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## THE RESILIENCY OF LIZARD COMMUNITIES TO HABITAT FRAGMENTATION IN DRY FORESTS OF SOUTHWESTERN PUERTO RICO

By

Kristen S. Genet

## A THESIS

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

# MASTER OF SCIENCE

Department of Zoology

#### ABSTRACT

## THE RESILIENCY OF LIZARD COMMUNITIES TO HABITAT FRAGMENTATION IN DRY FORESTS OF SOUTHWESTERN PUERTO RICO

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The effects of habitat fragmentation on lizard communities were quantified for a subtropical dry forest ecosystem in southwestern Puerto Rico. Diversity and abundance of 10 lizard species were determined for small (<1 ha), medium (1-10 ha), and large (>10 ha) forest fragments and were compared to sites in Guánica Forest, the largest continuous tract of dry forest remaining in Puerto Rico. Characteristics of the study sites and surrounding landscape were also quantified to assess the response of lizards to landscape-level phenomena; habitat characteristics of anoles were also quantified to assess the ecological status of the endangered Anolis cooki. Comparisons of lizard community composition and structure among fragments and continuous forest revealed that lizards were relatively resilient to the consequences of habitat fragmentation. although species richness was significantly positively correlated with fragment area. The ability of lizards to survive and maintain populations in this fragmented landscape indicated that conservation and/or restoration of small patches of secondary forest would likely lead to increased lizard populations that would be able to colonize additional forest patches as habitat becomes available.

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#### INTRODUCTION

Habitat fragmentation is one of the greatest threats to natural ecosystems and global biodiversity (Wilcox and Murphy 1985, Turner 1996, Dale and Pearson 1997). Thus, the causes and consequences of fragmentation are important considerations for developing conservation and management strategies for fragmented landscapes. Alteration, degradation, and fragmentation of tropical forest ecosystems as a result of human impact have received considerable recognition and attention as a source of loss of both biodiversity and ecosystem structure and function (i.e., Lugo *et al.* 1978, Murphy and Lugo 1986a, Janzen 1988a, b, Murphy *et al.* 1995), as rates of deforestation in the tropics and subtropics have increased over the past several decades (FAO 1993, Whitmore 1997).

Laurance *et al.* (1997) reviewed the effects of tropical forest fragmentation on ecosystem structure, diversity, and function. Bierregard *et al.* (1997) identified the major priorities for research, conservation, and management in these systems. Fundamental information on the natural history of species and knowledge of species-level responses to habitat fragmentation are lacking (Laurance and Bierregard 1997); this study addressed these issues concerning lizard community ecology in a highly fragmented subtropical dry forest landscape in southwestern Puerto Rico.

Tropical and subtropical dry forests are more imperiled than their moist and wet forest counterparts (Janzen 1988a, b, Redford *et al.* 1990, Murphy and

Lugo 1990, Lerdau *et al.* 1991, Murphy and Lugo 1995). Although it is true that tropical rain forests harbor a more speciose community, tropical dry forests support a rich array of biological interactions and responses to the more pronounced seasonality of these systems. Rather than limiting conservation efforts solely to numbers of species, interactions among and between species are also crucial components of a naturally functioning ecosystem that need to be protected and preserved (Janzen 1988a).

Subtropical and tropical dry forests are located in frost free regions where the mean annual biotemperature (air temperature corrected for extremely high or low temperatures,  $>30^{\circ}$  C and  $<0^{\circ}$  C, respectively) is greater than  $17^{\circ}$  C, mean annual precipitation ranges from 250-2000 mm, and the mean annual ratio of potential evapotranspiration to precipitation (PET/P) is greater than 1.0 (Holdridge 1967). The majority of forests within this classification are found in Africa, Central America and tropical islands, where they constitute 70-80% of the total forested area (Murphy and Lugo 1986b).

Although dry forests constitute approximately 42% of the total forested area in the tropics and subtropics (Murphy and Lugo 1986b, 1990), they are underrepresented in terms of research focus and published literature. Historically, dry forests extended over a much larger area than at present, but as a result of a long legacy of disturbance and deforestation, their original extent will probably never be known. It is thought that many of the dry savannas or thorn woodlands are derived from degraded or disturbed dry forests (Murphy and Lugo 1986b). Dry forests are perhaps a more endangered ecosystem than

moist or wet forests as a result of the greater human pressure and disturbances. In general, people prefer to live in the climate of the dry or moist tropics (*sensu* Holdridge 1967), and the forest structure and underlying soils have made these regions profitable to clear for agriculture and cattle ranching (Murphy and Lugo 1986b).

There are few remaining intact representatives of dry forest in Central America and the Caribbean (Janzen 1988a, b, Murphy and Lugo 1995). Two notable examples of dry forest under active management and protection are the Guanacaste National Park in northwestern Costa Rica (Janzen 1988b) and the Guánica Commonwealth Forest in southwestern Puerto Rico (Murphy and Lugo 1990, Murphy *et al.* 1995). Janzen (1988a, b) has stated that restoration ecology and habitat management will be the only solutions to salvaging the diverse array of species and biological activities in the world's tropical dry forests, and has actively pioneered such projects in the dry forests of Costa Rica. From the biological perspective, the task at hand is to devise a plan for sustainable land management strategies that meet the needs of the local people and contribute to the conservation of biodiversity (Lamb *et al.* 1997).

Species exhibit tremendous variability in their responses to habitat fragmentation. Species that are the most susceptible to the consequences of fragmentation, undoubtedly leading to eventual population declines and extinction, are those that have one or more of the following characteristics (modified from Turner 1996 and Laurance *et al.* 1997): (1) extreme sensitivity to habitat alteration or intolerance of conditions in the surrounding matrix (i.e.

habitat specialists), (2) large habitat area requirements, (3) vulnerability to any sort of exploitation, (4) unstable or highly fluctuating population dynamics, or ecological dependence on species with unstable populations, (5) naturally low population densities or patchy distributions (i.e., rare species), (6) limited dispersal abilities, or (7) low fecundity. Studying individual species or ecological assemblages of species will allow us to gain a successively more comprehensive understanding of how different groups of organisms respond to the pressures of habitat fragmentation.

Studying animals' responses to habitat fragmentation is necessary because many species are very vulnerable to habitat alteration and respond quickly to any changes in habitat structure and microclimate. Since dry forest systems are critical habitat areas for many species of vertebrates (notably high avian diversity; Kepler and Kepler 1970, Faaborg and Arendt 1990), assessing the ecological response of the fauna to habitat fragmentation is a necessary step in addressing biodiversity and conservation management strategies. Small sized, ectothermic species with short generation times may exhibit the most sensitive and rapid responses to habitat modification. Responses of vertebrate species in particular may have ramifications on the entire community structure as a result of higher order interactions.

Lizards (suborder Lacertilia) are probably the most common as well as the most conspicuous terrestrial vertebrates, inhabiting every region of Puerto Rico. The island supports a very diverse lizard fauna, with species accounts ranging from 33 (Rivero 1978) to 43 (Schwartz and Henderson 1991) species.

