

Variation in Iguanine Social Organization:

Mating Systems in Chuckawallas (*Sauromalus*)

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INTRODUCTION

Sauromalus is one of the few genera of lizards for which there are comparative data on social organization. Previous studies indicate that social organization varies not only among populations but within a single population among years. An understanding of this variation requires not merely a description of the types of social systems but an evaluation of their dynamic nature.

Social plasticity is well known in lizards (e.g., Rand, 1967b; Stamps, 1975) and was first documented when species territorial in the field formed dominance hierarchies in the laboratory (Noble and Bradley, 1933). This phenomenon is widespread in lizards and is not merely a laboratory artifact, as was demonstrated by Evans' classical field studies of *Sceloporus grammicus* (1946) and *Ctenosaura pectinata* (1951) and more recently by Stamps' (1973) work with *Anolis aeneus*. They showed that species may be territorial in one situation but form dominance hierarchies in another.

Hunsaker and Burrage (1969) suggest that there is a continuum from territoriality to dominance hierarchy. Many authors contend that this shift in social organization is due to the inability of males to defend territories under crowded conditions (e.g., Brattstrom, 1974). This is a plausible explanation for the phenomenon observed in the laboratory. However, it does not necessarily explain the existence of dominance hierarchies in the field and is even less applicable in explaining the more subtle variations in social organization which have been reported (e.g., Rand, 1967b).

In this chapter I review the previous reports of social behavior in chuckawallas (*Sauromalus*). I will attempt to identify the function of territoriality (*sensu*

strictu, Williams, 1966; see below) in these lizards by considering the behavior in terms of its potential costs and benefits. I then consider which factors affect costs and benefits, how they might be responsible for the observed social plasticity in *Sauromalus* and propose a predictive theory of social organization in these lizards.

SOCIAL ORGANIZATION

Berry (1974) investigated the ecology and social behavior of *Sauromalus obesus obesus* near Lone Butte, California. In 1969 and 1971 only the larger males or tyrants were territorial. These territories were aggressively defended against other large males and overlapped the home ranges of females, juveniles and subordinate males. There was a high level of aggression as subordinate males constantly challenged the territorial dominants. A stable dominance hierarchy, based on size, was maintained among subordinate males. Berry classified this a tyrant-subordinate system.

Chuckawallas feed primarily on the shoots and flowers of desert annuals. This food source may show radical fluctuations from year to year due to changes in the amount of rainfall. In the winter of 1969-1970 there was below average rainfall in California. Consequently, in 1970 the food supply was low and lizards were relatively inactive. Berry reported that aggressive interactions were only 15.6% of those in 1971 and there was virtually no courtship or copulation. During this year a dominance hierarchy formed around a rock pile and several nearby perennial sweet bushes (*Bebbia juncea*). The chuckawallas fed on the flower heads of these bushes.

In summary, Berry reported that in 1969 and 1971, when food was plentiful, only the larger adult males were territorial. Subordinate males aligned in a dominance hierarchy based on size. However, during the 1970 breeding season, when food was scarce, there was no mating and no territorial defense and some males formed a dominance hierarchy centered on a food source.

During the same drought year of 1970, Nagy (1973) studied a population of chuckawallas (*S. o. obesus*) on Black Mountain in the Mojave Desert, California. After all the annuals died in May, the lizards shifted their diet to perennials. He noted there was reduced activity, infrequent aggression and no reproduction. There was also extensive overlap of home ranges, both between and within sexes, and no territorial defense. Nagy reported similar home range sizes for males and females (males = 0.20 ha, females = 0.17 ha). In previous studies where male territoriality was observed, the home range of males was much larger than that of females (e.g., males = 0.57 ha, females = 0.17 ha; Johnson, 1965).

Prieto and Ryan (1978) described social organization of the Arizona chuckawalla, *S. o. tumidus*, in Organ Pipe National Monument, Arizona. In that study, all adult males defended well-defined territories that usually conformed to the boundaries of groups of rocks. These territories overlapped the home ranges of females and juveniles but were defended only against other adult males. Males introduced into the territories were challenged immediately by residents. I refer to this system in which all adult males defended territories as

"strict territoriality" to distinguish it from the tyrant-subordinate system reported by Berry.

