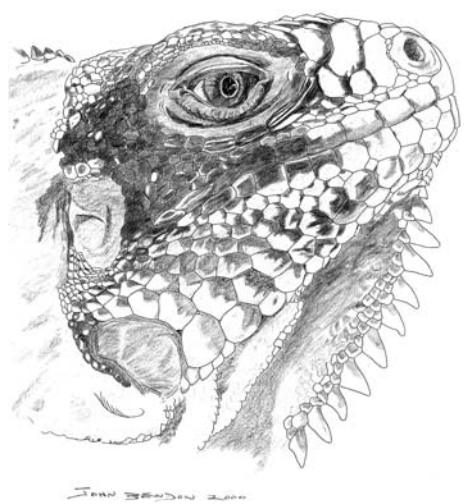
PART TWO

Behavior and Ecology



Introduction

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IGUANAS HAVE LONG FASCINATED behavioral ecologists because they offer an exception to almost every generalization. The implicit hope is that by explaining the exceptions, we might also be able to understand the rule. Whereas most lizards are insectivorous, iguanas feed mostly on plants. Whereas most lizards are territorial, iguanas often live together in groups. Much of lizard behavior and ecology can be explained by understanding the phylogenetic history of the groups. For example, most lizards are probably territorial simply because their ancestors were territorial and there has not been sufficient selective pressure to change that behavior. In contrast, iguanas are incredibly diverse, exhibiting a tremendous variety of behavior and ecology despite their shared phylogenetic history. By studying iguanas, behavioral ecologists can thus learn a great deal about the evolutionary origins and selective importance of many forms of behavior.

For example, much early iguana research focused on green iguanas and the ecological and behavioral ramifications of being an herbivore (e.g., see Burghardt and Rand, 1982; Burghardt, this volume). Leaves are particularly difficult to digest. Thus, iguanas may also aggregate to improve transmission of symbiotic organisms that help to break leaves down into digestible components (Iverson, 1982; McBee and McBee, 1982). Their activity periods may also be determined largely by the need to spend long hours digesting their food. Leaves are generally nutrient-poor and often loaded with toxic chemicals. Thus, iguana movement patterns may be dictated by the need to switch plant types often enough to gather enough calories without making themselves sick (Iverson, 1979). Plants tend to be seasonal, offering only occasional nutritionally-rich bursts of flowers and fruit. Thus, iguana groups may have formed originally as aggregations of animals taking advantage of these food bonanzas.

Another flurry of research involved the importance of nesting patterns and the green iguana tendency to lay eggs in communal nesting areas and only at particular times of the year. The requirements imposed by fierce competition for limited nesting sites leads to impressive homing behavior by which females migrate long distances to the same small spot of beach every year (e.g., Rand and Rand, 1976; Bock et al., 1985). Researchers moved on to studying the resulting simultaneous hatching of the eggs and the social associations formed among young iguanas shortly after emergence (e.g., Burghardt, 1977b; Greene et al., 1978; Werner et al., 1987).

More recent research in iguana behavioral ecology has broadened to other taxa and types of behavior. Perhaps because they are herbivores, iguanas are also unusually large lizards, and their size is likely to have had a major impact on their behavioral ecology. Recent iguana research has advanced from the basic relationship between body size and herbivory to consider how body size can affect details of iguana activity patterns and foraging behavior. For example, Wikelski and Carbone (this volume) use a complex model to describe whether Galápagos iguanas are likely to feed in the shallows or in deeper water, based on both water temperature and body size. Specifically, large animals are able to retain enough heat to forage in deep water. Iguanas are ectotherms and thus clearly constrained by external temperatures. Nevertheless, by shuttling back and forth between different temperature regimes, they can maintain far less extreme internal body temperatures and take advantage of a broader range of food resources. Similarly, Tracy (this volume) shows how larger chuckwallas (but not desert iguanas) can take advantage of higher elevations, where the activity season is longer. Both studies highlight how large body size combined with behavioral flexibility can open unexpected ecological niches. Iverson et al. (this volume) show that, although food abundance and iguana densities can clearly affect growth rates of individual animals, iguana populations as a whole may be relatively robust to short-term changes in their environments. For example, although supplemental feeding by human tourists has a clear impact on the growth rates of male iguanas living on the beaches where humans arrive, it seems to have had little impact on the growth rates of animals in the rest of the population.

Studies of social behavior have also advanced considerably. Older studies focused on the possibility of kin associations among juvenile iguanas (e.g., Werner et al., 1987) and the territorial mating and haremlike behavior of green iguanas (e.g., Dugan, 1982a; Rodda, 1992). More recent studies have uncovered even more sophisticated forms of social behavior. For example, Rivas and Levin (this volume) describe how male green iguanas will sometimes use their own bodies to shelter female siblings from predators. Although sibling groupings are known to be common in many animals, apparent acts of altruism of this sort are quite rare. In Martins and Lacy (this volume), we describe an appeasement display in the Turks and Caicos Island iguana, a headbob pattern that leads to reduced aggression from its recipients. Although several iguana species are often found in groups, an appeasement display is a fairly advanced form of social behavior, found usually in animals that have been evolving in groups for a long period of time (e.g., social insects, primates). Hayes et al. (this volume) describe the lek mating system of the Galápagos marine iguana, in which females choose among large groups of males on the basis of morphology, behavior, and parasite loads. The system is particularly interesting because females choose among males on the basis of many characters rather than on a single, simple measure, such as body size. Although altruism, advanced social behavior, and female choice are relatively common in birds and mammals, they are virtually unheard of in lizards or other reptiles. Iguana research can thus be a powerful tool to understanding the evolutionary origins of these forms of complex behavior.