Differences in surveys and species accounts are most likely attributable to unresolved and controversial taxonomic distinctions. The most diverse group within the lizard fauna is found among the *Anolis* lizards, with 12 species ecologically distributed throughout the island (Rand 1964, Roughgarden 1995). Lizards are among the higher order predators on the island. They are primarily insectivorous, but have a broad diet ranging from garbage scraps to other smaller lizards, making them important in terms of trophic structure of these tropical forest communities. Lizards also lend themselves well to ecological studies, as evidenced by the wealth of literature on this vertebrate group.

The vast majority of lizard studies in Puerto Rico have focused on communities within the Luquillo Rain Forest (e.g., Andrews 1971, Lister 1981, Reagan 1986, 1992). Of the diverse lizard fauna of the island, fewer than 15 species are found in the dry forest zone of the southwest (Rivero 1978). Studies of the lizards in the dry forest zone have investigated growth (Lewis 1986), activity budgets (Lewis and Saliva 1987), diet selection (Lewis 1989), and competitive interactions (Ortiz and Jenssen 1982, Jenssen *et al.* 1984). Ortiz (1990) reported on the status and distribution of *Anolis cooki*, and the impacts of competitive interference and habitat disturbance on this endangered species. Studies of this nature are of paramount importance in light of extensive human disturbances to natural habitats, and questions regarding faunal communities within fragmented and protected landscapes are in dire need of additional research.

Assessing the response of the dry forest lizard community is the first step in gaining a better understanding of how faunal assemblages respond to landscape-level habitat fragmentation phenomena. In order to protect and preserve biodiversity, it is critical to study at the landscape and regional level in addition to whole ecosystem studies (Noss 1983, Franklin 1993, Stohlgren et al. 1997). Through interpretation and analysis of historical land use and land cover maps (Vélez Rodríguez 1995a-f, Lugo et al. 1996, Kramer 1997) and current aerial photographs, temporal variability and changes in landscape structure and function can be inferred. In addition, abiotic landscape and fragment features can be combined with biotic attributes to assess landscape structure, function. and change in this highly fragmented and altered environment. This approach will provide an indication of the ecological associations of lizards in this region, which may subsequently provide valuable information concerning the conservation potential and future management strategies for this ecosystem and other similarly disturbed systems.

#### **Objectives and Hypotheses**

The overall objective of this study was to assess the ability of forest fragments to support native Puerto Rican dry forest lizard communities and to serve as refugia in the face of continuous habitat disturbance. Even small forest remnants have conservation potential and important biological, economic, and social values. These remnants can support assemblages of endemic species (Turner and Corlett 1996), increase ecosystem connectedness by allowing

dispersal or migration of some species (Powell and Bjork 1995), provide sources for recolonization of adjacent patches via metapopulation dynamics (Fahrig and Merriam 1985) or establishment in the matrix habitat through the 'rescue effect' (*sensu* Brown and Kodric-Brown 1977) or conserve local vegetation populations and seed sources (Nason *et al.* 1997), perform natural "ecosystem services" such as local soil stabilization and erosion control, and provide natural areas for recreation purposes.

One hypothesis underlying this work is that the fragments of Puerto Rico's dry forest region serve as refugia which contain source populations of native animal species (Brown and Kodric-Brown 1977, Fahrig and Merriam 1985). Characteristics such as area, plant community composition, microclimate, aspect, and disturbance history determine the potential of a fragment to serve as a refugium for a given species or assemblage of species.

The specific objectives of this study were:

- (1) to compare the diversity and abundance of native lizards in a large, relatively undisturbed, protected dry forest (Guánica Commonwealth Forest) and in forest fragments of varying sizes in the dry forest life zone. These data will be used to test the hypothesis that the diversity and abundance of lizards present in an array of fragments will collectively be comparable to those of Guánica Forest.
- (2) to determine variation in diversity and abundance of lizard species among fragments relative to fragment size, disturbance history, and characteristics of the landscape surrounding forest fragments. This objective will allow me

to test the hypothesis that the diversity and abundance of lizards will increase as total fragment area increases.

- (3) to determine (a) the minimum critical fragment size which contains a community of lizards similar to that found in undisturbed dry forest habitats, and (b) the minimum critical fragment size required to support 50% and 75% of the reference (Guánica Forest) lizard community.
- (4) to determine the influence of landscape-level phenomena on the distribution, diversity, and abundance of dry forest lizard species. These data will allow me to test the hypothesis that landscape characteristics such as land use adjacent to fragments and fragment isolation will influence lizard community composition of individual forest fragments.
- (5) to determine critical habitat requirements of selected lizard species in fragmented systems relative to continuous forest. The hypothesis to be tested is that fragment size and landscape position will affect habitat within fragments differentially such that habitat suitability for lizard species will be altered.

#### The Study Region

Ewel and Whitmore (1973) provided an excellent description of the subtropical dry forest zone on Puerto Rico and the U.S. Virgin Islands. In the dry forest life zone of southwestern Puerto Rico, annual precipitation ranges from 600-1100 mm, and Guánica Forest, situated in the approximate center of this region, receives approximately 860 mm of rainfall annually with considerable

year to year variability (Murphy *et al.* 1995). Guánica Forest covers an area of approximately 4000 hectares, the largest continuous tract of dry forest on the island. Originally, dry forests covered the majority of southern and western Puerto Rico (as well as smaller regions of the northeastern coast and surrounding islands and cays), but only 4% of the historical extent of dry forest remains today (Murphy and Lugo 1990). A more thorough discussion of land use history and changes in southwestern Puerto Rico can be found in Chapter 2.

The plant community of Guánica Forest, and the dry forest zone in general, can be characterized by three major vegetation associations: coastal scrub, deciduous, and semi-evergreen forest (Murphy and Lugo 1986a), although along the elevational gradient from coastal to upland sites these classifications can be refined to six floristically and structurally distinct categories (Murphy et al. 1995). Tree communities are usually stunted, rarely exceeding 15 m in height, with the possible exceptions of more humid and protected environments of ravines and valleys (Farnsworth 1993): the canopy is typically broad and sparsely leafed (Ewel and Whitmore 1973). The forest is typified by many multiple stemmed trees and a high density of small stems (< 5 cm DBH) reflecting regeneration by coppicing as a result of fence post harvesting or other disturbances (i.e., hurricanes) (Murphy and Lugo 1986a, S. Van Bloem, pers. comm.). In comparison to dry forest in other tropical and subtropical regions, Guánica Forest is structurally smaller in terms of canopy height, canopy foliage, and total biomass (Murphy and Lugo 1990). Possible explanations for these differences include profound seasonality with low rainfall

alternating with extreme drought (Murphy *et al.* 1995), harsh limestone substrate, and probably most importantly, the disturbance history (Murphy and Lugo 1990).

In spite of its harsh environment and structure, Guánica Forest harbors a rich diversity of wildlife and biological interactions. Both in terms of species richness and absolute abundance, Guánica Forest supports a more diverse assemblage of birds than the moist and wet forest zones in Puerto Rico (Kepler and Kepler 1970). Indeed, birds represent a valuable taxonomic group for research, and their responses to habitat fragmentation and alteration have been studied extensively in comparison to other faunal groups (Turner 1996, Bierregard *et al.* 1997). Previous studies of faunal assemblages within Guánica Forest have focused primarily on the avian communities (Faaborg and Arendt 1990 and references within); studies of other vertebrate and invertebrate communities are lacking.