Prieto and Ryan also observed the social behavior of an enclosed population of these chuckawallas. The adult males did not defend territories. One lizard was dominant and occasionally defended his basking site. He aggressively challenged other males and on one occasion disrupted a copulating pair and attempted to mate with the female. When the dominant individual was removed, another lizard immediately became dominant. There were several dominants during the study but never more than one at a time. They were frequently challenged and occasionally supplanted from their dominant position. The social structure in the laboratory enclosure was similar to that within a single territory of the tyrant-subordinate system.

Two species of giant chuckawallas, *S. hispidus* and *S. varius*, occur on islands in the Gulf of California. Case (1978, this volume) reported that these animals were not territorial and exhibited no obvious social hierarchy. Reproduction was infrequent, occurring only in the rainiest years and even then only 30% of the females were gravid. Case also noted that resources on the island were abnormally high in wet years and predation pressure low in comparison to mainland populations of *S. obesus*.

This brief review shows that there is a wide range in the expression of territorial behavior among chuckawallas (Table 21.1). The remainder of this chapter will attempt to define the function of territoriality in these lizards and consider the factors responsible for the observed variations in social organization.

Table 21.1: Variation of Social Organization in *Sauromalus*

Species	Location	Situation	Social System
Berry (1974)	California	Field 1970*	Dominance hierarchy
Nagy (1973)	California	Field 1971	Tyranny—subordinate
Prieto and Ryan (1978)	Arizona	Field	organization
Case (1978)	California	Lab Islands	Territoriality Despotism No apparent social organization

* Drought year in California.

THE ADAPTIVE SIGNIFICANCE OF TERRITORIALITY

The adaptive significance of any trait is best considered in terms of its potential costs and benefits. This concept was elegantly applied to the study of territoriality by Brown (1964) with his theory of economic defendability. Simply stated, this theory predicts that an animal will defend a territory only when the benefits accrued from possessing a territory exceed the costs of defense and maintenance.

Obvious costs of territorial defense in chuckawallas are time and energy expenditure and exposure to predators. Rand and Rand (1976) demonstrated that time and energy considerations are important in determining the intensity of

dispute interactions in nesting *I. iguana*. In chuckawallas, energy considerations may be even more important in years of low food supply. Nagy (1973:93) suggested that "chuckawallas apparently abandon costly social behavior and reproduction in years when succulent food sources are scarce."

Territorial defense by highly conspicuous displays probably increases the male's exposure to predation. Berry observed a large number of potential predators in her study area and noted that chuckawalla remains were found in coyote and soaring birds, some of which were known predators. Prieto and Sorenson (1975) demonstrated that chuckawallas respond to post-anal gland secretions of potential snake predators. The evolution and maintenance of these behaviors suggest that predation might be an important selection pressure.

Rand (1967a) discussed the potential benefits of territoriality in iguanid lizards. He suggested that a selective advantage is accrued to territorial individuals by increasing the possibility of (1) offspring survival, (2) securing environmental resources, (3) mating, and any combination of these benefits.

The Function

In an attempt to understand why there is variation in social organization we must first consider the selection pressures responsible for its evolution. Williams (1966) emphasized the necessity of distinguishing between *function* and *incidental consequences* of adaptation. The function of a causal mechanism implies that the mechanism was shaped by selection for the goal attributed to it. Fortuitous effects of the mechanisms are considered incidental consequences, even if these effects are advantageous to the individual. For example, if territoriality has evolved because of the selective advantage accrued to the individual by obtaining a specific, critical resource, then the defense of other resources which happen to occur in the territory is an incidental consequence and not a function of territoriality.

I will suggest the function of territoriality in chuckawallas by examining each of the benefits proposed by Rand in terms of potential costs and benefits. The hypothesis that the function of territoriality is to achieve a specific benefit will be rejected if alternate means of attaining this benefit, without incurring the costs of territorial behavior are apparent.

Offspring Survival

Parental care in lizards usually is restricted to prehatching investment, although some limited care of neonatal offspring has been reported (Evans, 1959). There are no obvious examples of parental care in chuckawallas and it is not known how nest site selection affects hatching success. Also, there are no suggestions that the male's territory influences juvenile mortality. Therefore, there is no direct evidence that territoriality in chuckawallas affords any benefit in offspring survival.

Securing Environmental Resources

A careful examination of chuckawalla ecology reveals at least three impor-

tant environmental resources contained in the territory: food, basking sites and rock crevice retreats. All of these resources are of obvious advantage to the territory holder, as suggested by Berry. However, by considering the spatial and temporal distribution of these resources in concert with the behavioral ecology of the lizards, it can be determined if these resources are economically defendable: that is, if costs are minimized and benefits maximized through territoriality.

