking nest burrows, but also from subadults and males seeking shelter after the nesting season. Guarding females are consequently aggressive towards all conspecifics. By reducing their daily home range, spent females can resume foraging and guard their nest sites simultaneously, typically watching for intruders while perched in nearby food plants (Iverson, 1979).

Descriptions of nesting activities in two similar races of Galapagos marine iguanas (*A. c. cristatus* on Fernandina I. and *A. c. venustissimus* on Hood I.) show how local differences in ecology can affect nesting behavior. From positions on nearby rocks, female iguanas on Hood I. keep watch over their egg-laying sites for a few days after filling the nest burrow, occasionally descending to check the spot with tongue flicks and to scrape more dirt over the egg cache (Eibl-Eibesfeldt, 1966). Neither Eibl-Eibesfeldt nor Carpenter (1966) found such guarding behavior on Fernandina and females there are less prone to fighting over burrows than are the Hood iguanas (Eibl-Eibesfeldt, 1966). These authors emphasize that both populations are faced with a natural scarcity of suitable digging sites and are forced to nest in aggregations. Nevertheless, one important ecological difference between the two islands is evident, in contrast to the open nesting beaches on Fernandina, the area used by *Amblyrhynchus* on Hood I. offers very little loose sand above the high tide line; females must dig their burrows in small patches of hard, gravelly soil upon the plateau, and many burrows are abandoned because of lava blocking the way to further digging (Carpenter, 1966).

With respect to nesting opportunities, the situation on Hood I. closely parallels that on Mona. Presumably difficult digging encourages females to exploit the efforts of their neighbors, before and after nest covering. In both cases this pressure has been countered by extended nest-guarding behavior and may have led to the reduction in male/female sexual dimorphism. Eibl-Eibesfeldt (1966) noted that, unlike the other races of the

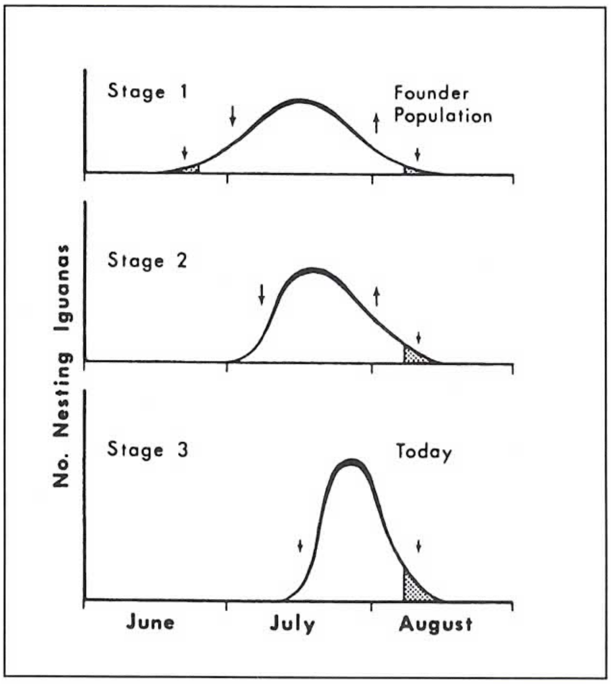

Figure 1: Model for the evolution of a late, abbreviated iguana nesting season where competition among females for suitable nest sites is keen. Stippled areas represent nesting efforts under environmental conditions marginal for incubation, hatching, and/or survival of first-year young. Arrows indicate the action of selection. The curve is driven to the right by egg loss in females that nest early to those nesting later and is kept to the left by limitations from the physical environment.

marine iguana, the Hood females assume a bright, male-like coloration during the egg laying season. Individuals so ornamented may hold a competitive advantage by being better equipped to intimidate other females by means of an impressive challenge display. Similarly, female Galapagos land iguanas, *Conolophus subcristatus,* on Isla Fernandina take on male-like colors shortly after breeding and throughout nesting (Werner, pers. comm.), a condition that accompanies intrasexual strife over nest sites and nest guarding (Werner, 1982).

Communal Nesting as a Modifier of Nesting Phenology: The nesting season of *Cyclura stejnegeri* on Mona Island is extremely short and nearly identical in duration and timing year after year. The entire season lasts 18 days (±4 days), with over 80% of the oviposition falling into an 8-day period island-wide. Yet, Mona's subtropical, maritime climate does not seem sufficiently limiting to explain such concentrated nesting.

I suggest that competition between communally nesting females for favorable nest sites can act as a nesting synchronizer. In Figure 1, three hypothetical stages are outlined for the evolution of an abbreviated nesting pattern from a less restrictive seasonal pattern with limits imposed only by climate and associated variables, such as food availability. Two assumptions have been made: (1) extended nest guarding is an advanced form of parental care in iguanine lizards and is derived from nest-hole defense that characteristically accompanies burrow digging and filling operations, and (2) the island's climate limits successful nesting to a period of two months, mid-June to mid-August, an intentional simplification.

In Stage 1, accompanying the expansion of the founder population the genetic contributions of two classes of females would be strongly selected against, those nesting outside the June-August season and those nesting early in the season. Early females run a high risk of losing their eggs to disturbance by the late-comers. Clearly, the outcome would be pronounced directional selection.

As directional selection proceeds, in Stage 2, a greater proportion of the population would nest synchronously later in the season resulting in intensified competition. This would be accompanied by increased nesting in places with more difficult digging and less favorable incubation conditions. Late nesting would probably take heavy toll on hatchlings that miss optimum periods for emergence, dispersal, feeding, and getting established at a retreat before the onset of the dry season in January. Furthermore, tendencies towards extended nest guarding would be favored in females that nest relatively early.