## Chapter 1

## The Reference Lizard Community of Guánica Forest

#### Introduction

Lizards (Reptilia, Lacertilia) are ubiquitous inhabitants of subtropical and tropical regions. Past surveys of the island of Puerto Rico have recorded 33 (Rivero 1978) to 43 (Scwartz and Henderson 1991) species on the main island as well as the surrounding smaller islands and cays. These species represent five families: Gekkonidae, Teiidae, Scincidae, Anguidae, and Polychridae. Within this diverse assemblage, 13 species (eight of which are endemic to the Puerto Rican Bank) and four families are represented in the dry forest life zone (sensu Holdridge 1967), although some species within this subset have restricted habitat requirements or represent rare and/or endangered species which are not continuously distributed throughout the dry zone (Table 1.1, Rivero 1978, Schwartz and Henderson 1991). Along with snakes and some birds, lizards are predominantly carnivorous and occupy the higher trophic levels in the dry forest ecosystem. Any perturbations in their community composition or population density have the potential to subsequently affect the entire ecological community.

Anoline lizards (Polychridae, genus *Anolis*) have been present in the Caribbean throughout its geologic history; the lineage extends back at least into the middle Jurassic, approximately 175 million years ago (Estes 1983, Roughgarden 1995). Puerto Rican *Anolis* are derived from the Central

Caribbean Complex lineage (Shochat and Dessauer 1981), and a single successful colonization event (likely from Hispaniola; Reagan 1996) and subsequent radiation are theorized as the origin of the current anole fauna (Williams 1969). Modern *Anolis* lizards are very conspicuous and widespread vertebrates in Caribbean terrestrial ecosystems (Williams 1969, 1976, Moermond 1979). These lizards are diurnal, primarily insectivorous, and are ecologically distributed along a vertical gradient throughout every habitat type in Puerto Rico (Rand 1964). These lizards are fundamentally arboreal, but some ecomorphs (*sensu* Williams 1983) are well adapted to grass and bush environments. Little is known about anole survivorship and longevity, but preliminary data suggest that some of the smaller species (e.g., *A. stratulus*) have a mean population turnover time of 1.4 years and a relatively constant mortality rate throughout their lifetimes; survivorship for larger species may be higher, but no estimates are available (Reagan 1996).

Table 1.1 Families and species of lizards represented in the dry forest zone of southwestern Puerto Rico (compiled from Rivero 1978, Schwartz and Henderson 1991).

Polychridae	<u>Teiidae</u>	Gekkonidae	<u>Scincidae</u>
Anolis cristatellus	<sup>T</sup> Ameiva exsul	<sup>T</sup> Sphaerodactylus nicholsi	*Mabuya mabouya
<sup>†</sup> Anolis cooki	<sup>†</sup> Ameiva wetmorei	<sup>†</sup> Sphaerodactylus roosevelti	
<sup>†</sup> Anolis stratulus		*Sphaerodactylus macrolepis	S
<sup>†</sup> Anolis pulchellus		Phyllodactylus wirshingi	
<sup>†</sup> Anolis ponc <del>e</del> nsis	•	*Hemidactylus brooki	

\* species which are rare or patchily distributed and not encountered during this study.

species endemic to the Puerto Rican Island Bank (Puerto Rico, Virgin Islands, and surrounding islets and cays).

Within the dry forest life zone of southwestern Puerto Rico, there are 5 species of Anolis lizards (Table 1.1). Of these, Anolis cristatellus (Duméril and Bibron), A. pulchellus (Duméril and Bibron), and A. stratulus (Cope) are widely distributed across the island and found in both xeric and mesic environments, while A. cooki (Grant) and A. poncensis (Stejneger), are restricted to the drier southwestern region of the island. Anolis lizards are among the most thoroughly studied organisms, and this collection of species is no exception. The more widespread species have been studied more intensively: research topics have included interspecific interactions (Hess and Losos 1991), distribution and abundance (e.g., Philibosian 1975, Gorman and Harwood 1977, Reagan 1992, Dial and Roughgarden 1994), habitat and resource partitioning (e.g., Schoener and Schoener 1971a, b, Lister 1981, Goto and Osborne 1989), and foraging (Reagan 1986). Research in the dry forest zone has emphasized competitive interference between A. cristatellus and A. cooki (Ortiz and Jenssen 1982, Jenssen et al. 1984); this interference has implications for the status and distribution of the threatened A. cooki, a candidate for the federal endangered species list (Marcellini et al. 1985, Ortiz 1990).

Members of the family Teiidae (represented by the genus *Ameiva* in the dry forest life zone) are considered insectivorous, but stomach contents analysis has determined that they are opportunistic and generalized omnivores (Rivero 1978, Lewis 1989). These lizards are characterized by extremely long tails and continual active foraging through the forest substrate (Rivero 1978, Scwartz and Henderson 1991). They are adapted to digging under rocks or other substrate

debris in search of food, and have been found to excavate burrows as deep as 30 cm in sandy soils (Rivero 1978). *Ameiva* spp. are diurnal, foraging most vigorously during the warmest midday hours; they can actively thermoregulate by basking or seeking shelter (Rivero 1978).

Two species of teiid lizards inhabit the dry forest of southwestern Puerto Rico, *Ameiva exsul* (Cope) and *A. wetmorei* (Stejneger). The distribution of *A. exsul* is restricted to the warm and sandy lowlands around the entire perimeter of the island (Heatwole and Torres 1967, Schwartz and Henderson 1991). This species seems to prefer open forest or roadside conditions, and does very well in human-altered environments. *Ameiva wetmorei*, on the other hand, has a much more restricted distribution, being found only in the arid region of southwestern Puerto Rico and on Caja de Muertos island (Rivero 1978, Schwartz and Henderson 1991). This species is found in open, dry scrubby habitats; its activity patterns and natural history characteristics are very similar to those of *A. exsul* (Heatwole and Torres 1967). Previous studies of these lizards have focused primarily on the more abundant, larger *A. exsul* (Lewis 1986, 1989, Lewis and Saliva 1987); little is known about the ecology of *A. wetmorei*.

The remaining Puerto Rican dry forest lizard species belong to the family Gekkonidae. This large and diverse family in the tropics and subtropics is characterized by generally immovable eyelids, nocturnal or crepuscular habits (although some species can be diurnal as well), and expanded toepads which are covered with lamellae and setae that aid them in navigating smooth vertical surfaces (Rivero 1978). Many species of geckos have become well established

in and around buildings and residences (Rivero 1978). The geckos of the dry forest zone can be found in leaf litter and under rocks; some populations are also very successful in littoral situations under accumulations of palm trash (Rivero 1978).