Chuckawallas are xeric herbivores. Consequently, they are especially subject to the vagaries of climate as manifested by fluctuating food supplies. As previously mentioned, social organization is affected when food is scarce (Berry, Nagy). Therefore, it might be predicted that food defense is an important function of territoriality.

In 1970 when a tyrant-subordinate system was present, Berry noted that food sources were utilized readily by subordinate males in "free zones" outside of the territories. Prieto and Ryan also showed that food sources were not contained exclusively in the territories. In fact, territorial males only descended from their rocks and left their territories during feeding. These were the only occasions when adult males were observed in close proximity with no aggressive interactions. Furthermore, in Nagy's study when food supplies started to decrease in May, there was no increase in home range size, as might be expected if the territory was food based (Simon, 1975). Females and juveniles also might be expected to partake in defense of food resources if food was critical. It seems likely that the acquisition of a food source is an incidental consequence and not a function of territoriality.

Raised areas were utilized for basking, display and the lookout stations. Lizards were often seen basking in groups, but these groups never contained more than one adult male (Prieto and Ryan). Rock crevices were utilized for sleeping and were especially important for predator avoidance. By inflating its body a chuckawalla can increase its volume by 58% (Salt, 1943) and safely lodge itself in crevices. Basking sites and rock crevices were abundant outside the territory and there was no obvious difference in quality among sites on and off the territory. It does not appear necessary to incur the costs of territorial defense to obtain these resources. This is also suggested by the fact that males did not attempt to exclude females, juveniles or subordinate males from these sites. For obvious reasons, a male might not exclude a potential mate from utilizing these resources. However, if resources are critical enough to warrant the costs of defense, we might expect the exclusion of subordinate males.

Territorial defense does not appear to minimize the costs of obtaining environmental resources. Therefore, resource defense is probably a consequence of territoriality and has had little importance in the evolution of this behavior.

Mate Acquisition

In most species the asymmetries of parental investment have resulted in mating systems which exhibit male-male competition and female choice (Williams, 1966; Trivers, 1972). Therefore, current theory predicts the evolution of behavioral strategies which maximize the male's ability to compete for females.

Is territoriality a means by which chuckawallas increase their ability to com-

pete for females? Berry, and Prieto and Ryan, reported that males' territories overlapped the home ranges of females and juveniles and they were not aggressively challenged by territorial males. This is consistent with the hypothesis of a mate acquisition territory. Exclusion of females and pre-reproductive males would accrue no benefits if the primary function of the territory was mating, but it would be sure to increase the costs of territorial defense. In Berry's study, only large males were territorial and the smaller, nonterritorial and subordinate males were chased from the territory when detected by the tyrant. This is also consistent with the mate acquisition hypothesis since all reproductive males are potential competitors. Berry stated that possession of a territory not only increases the territory holder's possibility of mating with a female but also decreases the possibility of female-subordinate male matings. The latter point is especially important in species which store sperm, as do most iguanid lizards (Cuellar, 1966).

These studies suggest that a selective advantage accrues to territorial males because of their potentially increased ability to fertilize females. Therefore, mate acquisition seems to be the primary function of territoriality while defense of various environmental resources is probably only an incidental consequence of this adaptation.

VARIATION IN SOCIAL ORGANIZATION

If mate acquisition is the function of territoriality, as suggested in the previous section, then we expect males to adjust their territorial strategies in such a way as to maximize the number of mates they acquire. There are two ways in which a territorial male can increase his ability to fertilize females: increasing the size and the intensity of defense of the territory. A larger territory will overlap the home ranges of more females and therefore should increase the male's accessibility to females. An increase in the intensity of defense also increases the male's probability of successful fertilization. A male that reduces the access of females to other males, either by excluding all males from the territory or by behaviorally dominating them, decreases the chances of female cuckoldry and hence reduces potential sperm competition.

This is not to imply that females play no role in mate selection. There are no data that indicate the extent of female choice in chuckawallas, or any other iguanines (Dugan and Wiewandt, this volume). However, if females do exercise considerable mate choice, there are reasons to believe they would preferentially select males which vigorously defend large territories (cf. Werner, this volume).

Factors Affecting Costs of Territoriality

In the absence of associated costs, males should intensively defend territories of infinite size. Obviously there are costs incurred by territoriality, including time and energy expenditure and exposure to predation. As a male attempts to enhance his access to mates by increasing the size and defense of his territory, there is an increase in associated costs. Therefore, a male should adjust the potential costs and benefits of territoriality by employing a strategy (e.g., a specific size and intensity of defense) which maximizes mate acquisition.