Stability is attained, in Stage 3, when selection against late nesting balances that against early nesting. In addition to the limitations imposed by climate, females arriving relatively late in the season may have difficulty finding suitable unoccupied sites once nest-guarding behavior is established in the population. Nesting early is advantageous only if a female is able to protect her eggs until most other females have departed from the nesting area. How long she can profitably afford to stay to fight off intruders must vary with the costs involved. Under conditions of intense competition, nest defense is energetically taxing and the risk of physical injury is considerable.

In the context of intense female/female competition for nest sites, large body size and delayed maturity should also be favored by selection if mature females have no natural predators, as on Mona, and can benefit from long life expectancy. Clearly, large females can exploit the efforts of other nesting females and defend their interests more effectively than small individuals. The highest pay-off, in terms of adult survivorship and reproductive success, should therefore go to females that postpone breeding until reaching an age and stature at which the costs of competition are lowered. I suspect that the evolutionary consequences of male/male competition for mates and female/female competition for nest sites are sufficiently similar to explain much of the male/female convergence in appearance found in Mona's iguana population (Wiewandt, 1977, 1979).

Summary and Conclusions

All lizards of the subfamily Iguaninae are oviparous, and most have short, predictable, annual nesting seasons. Populations differ with respect to age at maturity, nesting phenology, nesting place, gregariousness, parental care, and size of clutches, eggs, and hatchlings. Primary determiclutches, eggs, and hatchlings. Primary determinants of nesting patterns include climate, predation pressure, competition, and the quality and quantity of nest sites. Nesting phenology is broadly defined by climate, particularly as temperature and moisture conditions affect length of the activity season, incubation, hatchling emergence, and food availability. Decreasing predation intensity permits longer life expectancy, slower growth, later maturity, and smaller clutches, with increased investment in individual progeny. Scarcity of favorable nest sites encourages nesting migration and aggregation. Intense competition among females probably selects for seasonally late, synchronous nesting, nest guarding, delayed maturity, and reduced sexual dimorphism.

The degree of sexual dimorphism evident in iguana body size, form and color must be cautiously interpreted. There is no evidence for sexual dimorphism favored by food resource partitioning in iguanine lizards. Where studied, diets of both sexes are essentially identical. Even in the marine iguana, separation of foraging niches appears to be a consequence of, rather than an explanation for, size dimorphism (Boersma, 1982; Trillmich, 1979). Just as sexual selection may be strongly operative in male iguanas (Dugan and Wiewandt, 1982), promoting intersexual character divergence, other selective pressures acting specifically on the female sex may promote character convergence. For example, keen female-female competition for nest sites apparently favors large body size and other male-like attributes that would enhance a female's competitive ability. Other factors, such as ecologically imposed upper limits to nest volume (as suggested here for *Amblyrhynchus*), may have the opposite effect by selecting against large females, thereby increasing size dimorphism. Furthermore, because the cost of reproduction (with respect to energy budgets and exposure to predation) varies between the sexes in different ecological settings, optima for adult male and female body size can be expected to differ.

Understanding life history patterns and identifying factors responsible for their evolution require much more than a tally of life history attributes. Failure to recognize and investigate the complexities of an animal's ecological and social position in its community has been an interpretive stumbling block in most treatments of reproductive effort. Valid comparisons between and within species must be selectively drawn from broad, integrative studies conducted over extended periods of time; few such studies are presently available.

[1] Müller (1972, p. 121) says "Clutch size is dependent upon female body size, varying between 14 (in one or two year-old *I. iguana*, SV: 16-21 cm) and 70 in larger females (SV: 35-40 cm)." This statement, which suggests that females 16-21 cm SVL lay clutches of 14 eggs, is evidently in error. Data in Figure 1 and Table 1 of Muller (1968) indicate that females do not begin nesting before an age of 21 mos., at 20.1 cm SVL. Instead of selecting the 15.8-21.1 cm size class, measured in April/May, he should have cited his Dec./Jan. data of 20.1-23.3 cm SVL (probably the same cohort) taken just prior to nesting.

[2] In this study, I have chosen to retain the name *Cyclura stejnegeri* Barbour and Noble for the Mona iguana, even though Schwartz and Carey (1977) favor the trinomen *C. cornuta stejnegeri*, which emphasizes its close relationship to the Hispaniolan rhinoceros iguana, *C. cornuta*. Schwartz and Carey's evaluation was severely hampered by necessarily small sample sizes and their choice of only two taxonomic criteria — body coloration and scalation. Because Mona is thought to have always been well removed geographically from neighboring islands, on theoretical grounds one would expect the Mona iguana to be far less similar to Hispaniolan populations than they are to each other. Until further data become available to permit comparisons within this population complex, no meaningful species/subspecies designations can be made. The limited comparative information that I have been able to collect about the life history of Hispaniolan *C. cornuta* suggests that Mona females differ significantly in reproductive tactics (see Table 2 and text).

Acknowledgements

I wish to thank several persons who helped make this synthesis possible by generously sharing their field experiences, opinions, and in some cases, unpublished data: Walter Auffenberg, Dee Boersma, Michael Carey, Jude Duval, Donald Harker, John Iverson, A. Stanley Rand, R. Wayne Van Devender, Peter Vogel, and Dagmar Werner. I am also grateful to the Florida State Museum for permitting me free access to their reprint collections. Colleagues who offered valuable suggestions for improving the content and readability of an early version of this paper are Gordon M. Burghardt, Martha Crump, Dennis Harris, John Iverson, A. Stanely Rand, and especially Kentwood Wells.

G.M. Burghardt and A.S. Rand, editors. 1982. *Iguanas of the World: Their Behavior, Ecology and Conservation.* Noyes Publications, Park Ridge, New Jersey. 473 pp.