Of the five species of geckos that are present in the dry forest zone of southwestern Puerto Rico, two (*Sphaerodactylus macrolepis* Günther and *Hemidactylus brooki* Gray) are relatively uncommon in natural forested habitats (Table 1.1). *Sphaerodactylus macrolepis*, although it is generally the most common and widespread gecko in Puerto Rico, is absent from the most xeric habitats typical of the dry forest (Rivero 1978, Schwartz and Henderson 1991). *Hemidactylus brooki* can be found in the dry forest region, but is associated primarily with human dwellings and rarely occurs in naturally forested habitat (Schwartz and Henderson 1991).

The other two *Sphaerodactylus* species, *S. nicholsi* (Grant) and *S. roosevelti* (Grant), are restricted to dry coastal areas (Thomas and Schwartz 1966); *Phyllodactylus wirshingi* (Kerster and Smith) has a similar distributional range (Schwartz and Henderson 1991). These geckos are primarily ground-dwellers, inhabiting the forest floor in piles of leaf litter and underneath rocks (Rivero 1978), although some individuals are also found under peeling bark near the base of dead trees such as *Leucaena leucocephala* (*pers. obs.*). Other than comments and observations provided in the original descriptions of these species, very little is known of the habits and ecology of any of the Puerto Rican gekkonids (Hass 1991).

Although some assemblages or individual species of dry forest lizards have been studied extensively, additional investigations of community composition and abundance would provide meaningful contributions to what is already known about basic lizard biology. The objectives of this chapter are to determine the baseline conditions and characteristics of a relatively undisturbed lizard community in southwestern Puerto Rico's dry forest life zone. This community will serve as a reference against which other lizard communities (disturbed or otherwise impacted) can be compared (Chapter 2).

#### **Materials and Methods**

#### Study Region

The dry forest life zone (*sensu* Holdridge 1967) of southwestern Puerto Rico encompasses an area of approximately 121,640 hectares (ha) extending approximately 120 km eastward from Cabo Rojo on the extreme southwestern corner of the island, and depending upon local topography, the northern boundary of the dry zone ranges from 3 - 20 km inland (Figure 1.1 inset, Ewel and Whitmore 1973). The vast majority of Puerto Rico's dry forest habitat occurs in this region, although only approximately 4% (roughly 5000 ha) remains of the original forested area (Murphy and Lugo 1990, Murphy *et al.* 1995). Dry forests are also found along the northeastern coast of the island and constitute the predominant life zone classification on all surrounding islands (Culebra, Vieques, Caja de Muertos, Mona, and Desecheo) (Ewel and Whitmore 1973).

The dry zone in the southwestern region of the island lies in the

orographic rain shadow of the Cordillera Central, and receives between 600-1100 mm of precipitation annually, variable with specific location and seasonality (Ewel and Whitmore 1973). There are two wet and dry periods annually; most of the rainfall occurs in either the longer wet season from August until November or the shorter wet season during the month of May.

#### Guánica Commonwealth Forest

Guánica Forest, one of the best remaining representatives of dry forest habitat, is situated at the approximate center of the dry zone's east-west orientation, where it receives approximately 860 mm of rainfall annually (Ewel and Whitmore 1973, Murphy and Lugo 1990). The area was designated a Commonwealth Forest in 1917, and has been protected and managed to varying degrees since the 1930's. In 1982, protection and management were heightened when Guánica Forest became a Biosphere Reserve in the UNESCO Man in the Biosphere program.

Guánica Forest's boundaries currently encompass approximately 4000 ha, significantly increased from the original 2079 ha reserve (Lugo *et al.* 1996). This area has been subjected to a wide variety of activities and uses throughout its history, including tree plantations (*Haematoxylum campechianium* and *Swietenia mahogani*), charcoal and fencepost production, agriculture (both cultivated crops and livestock), and human settlements (Murphy *et al.* 1995). Most of these activities ceased by the 1930's or 1940's, but fencepost harvesting continued until the 1970's (M. Canals Mora, *pers. comm.*).

Guánica Forest is divided into two sections, separated by Guánica Bay and the town of Ensenada. The western portion represents a smaller, more recently acquired, and less intensively managed tract than the eastern portion. The forest supports a wide array of vegetation types and associations, with three primary categories: coastal scrub, deciduous, and semi-evergreen forest along the gradient from coastal to upland sites exceeding an elevation of 200 m. An additional feature of Guánica Forest is the extensive cave system that has resulted from dissolution of limestone. Collapsed cave systems now form narrow ravines and canyons along a north-south orientation in the forest, supporting flora and fauna in a more mesic environment which often floods in the wet seasons and during large storms (Farnsworth 1993).

## Reference Site Selection

Four sites were selected within the continuous eastern portion of Guánica Forest for this study (Figure 1.1). These sites represent the vegetation types and topographical features described above, and match the characteristics of additional study sites (forest fragments, discussed in Chapter 2). Each site measured 100 ha (with the exception of the ravines), and was delineated using topographic maps (USGS standard 1:24,000 quandrangle maps for Guánica and Punta Verraco). These areas within Guánica Forest included a coastal scrub (Co, Figure 1.1) along the southern coast and two upland forest sites in the central and northern section of the forest. The central site (Ce, Figure 1.1) included predominantly south-facing slopes, while the slopes in the northern site



are labeled as follows: Co=coastal scrub, Ce=central site of upland forest on predominantly south-facing slopes, N=northern site of upland forest on predominantly north-facing slopes, R1-R6=ravines. The Land use map of Guanica Forest (eastern section) and vicinity. Study sites within the reference site relative size and location of fragment sites 4, 7, and 10 are also shown on this map. Figure 1.1

(N, Figure 1.1) were primarily north-facing. Six ravines (R1-R6, Figure 1.1) were selected for sampling from topographic maps and personal observations; this site was not a continuous 100 ha as the others, rather the number of ravines was selected to match the sampling regime for each of the other sites (Table 1.2).

Due to differences in the biology and activity patterns of the 10 commonly encountered dry forest lizard species, two distinct survey strategies were required to obtain accurate estimates of diversity and abundance. Seven members of the genera *Anolis* and *Ameiva* are either arboreal or free-ranging lizards and abundant and conspicuous diurnal species. These species were censused along 100 m transects of fixed area. Three members of the genera *Sphaerodactylus* and *Phyllodactylus* are primarily nocturnal and/or fossorial, making transect surveys unrealistic to obtain accurate diversity and abundance measures. These species were sampled by carefully searching through litter and ground debris in 2 x 2m plots. The sampling design for the reference site is summarized in Table 1.2. The number of transects and plots represented the necessity of efficient and accurate sampling, coupled with time and labor intensive survey strategies. Species-area curves were constructed as a measure of sampling efficiency at each site (Appendix A).