If costs of territoriality among individual males and populations were identical, we would expect little variation in male mating strategies. I suggest that variations in social organization can be understood by examining changes in the costs of territoriality. To do this, it is helpful to consider cost in the context of a probability function. For example, the potential cost of predation, being devoured by a predator, is identical for two individuals in different populations. However, the probability of incurring this cost is determined, in part, by the number of predators present in the area, a factor which is sure to vary among populations. In the following discussion, "cost" is considered a product of the potential cost and the probability of incurring that cost.

Size-Dependent Cost and Alternative Mating Strategies

There are important differences in the expression of territoriality among males of the same population. Berry suggested that the ability to maintain a territory is size dependent. Not only should larger males dominate in physical combat but they should be involved in fewer interactions which culminate in combat, since the probability of a contest escalating is inversely related to the degree of asymmetry in size among the contestants (Maynard Smith and Parker, 1976). Therefore, the costs of territoriality will increase more slowly with increases of size and defense of territory for larger males. Males of different sizes will employ different territorial strategies to maximize mate acquisition.

Not all sexually mature males defend territories (Berry). It should not be assumed that these males are incapable of maintaining a territory. The asymmetrical costs of territoriality might be such that for smaller males a territorial strategy is not an economically feasible means for acquiring mates (Figure 21.1). This might especially be true for long-lived species with indeterminate growth where a nonterritorial strategy should increase the possibility of survival to the next breeding season and allow a more rapid growth rate.

Nonterritorial males capable of territorial defense are not necessarily forfeiting the possibility of mating. Although it was not a common occurrence, Berry observed subordinate males attempting courtship with females. The possibility of these males fertilizing a female may be small but the costs are negligible. This nonterritorial strategy may represent a viable alternative for mate acquisition. Size-dependent mating strategies have been reported in other species with indeterminate growth (e.g., bullfrogs, Howard, 1978).

Asymmetrical Costs Among Populations

Differences in costs of territoriality among populations and within the same population among years, might similarly account for observed variation in social organization among populations. It is necessary to examine population parameters which might influence costs of territoriality.

Extending the previous discussion, the distribution of male sizes within the population ultimately will influence social organization. With an increase in the variance of male size we predict greater variation in the size and intensity of defense of territories and a larger number of males employing alternative mating strategies. As previously discussed, predation pressure is another parameter influencing costs which is sure to vary among populations. However,

these two parameters are not subject to rapid fluctuations and may be of little importance in explaining shifts in social organization among years within one population.

The more interesting population parameters concern the ratio of fertilizable females to available males (operational sex ratio, OSR; see Emlen and Oring, 1977, for a detailed discussion of this concept) and how these females are distributed in space. As the OSR becomes skewed toward males there is increased competition for mates and hence greater costs of territoriality. Also, given a constant OSR (the precise ratio is unimportant) mate competition will increase with the variance of females per territory. Competition should be most intense when there are a large number of a sexually active males and relatively few receptive females and the females are clumped in space.

Distribution of male sizes, predation pressure, OSR, and the spatial distribution of females probably are all important parameters influencing costs of territoriality. The latter two parameters might be more relevant in explaining rapid shifts in social organization because of their relative instability (see below).

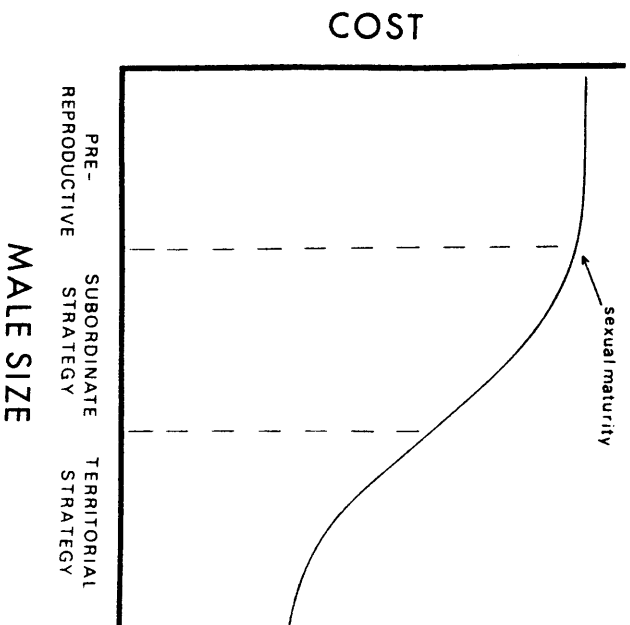


Figure 21.1: Costs of territorial maintenance should be inversely related to male size. This figure represents how asymmetrical costs of territoriality, among males of different sizes, might influence male mating strategies.