Future research on iguana behavioral ecology seems likely to focus on the more sophisticated aspects of their behavior and the mechanisms underlying the rapid change responsible for the incredible diversity of iguana behavior. Have green iguanas evolved any special mechanisms for kin or sex recognition that allow for their unusually altruistic behavior? Have marine iguanas evolved specialized mechanisms for mate choice? What sorts of evolutionary interactions are responsible for the complex relationships observed between herbivory, large body size, and differences in activity patterns? Why has complex behavior evolved so rapidly in iguanas? What are the behavioral, morphological, physiological, and genetic mechanisms controlling complex social behavior? Has learning played an important role, or are genetic changes responsible for the major differences between iguanas and other lizard taxa? Will human impact on natural populations also lead to similarly rapid levels of change? How might we protect iguanas from these latter sorts of artificial changes?

Future research is also likely to have a strong conservation focus. As discussed in the final section of this book (Alberts, this volume), many iguana species are seriously endangered or threatened with extinction. Behavioral ecology is an important issue in the conservation of most species (e.g., Clemmons and Buchholz, 1997), but has been particularly important in iguana conservation efforts. Behavioral traits can be critical in determining what constitutes a unique taxonomic unit or species, developing husbandry procedures for animals in captivity, and determining exactly how animals should be managed in the wild. They can also provide an important type of diversity, which warrants preservation (e.g., Stone et al., 1994). Although iguanas, being lizards, may not seem as complex behaviorally as many bird and mammal species, they have large brains and complex social and foraging behavior (e.g., Burghardt, 1977a), all of which suggest that their behavior may be of importance to conservation efforts.

Many conservation tools currently being applied to iguanas (see the last section of this book) can affect the behavior and ecology of the animals being protected. For example, several iguana ecotourism sites have been established recently to offer an opportunity for environmental education and to protect iguanas by focusing human impacts on a small, confined part of the population. Unfortunately, we know little about the effects of ecotourism and supplemental feeding on behavior (but see Lacy and Martins, 2003; Iverson et al., this volume; Knapp, this volume), and further research is desperately needed to understand the larger-scale impacts of this approach on the unusually complex behavior and ecology of iguanas.

Headstart and translocation programs, in which young animals are captured in the wild and then raised in captivity or simply introduced into a new area, are also becoming popular (e.g., Alberts et al., Knapp and Hudson, Wilson et al., all in this volume). When iguanas are brought into captivity in a headstart program, how can we ensure that are they presented with adequate stimuli to generate normal behavioral development? In some species, proper development may require exposing the animals to predators so that they develop antipredator skills or presenting the animals with food in ways that require them to process and handle those items as they would in the wild (e.g., Alberts et al., this volume). It may also be important to expose developing iguanas to the natural social interactions of older animals from the same population. Translocation attempts may suffer if enough animals of the right sexes and ages are not introduced together, or if they do not all originate from the same population and thus differ in behavior. Although we still have very little information to answer the above questions, the few current attempts at headstarting seem to have been largely successful, leading to large, healthy animals, which exhibit relatively normal behavior (e.g., nesting in the wild). More detailed behavioral research is needed, however, to determine whether the introduced animals exhibit the full diversity of behavior and ecology of natural populations, which may be critical to long-term survival of these species.

Finally, behavioral research may also be important in determining the most appropriate unit of conservation (e.g., Clemmons and Buchholz, 1997). Population differences of the magnitude observed in iguanas (e.g., Bissell and Martins, Hayes et al., Malone and Davis, Welch et al., all in this volume) can have important ramifications for conservation and management plans, as they suggest that different populations may be behaviorally, morphologically, and/or genetically unique and worthy of individual conservation. Animals that differ in their behavior may not be able to communicate with each other effectively, to find food or shelter in each other's environments, or to avoid unfamiliar predators (e.g., Snyder et al., 1996). As groups of animals become increasingly different from one another, individuals from one group will stop mating or interacting in any way with those from another group; the groups may eventually become genetically distinct populations or even separate species. Iguana behavioral ecology is thus quite likely to play a role in speciation and population subdivision. By determining which groups are behaviorally and/or ecologically different and how those differences affect individual animals' abilities to interact with each other, we can help make informed decisions about the taxonomic level at which the animals should be conserved.

Almost everyone is fascinated by iguanas. Although to the general public, iguanas are the lizard of choice for creating such reptilian monster images as Godzilla, to behavioral researchers, they offer an unparalleled opportunity to study the mechanisms underlying the evolutionary origins of complex and unusual forms of behavioral ecology. By comparing iguanas to other lizards, we can begin to understand how animals evolve active mate choice and complex social behavior and also how morphology and physiology constrain or create behavioral choices. Further research is also needed to determine if some of the less studied taxa (e.g., *Ctenosaura*) are similarly complex in terms of their behavior. We hope that this volume will help to excite and inspire future researchers to answer some of these fascinating and important questions.