## Transect Sampling

Other investigators have often used transect surveys to efficiently and accurately estimate lizard population densities (Rand 1964, Schoener and Schoener 1971a, b, Reagan 1992). Thus, this method was chosen for sampling

	Summary	or sampling design	in Guarrica Co	mmonwealth F	01031
Site ID	Area (ha)	Total area of transects (m <sup>2</sup> ) (# of transects)	Number of 10m x 10m plots <sup>†</sup>	Number of 2m x 2m plots	Site Walk <sup>‡</sup>
Coastai (Co)	100	2520 (6)	8	24	yes
Central (Ce)	100	2520 (6)	8	24	yes
North (N)	100	2520 (6)	8	24	yes
Ravines (R)	*	2520 (6)	6	18	no

 Table 1.2
 Summary of sampling design in Guánica Commonwealth Forest

<sup>+</sup> Located at the beginning of each transect and additional randomly established individual plots

<sup>+</sup> Presence/absence data only

\* Ravines were not continuous 100 ha, rather six individual ravines were selected to match the sampling design of the other three sites.

visually conspicuous lizards above the litter layer. Lizard surveys were conducted along six randomly located 100 m transects in each of the study sites during the summers of 1997 and 1998 (coastal, central, and north sites were sampled in May - August, 1997; these were resampled and ravines were added to the design in July-August 1998). In the field, the transect locations were determined with the aid of topographic maps, a compass, and landmarks. When site topography allowed, sampling locations were stratified using four aspect categories (N-, S-, E-, and W-facing slopes). The number of transects established within each category was determined by the proportion of the total area comprised by that category at each site. Each 100 m transect ran perpendicular to the slope, and was subdivided into sample plots at 5 m intervals. Lizards were censused in each plot by slowly walking along the fixed-area transect and stopping to identify and count the individuals within a 2.5 m radius (Figure 1.2). Methods used in this study were modifications of the Frye strip census method (Overton 1971) utilized by Reagan (1992). A fixed area transect was used to improve the accuracy of the area estimation, as visually estimating angles or distances to individuals can be imprecise (Heckel and Roughgarden 1979). *Anolis* spp. and *Ameiva* spp. were censused with this method because they are visually conspicuous. The mean number of individuals of each species per m<sup>2</sup> was calculated and used to estimate the density of lizards on a per hectare basis (#/ha); relative abundance was determined by dividing the density of each species by the total density of all species combined.

Each transect plot was carefully surveyed visually until all individuals had been detected (approximately 5 minutes, but duration was highly dependent on structural diversity and density of the vegetation). All transects were surveyed by a single observer to eliminate any observer bias. Locations (i.e., perches) of each lizard were recorded to ensure that no lizards were counted more than once. Each transect was surveyed twice to ensure that all individuals were counted. Adult *Anolis* lizards exhibit remarkable fidelity to their perch and territory (Rand 1964, Philibosian 1975), and a second survey of the transect was made within a few hours (to account for diurnal differences in activity and abundance, Reagan 1986). This method yielded more accurate counts of

individuals in the sampling area than from one survey alone. Juvenile anoles may be more mobile and introduce error into this method, but Andrews and Rand (1983) suggested that the mean distance between captures of juvenile *A. limifrons* at Barro Colorado Island in Panama was 2.9 m, a distance contained within the area of the circular transect sample plot.

Figure 1.2 Transect sampling design





At the beginning of each transect a 10m x 10m plot was established and three 2m x 2m subplots were randomly selected within each. Because the area sampled with 10m x 10m plots was substantially less than that sampled with the transect methods, two additional 10 x 10 m plots were also randomly established within each site, with the exception of the ravines (refer to Table 1.2 for a complete summary of sampling design). Plot sampling accounted for less total

area sampled than transect sampling because of the greater time commitment involved in careful searches of subplots.

Each subplot was thoroughly searched for geckos by examining and clearing away all leaf litter and overturning all rocks to investigate potential refuges within the substrate. After each plot was searched, all litter and rocks were replaced to minimize impacts on substrate habitat. The following data were recorded for each subplot: (1) species identification of each individual, (2) number of individuals of each species, (3) percent rock cover, (4) average litter depth (cm), and (5) canopy cover, visually classified as open, partially open, or closed. Percent rock was visually estimated, and litter depth was determined by taking the mean of three random measurements within each subplot.

In addition to the quantitative transect and plot sampling methods described above, qualitative focal searches (site walks) of study sites sampled in 1997 were made during the summer of 1998 to ensure that the species lists for each site were complete and accurate. A species list was considered complete if all ten dry forest lizard species were present at any given site. Site walks yielded only qualitative presence/absence data, and were conducted only at sites with incomplete species lists. Data from the sites which were resampled in 1998 were used to test for temporal differences in lizard community composition and abundance. All statistical analyses were performed with Systat (version 5.0, Evanston, IL).
#### Results

The survey of the reference lizard community of Guánica Commonwealth Forest yielded 10 species representing three families and four genera (Table 1.3). The distributions of these lizard species were rather patchy, even within a continuous forest. *Anolis cristatellus, A. exsul, A. wetmorei,* and *S. nicholsi* were found at all sites. *Anolis cooki* was found only at the coastal site and a single individual was found in a ravine in close proximity to the coast.

Lizard communities at all sites were consistently dominated by two species, *A. cristatellus* and *S. nicholsi* (Figure 1.3), which represented at least 75% of the lizard community at all sites. The occurrence of the remaining eight species differed among sites. Both *Ameiva* spp. occurred at all sites, but the remaining species were absent from one or more sites (Table 1.3). Differences in proportional community similarity (Table 1.4) reflect differential community composition relative to available microhabitat characteristics. The dominance of *A. cristatellus* and *S. nicholsi* at each site clearly resulted in relatively low diversity (Shannon Index, H') and evenness (H'/H'<sub>max</sub>) estimates (Table 1.5). Lizard community composition did not differ significantly among the four habitat types (sites) (Kruskal-Wallis ANOVA, p=0.454). Additionally, absolute abundance of lizards did not differ in Guánica Forest between 1997 and 1998 (paired *t* test, p=0.908).

Individual species or groups of species showed significant differences among sites. Because of low sample size in all habitats, it was very difficult to determine whether the data were normally distributed. Both parametric and

nonparametric analyses of variance (ANOVA and Kruskal-Wallis ANOVA, respectively) were used to test for statistically significant differences among sites( $\alpha$ =0.05) and results are reported for both methods.



Figure 1.3 Five most predominant species comprising the lizard community in Guánica Forest. Species composition was not significantly different among sites (Kruskal-Wallis ANOVA, p=0.454).

Table 1.3	Lizard species present in study sites within Guanica Forest	ł
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Species	Coastal	Central	North	Ravines	Total
Anolis cristatellus	X	Х	Х	Х	Х
Anolis cooki	X			Х	Х
Anolis stratulus		Х	Х	Х	Х
Anolis pulchellus	X	Х	Х		Х
Anolis poncensis	X	Х			Х
Ameiva exsul	X	Х	Х	Х	Х
Ameiva wetmorei	X	Х	Х	Х	Х
Sphaerodactylus nicholsi	X	Х	Х	Х	Х
Sphaerodactylus roosevelti	X	X	X		Х
Phyllodactylus wirshingi	X		X	X	X
Total species richness	9	8	8	7	10

 Table 1.4
 Proportional Similarity of Sites within Guánica Forest

Site	Coastal	Central	North
Central	0.75		
North	0.59	0.65	
Ravines	0.81	0.71	0.58

Table 1.5Lizard community composition in Guánica Forest. Relative<br/>abundance of the ten species indicates dominance of A. cristatellus<br/>and S. nicholsi. Community diversity and evenness metrics also<br/>reflect this pattern.