Environmental Parameters and Fluctuating Costs

Berry and Nagy showed that following winters of below average rainfall there was a drastic decrease in food supply. In these years there were fewer sexually active females and lizards of both sexes clumped around available food sources. Variation in rainfall manifested by fluctuating food supplies seem to influence both the OSR and the spatial distribution of females. Figure 21.2

summarizes the division of territorial costs by illustrating how environmental, population and individual parameters might interact to determine male mating strategies.

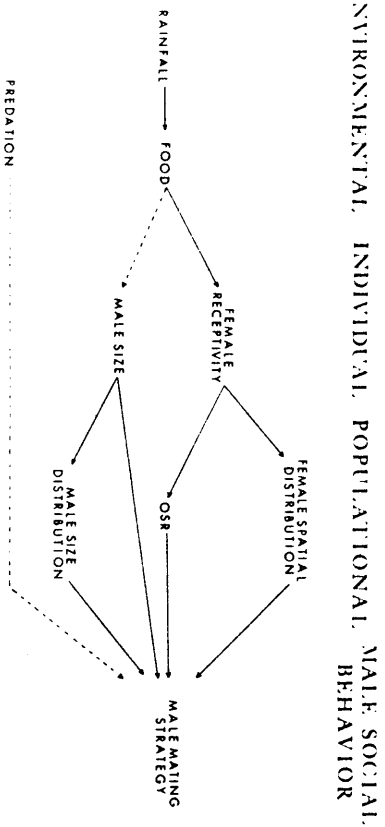


Figure 21.2: Interactions of environmental, individual and population parameters determine male mating strategies. Solid lines represent factors which may be responsible for rapid shifts in social organization. Dashed lines represent less direct effects.

Territorial Costs as Predictors of Social Organization

I suggest that certain factors causing fluctuations in costs of territoriality are responsible for the observed variation in chuckawalla social organization. This is a *post hoc* explanation of how chuckawalla social systems are organized and is in a large part speculative. However, it can also serve as a predictive theory which can be subject to further testing if the proper data are collected.

Figure 21.3 demonstrates how an increase in costs might affect social organization. When costs are minimal territorial behavior should be widespread, as in the strict territorial system (Prieto and Ryan). As costs increase territoriality tends to become a nonadaptive strategy for smaller males (see also Figure 21.1). These males then switch to the less costly subordinate strategy (tyrant-subordinate system, Berry).

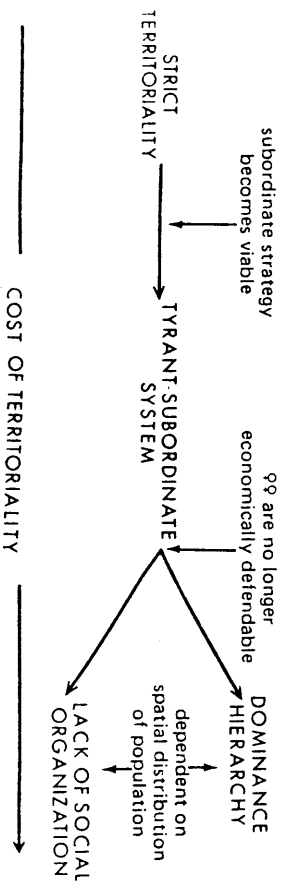


Figure 21.3: Costs of territoriality influence social structure. This figure illustrates how increased costs might be responsible for the observed variation in *Saurornotus* social organization.

A drought preceding the 1970 breeding season resulted in a drastic decrease in annual plants, the primary food of chuckawallas (Berry, Nagy). Territoriality was not observed in either of the two populations. Berry reported a dominance hierarchy around a food source and Nagy noted an almost total lack of social interactions. There are two possible causes for these types of social organization. As less food is available the relative energetic investment in territorial defense increases. Consequently, the costs increase and territorial behavior may no longer be an economically efficient strategy. The second cause relates to the effect of decreased food availability on the females' reproductive physiology. Nagy reported that only one of 18 females had enlarged follicles. Such a drastic decrease in fertilizable females would greatly skew the OSR toward males, causing an increase in male competition and an additional increase in territorial costs.