Species	<u>Coastal</u>	<u>Central</u>	North	Ravines	Total
Anolis cristatellus	0.23	0.38	0.55	0.27	0.33
Anolis cooki	0.02	0	0	<0.01	<0.01
Anolis stratulus	0	0.01	0.01	0.01	0.01
Anolis pulchellus	<0.01	<0.01	<0.01	0	<0.01
Anolis poncensis	<0.01	<0.01	0	0	<0.01
Ameiva exsul	0.04	0.02	0.01	0.01	0.02
Ameiva wetmorei	0.01	<0.01	<0.01	<0.01	<0.01
Sphaerodactylus nicholsi	0.53	0.42	0.26	0.67	0.53
Sphaerodactylus roosevelti	0.09	0.17	<0.01	0	0.05
Phyllodactylus wirshingi	0.09	0	0.18	0.04	0.07
Diversity (H')	0.59	0.48	0.45	0.35	0.49
Evenness (J')	0.62	0.57	0.53	0.45	0.49

Absolute abundance of lizards sampled along transects and in plots differed significantly among sites within Guánica Forest (Tables 1.6 and 1.7). Individual species also exhibited statistically significant associations with the habitat types represented by the four sites in the forest; abundance of *A. cristatellus, A. cooki,* and *S. nicholsi* all differed significantly among sites. *Anolis cooki* was significantly more abundant at the coastal site while *S. nicholsi* was more abundant in ravines than any other site.

Table 1.6Variables which differed significantly among sites in GuánicaForest, Kruskal-Wallis ANOVA.

Variable	<u>p value</u>
Anolis cristatellus abundance	0.003
Anolis cooki abundance	0.013
Sphaerodactylus nicholsi abundance	0.018
Absolute transect abundance (# Anolis and Ameiva per transect)	0.005
Absolute plot abundance (# geckos per plot)	0.04

Measured habitat variables (% rock cover and litter depth) differed significantly among sites (ANOVA, p<0.001). Percent rock cover in 2 x 2m subplots was arcsine-square root transformed prior to analysis so that the data more closely approached a normal distribution (Zar 1984). Plots sampled in the central site had significantly lower percentage rock cover and a deeper litter layer than the other 3 sites (Figures 1.4 and 1.5, respectively). Density of *S. nicholsi*, which is a species associated with substrate habitats, is significantly correlated with litter depth (Spearman Rank correlation,  $r_s$ =0.227, df=90, p<0.05).

Although slope degree and angle were not measured, there were no significant differences in the composition of the lizard community or abundances of any individual species or groups of species with respect to aspect. Although aspect may be very important in structuring plant communities in the dry forest (Ramjohn *et al., unpubl. data*), it did not appear to play an important role in structuring lizard communities in this region.

among sites. Nu with matching su number of individ	umbers represent m uperscripts differ sig duals per site	ean (SE) densities ( nificantly from one a	# individuals/ha), a another (Tukey's Ht	ind values within a rov SD, p<0.05). n = total
Species	<u>Coastal</u>	Central	North	Ravines
Anolis cristatellus	275 (63) <sup>ab</sup>	461 (119) <sup>6</sup>	651 (64) <sup>ª</sup>	877 (15) <sup>86</sup>
	n=68	n=114	n=161	n=217
Anolis cooki	24 (9) n=6	0- D=0	_0 U=U	4 (4) n=1
Anolis stratulus	0	8 (5)	8 (8)	32 (23)
	0=u	n=2	n=2	n=8
Anolis pulchellus	*	*	*	ο
				<b>0=</b> 0
Anolis poncensis	*	•	0	0
			0=u	0=u
Ameiva exsul	42 (14)	24 (11)	6 (4)	32 (24)
	n=11	n=6 _	n=2	n=8
Ameiva wetmorei	9 (3)	6 (4)	4 (3)	2 (2)
	n=2	n=2	n=1	n=2
Sphaerodactylus nicholsi	625 (343) <sup>ª</sup>	521 (219) <sup>b</sup>	313 (152) <sup>°</sup>	2222 (852) <sup>abc</sup>
	n=6	n=5	n=3	n=16
Sphaerodactylus roosevelti	104 (104)	208 (208)	*	0
	n=1	n=2		0=u
Phyllodactylus wirshingi	104 (104)	0	208 (136)	139 (139)
	n=1	n=0	n=2	n=1
* species that were recorded a	at a site but not duri	ng quantitative sam	pling, precluding de	ensity estimation.

> Densities of lizards in Guánica Forest. One way ANOVA was used to test for differences Table 1.7

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Figure 1.4 Differences in percentage rock cover in  $2 \times 2$  m subplot among sites (mean <u>+</u> SE). Points with matching letters indicate significant pairwise differences (Tukey's HSD, p<0.05).



Figure 1.5 Differences in litter depth in  $2 \times 2 \text{ m}$  subplots among sites (mean  $\pm$  SE). Points with matching letters indicate significant pairwise differences (Tukey's HSD, p<0.05).

#### Discussion

Guánica Forest is the most extensive tract of dry forest in Puerto Rico, and it supports the richest and most complete native dry forest lizard community on the island. This large and continuous forest offers a wide variety of habitat types that accommodate many species' ecological preferences. Of the 13 species that have been recorded in the dry zone of southwestern Puerto Rico (Table 1.1, Rivero 1978, Schwartz and Henderson 1991), 10 were found within Guánica Forest during this study.

The three species that are absent from the reference community were *Sphaerodactylus macrolepis*, *Hemidactylus brooki*, and *Mabuya mabouya*. *Sphaerodactylus macrolepis* has been reported to occur in the more humid ravines within the northern boundaries of the forest (M. Canals Mora, *pers*. *comm*.), but was not encountered during my surveys as a result of its relative rarity and patchy distribution in the most arid parts of the island. *Hemidactylus brooki* is primarily edificarian, and although it is rarely encountered in natural forested situations, this species is very abundant in and around buildings (Schwartz and Henderson 1991, *pers. obs.*). *Mabuya mabouya* is also very rare in Puerto Rico, with fewer than 15 specimens ever collected from the island (Rivero 1978).

Anolis cooki was significantly more abundant at the coastal site than at any other site within Guánica Forest. One individual was recorded from a ravine in close proximity to the coast, but this species was conspicuously absent from inland and upland locations. Previous studies have indicated that *A. cooki* is

restricted to a limited number of discontinuous coastal scrub habitats within 1 km of the coast in southwestern Puerto Rico (Marcellini *et al.* 1985, Jenssen 1990). Over the past two decades, field studies have documented disappearing populations, reductions in the extent of its previous distribution, and microhabitat invasions by *A. cristatellus* where the two species were previously allopatric (Jenssen *et al.* 1984, Marcellini *et al.* 1985, Ortiz 1990). *Anolis cooki* is of special concern for local conservation officials, who take its distribution into consideration in current management and development planning (M. Canals Mora, *pers. comm.*). The implications of competitive interference between these two species is addressed in the third chapter of this thesis.