Territorial behavior was no longer a viable strategy for obtaining mates in the populations studied in 1970. Why did one population exhibit a dominance hierarchy (Berry) while one showed an almost total lack of social interactions? Dominance hierarchies are a result of continual dominant-subordinate interactions between individuals. When chuckawallas were enclosed in a laboratory a dominance hierarchy emerged (Prieto and Ryan). In the tyrant-subordinate system a dominance hierarchy, similar to the laboratory situation, was present among individuals on the same territory.

Dominance hierarchies do not occur if individuals are distributed in such a way that interactions among individuals are minimized. The distribution of lizards should be influenced by resource distribution. Berry reported a dominance hierarchy centered on a rock pile which contained the only sweet bushes in the area. In Nagy's study there were few social interactions, even though lizards were in close proximity on several occasions. There is the possibility that Nagy observed few social interactions because there was already a well-formed dominance hierarchy. However, Nagy did observe aggressive interactions during apparent defense of a rock site. There are no comparable data on resource distribution for the two studies, but perhaps the highly clumped distribution of the food source noted by Berry facilitated the rate of individual encounters resulting in the formation of a dominance hierarchy.

There is little information on the social behavior of the insular giants, *S. hispidus* and *S. varius*. Case (this volume) reported that these animals were not territorial and groups of adults, usually a male and one or more females, sometimes shared the same burrows and rock crevices. He also noted that recruitment is quite low in these populations. There is no reduction in clutch size but breeding takes place only in very wet years and only a small portion of the females become gravid.

Case (1978) suggests that resources are abnormally high and territoriality is not profitable (but see Case, this volume). However, if territoriality is a mate acquisition strategy perhaps the low reproductive rate is responsible for the lack of territoriality and the high resource abundance accounts for the absence of a dominance hierarchy. Precisely why there is a low reproductive rate in these populations is enigmatic. But it should be noted that when Case discusses an abnormally high abundance of resources he is referring to perennials, a food source which mainland chuckawallas eat only after the supply of annuals has

been depleted. Perhaps the low rates of reproduction are caused by a less than optimal diet.

SUMMARY AND CONCLUSIONS

Previous studies indicate significant variation in *Saurornalus* social organization. An analysis of the costs and benefits of chuckawalla territoriality suggests that territories function (*sensu strictu*, Williams) in mate acquisition. Male size, predation pressure, OSR, and the spatial distribution of females are important parameters determining the cost of territorial maintenance. The latter two factors are influenced by rainfall and food and undergo rapid shifts due to the vagaries of the desert climate. Fluctuating costs of territoriality might explain the observed variation in chuckawalla social organization.

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Section VI

Conservation and Management

As with many, perhaps most, tropical animals, iguanine lizards are endangered. They are large, which means both that they are conspicuous and that their populations are relatively small. Many species occur on small islands as parts of fragile systems that are easily disrupted by habitat modification, particularly by the introduction of exotic competitors or predators.

The current status of all iguanines cannot be presented here—we do not know enough. But we do have some information from Chapter 22 by Fitch, Henderson, and Hillis, from which it appears that *Ctenosaura similis* and *Iguana iguana* in Mexico and Central America are still common but rapidly becoming less so. Many ground iguanas are threatened with extinction as the table provided by Wiewandt depressingly catalogues. Banded iguanas discussed in Chapter 23 by Gibbons and Watkins, are common only on small islands and Case (Chapter 11) notes the decreasing populations of the giant chuckawallas that he attributes to capture by people. Other previous chapters also contain pertinent conservation and management information.

The threats to the continued existence of iguanines vary from species to species, but overall one of the most important is habitat modification by humans both directly and indirectly. Such modification is due to diverse influences. For example: tourist developments in the Caicos destroy ground iguana habitats; the disappearance of vacant lots in Panama City eliminates places for urban green iguanas to breed; cutting of mangroves in Mexico destroys iguana habitat; hydroelectric dams flood the sand bars on which iguanas breed. Perhaps most important is the increasing rate at which forest is being converted into pasture. Even in areas where humans are not directly changing the environment the introduction of exotic animals (such as goats that change the vegetation and compete directly with iguanines for food, pigs that dig up their eggs, cats and dogs that prey directly on them) have negative and sometimes disastrous effects on populations, particularly those that have evolved without mammalian predators and competitors.