Although *A. cooki* was present in the coastal regions of Guánica Forest, it was by no means abundant. Ortiz (1990) reported that *A. cooki* was locally abundant where present, but low population densities reported here could be indicative of increased competitive pressure from *A. cristatellus*. Another potential explanation for low *A. cooki* densities is misidentification, which could lead to underestimates of actual abundance. It is very difficult to visually distinguish between these two species in the field, but following the recommendations of Marcellini and Jenssen (1983), accurate species identifications were possible for adult individuals as long as the tail had not been recently autotomized. Williams (1972) was the first to suggest that *A. cooki* was potentially threatened by extinction, and evidence of competitive interference and displacement into less desirable habitats (both attributable to the more abundant and widespread *A. cristatellus*) indicates that *A. cooki* is under intense

ecological pressure and has an uncertain future (Ortiz and Jenssen 1982, Jenssen *et al.* 1984, Marcellini *et al.* 1985, Jenssen 1990).

Another anoline lizard, A. poncensis, is restricted to the arid regions of southwestern Puerto Rico (Schwartz and Henderson 1991). In this study, it was found to occur only at the coastal site in Guánica Forest, but was not encountered often or at all during quantitative transect sampling. This species is a grass-bush ecomorph, and shares much of its habitat with A. pulchellus, a much more widely distributed species which is often found at extremely high population densities in grassy habitats (up to 20,000 individuals/ha, Gorman and Harwood 1977). Where sympatric, A. poncensis often occupies bushes and fenceposts while A. pulchellus seems to prefer the more exposed grassy areas (Rivero 1978). To my knowledge, the potential for competitive interference and displacement between A. poncensis and A. pulchellus has not yet been assessed, although these two species may represent a dynamic situation similar to that discussed above for A. cooki and A. cristatellus. While this was not a question addressed in this study, it is nonetheless a potentially interesting avenue for future research.

The four sites represented different habitat types within a continuous forest; habitat variables differed significantly among these sites. The site in the central portion of Guánica Forest had significantly less rock and deeper leaf litter compared to substrate characteristics of the other three sites. Geckos would be expected to respond to variations in substrate habitat, as they are found primarily in and among substrate debris in all habitat types in the dry forest

region (Rivero 1978). Sphaerodactylus nicholsi abundance showed a significant positive correlation with leaf litter depth, but *S. nicholsi* was surprisingly much more abundant in ravines than at the central site where the litter layer was deepest. While *S. nicholsi* prefers a dry habitat (Thomas and Schwartz 1966), their soil and leaf litter arthropod prey may be more abundant in the more humid substrate habitat of ravines. The distribution and abundance of *S. nicholsi* in Guánica Forest may represent a tradeoff between their preference for a xeric habitat and the need for an abundant and stable food supply. *Sphaerodactylus roosevelti* and *P. wirshingi* abundance would also be expected to vary with substrate characteristics, but their low occurrence in this study precluded the detection of any significant patterns.

Anolis cristatellus abundance also differed significantly among the four sites in Guánica Forest. This species was least abundant at the coastal site, where it is partitioning the habitat and competing with the other trunk-ground ecomorph, *A. cooki*. Since anoline lizards are largely arboreal, the density of individuals may also be influenced by the number and distribution of trees present in the habitat. Although not specifically addressed in this study, the four sites very probably differ in the distribution of trees and tree species composition, leading to differences in *A. cristatellus* density. The ravines contain larger mature trees and more abundant vines and lianas than the surrounding dry forest (Farnsworth 1993), which provide a greater density of perches for these arboreal lizards. Within the reference site, semi-evergreen forest has higher basal area as compared to deciduous and scrub forest types, but stem

density is greatest in deciduous forest (Lugo *et al.* 1978, Castilleja 1991, Ramjohn *et al. unpubl. data*).

The total number of lizards encountered during quantitative sampling varied greatly among species. While patterns potentially exist to explain distribution and abundance of other species within this community, their infrequent occurrence did not allow determination of any noticeable trends. Increasing the number of transects and plots as well as sampling additional habitat types and geographic locations within Guánica Forest would greatly improve the reliability of these results. Altering the survey methods would also lead to more accurate density estimates. Some species (i.e., *Anolis stratulus*) are present in great numbers higher in the canopy than can be accurately detected from ground-level observations, and vertical transect methods yield dramatically higher density estimates than ground transects (Reagan 1992, 1996). The relative abundance and density estimates reported for *A. stratulus* are likely to be underestimates for these reasons.

In conclusion, the reference lizard community of Guánica Forest is comprised of 10 species, some of which are differentially distributed throughout the four different forest habitat types sampled in this study. This continuous forest provides excellent habitat for dry forest lizards, and provides baseline conditions against which data from other areas can be compared. Remaining dry forest habitat in southwestern Puerto Rico exists as fragments of varying size, degree of isolation, and vegetation type; it is important to determine the impact of large scale habitat fragmentation on the distribution and abundance of

dry forest lizards to assess the status and conservation potential of both the species and the forest fragments. The influences of fragment and landscape characteristics will be addressed in the following chapter.

# Chapter 2

# Lizard Community Composition and Structure in a Fragmented Subtropical Dry Forest Landscape

### Introduction

Habitat fragmentation, resulting in reduction of total habitat area and isolation of forest fragments, has been recognized as a major threat to tropical forest ecosystems (Turner 1996, Dale and Pearson 1997, Laurance and Bierregard 1997). Typically, fragments are able to support only a subset of the biological community found in a continuous forest, and the composition and complexity of the fragment community depends on a variety of fragment characteristics including size and degree of isolation from other forest patches (Cutler 1991).

The theory of island biogeography (MacArthur and Wilson 1967) was developed to describe continental mainlands and true islands surrounded by ocean; it has since been adopted and tested for habitat 'islands' (fragments) surrounded by an 'ocean' of alternative land uses (e.g., Harris 1984, Bierregard and Dale 1996). The theory of island biogeography predicts that the rates of immigration and extinction in a habitat 'island' (fragment) are regulated by the size of the island and the distance to the nearest 'mainland' source of colonizers (MacArthur and Wilson 1967, Quinn and Harrison 1988). Understanding the consequences of habitat fragmentation on fragile tropical forest ecosystems will aid in the preservation and conservation of biodiversity worldwide. Turner (1996) emphasized that determining the long-term viability of fragments and their

extinction-colonization equilibria will be the greatest contribution to the development of feasible and effective conservation strategies.

Globally, tropical and subtropical dry forests have been more severely impacted by human activities than wet tropical forests (Tosi and Voertman 1964). The climate, soils, and topography of dry forest regions make them very attractive for settlement and conversion to agriculture. Most of the dry forest habitat in Puerto Rico and elsewhere has been extensively disturbed or completely eliminated as a result of human activities (Murphy *et al.* 1995). In southwestern Puerto Rico, most dry forest habitat exists as islands of remnant and recovering forests sparsely scattered throughout a highly human-dominated and disturbed landscape.

These trends of disturbance and deforestation are characteristic of the entire island; 95% of the island was forested during pre-colonial times, but by 1948 only 5% of the forest remained, mostly in steep and topographically inaccessible areas (Birdsey and Weaver 1982). Puerto Rico has since experienced a shift in its economy from a predominantly agricultural to an industrialized society with greater emphasis on manufactured products (Morales-Carrion 1983, Dietz 1986). This shift has reduced anthropogenic impacts on the remaining forested areas, and by 1985 the forested area had increased to 34% (Birdsey and Weaver 1987). In the vicinity of Guánica Forest, the amount of forested land has steadily increased since 1936 (Lugo *et al.* 1996).

Anthropogenic disturbance of forested landscapes has long-term effects, both in duration and environmental consequences. It is imperative that tracts of recovering as well as remnant forest be preserved; structure and diversity of secondary forests are able to support rich ecological communities, although the species composition of undisturbed dry forests may not be reached for centuries, if at all (Aide *et al.* 1996, Thomlinson *et al.* 1996, Rivera and Aide 1998).

The remnant and recovering fragments of dry forest in southwestern Puerto Rico are scattered throughout a landscape dominated by agriculture and urban development. Much of the native biota of this region is restricted to these isolated fragments, and understanding how certain species or groups of species respond to habitat fragmentation will greatly contribute to the management and conservation of remaining dry forest patches. Vertebrates (especially birds and mammals) have been a popular group of study organisms for fragmentation research (Turner 1996, Bierregard *et al.* 1997). Previous studies indicated that species which have large area requirements, poor dispersal capabilities, limited abilities to cope with disturbance, or low population densities are particularly susceptible to local extinction in the face of habitat fragmentation (Turner 1996, Laurance *et al.* 1997).

The dry forest zone of southwestern Puerto Rico is a critical habitat area for many species of vertebrates. In this region, lizards are conspicuous and abundant as well as ecologically important organisms in terms of community structure and trophic interactions (e.g., Lewis 1989). Habitat fragmentation has the potential to negatively affect the lizards via reduced habitat suitability and

availability resulting from altered microclimatic regimes, or limited dispersal opportunities resulting from isolation (Saunders *et al.* 1991). Previous studies concerning the effects of habitat fragmentation on lizard communities found that the species composition of fragmented habitats was biased towards generalists and more related to site ecology than degree of isolation from other fragments (Kitchener *et al.* 1980, Kitchener and How 1982, Sarre *et al.* 1995). Species found in small woodland remnants where habitat alteration had resulted in reduced tree density, understory shrub cover, and litter were subsets of those which occurred there prior to fragmentation (Smith *et al.* 1996). In other anthropogenically influenced habitats, the most disturbed areas supported the least diverse lizard communities (Lenart *et al.* 1997).

Certain ecological characteristics may allow some species to persist in disturbed habitats, at least in the short term. The majority of dry forest lizard species in southwestern Puerto Rico can be classified as ecological generalists (Schwartz and Henderson 1991), which may confer an advantage in this fragmented landscape. In areas where forest disturbance and degradation are a continual threat to the native biota, habitat specialists (with narrow ecological preferences or restricted to areas of 'natural' vegetation) do not persist as well as generalists that can tolerate a wider range of habitat conditions, including more degraded habitats (Kitchener 1982, Kitchener and How 1982, Sarre *et al.* 1995). Lizards have been found to be relatively resilient to habitat fragmentation. For example, lizards have not suffered any extinctions and have persisted even in small remnants in the Australian wheatbelt (Kitchener *et al.* 

1980). Overall, generalist species have less specific habitat requirements and are also better able to migrate between fragments, despite having to cross less hospitable habitat that most often surrounds isolated forest remnants.

Assessing the response of the dry forest lizard community is a first step in gaining a better understanding of how faunal assemblages respond to landscape-level habitat fragmentation phenomena. Provided that the trend of forest recovery continues in Puerto Rico, native lizards will likely be able to colonize and establish populations in additional patches of recovering forest as they become available. The objectives of this study were to: (1) evaluate the response of the lizard community to fragment and landscape characteristics in the dry forest zone, (2) compare lizard communities in fragments of varying sizes to the reference community of Guánica Commonwealth Forest, (3) assess the ability of fragments to support representative lizard communities, and (4) evaluate conservation potential and management opportunities for forest fragments in this region.

#### **Materials and Methods**

#### The Study Region

The southwestern region of Puerto Rico contains the majority of the dry forest habitat on the island, although this habitat exists primarily as isolated patches interspersed throughout a landscape dominated by agriculture (pasture) and urban/residential areas. The dry forest life zone (*sensu* Holdridge 1967) of southwestern Puerto Rico is typified by low rainfall (600-1100 mm annually), warm temperatures (mean annual biotemperature >17° C), and a ratio of potential evapotranspiration to precipitation (PET/P) which exceeds unity (Ewel and Whitmore 1973). Study sites were located throughout the dry forest life zone (approximately 18° N and 66° 35' W to 66° 12' W). Guánica Commonwealth Forest, a continuous and relatively undisturbed dry forest, is located in the approximate geographic center of this region (Figure 2.1). It encompasses roughly 4000 ha and represents one of the best remaining examples of subtropical dry forest in the world (Murphy and Lugo 1990), making it a suitable reference site for this study. Lizard habitats and species composition of Guánica Forest were discussed in the previous chapter.

#### Dry Forest Fragment Study Sites

Previous studies by Ramjohn *et al.* (*unpubl. data*) have identified more than 300 fragments (open and closed forest) representing both remnant and recovering patches of dry forest habitat in southwestern Puerto Rico; the vegetation has been surveyed and studied extensively in 41 of these fragments (Ramjohn *et al. unpubl. data*). To assess the impact of habitat fragmentation on the native dry forest lizard communities, a subset of these fragments was selected for study. The twelve fragments chosen for lizard community sampling ranged in area from 0.006 ha (a single isolated tree and surrounding shrubs) to >800 ha (Figure 2.1). Four fragments were selected in each of three size categories: small (<1 ha), medium (1-10 ha), and large (>10 ha). The 12





fragments contained a range of habitat conditions and vegetative associations, including both coastal scrub and upland deciduous forests. These fragments differed in a variety of characteristics, providing the basis for comparisons among fragments and between fragments and the reference site, Guánica Forest. Sites within Guánica Forest were chosen to match the characteristics of the fragments (see Chapter 1).

The 12 forest fragments varied in size, shape, topographic location, vegetation composition and structure, degree of past and present disturbance, as well as the type of substrate. For instance, one fragment was located in close proximity to the coast and situated on limestone outcroppings almost completely lacking soil (Site 16, Figure 2.1). Other fragments were located on abandoned pastures and had more well-developed soils (Sites 30, 36, 40; Figure 2.1). In addition, some sites have been under extreme pressure from human activities for prolonged periods of time (Sites 5, 10, 16; Figure 2.1) while others have remained virtually untouched following their isolation from adjacent forests (Site 4, Figure 2.1). Most of the fragments were located in relatively inaccessible areas such as ravines, steep slopes, and hilltops that were not suitable for agriculture or urban development. Although such a large number of factors could not be controlled in this study, the range of environmental conditions present in the fragments allowed comparisons valuable for generating additional hypotheses about the complex effects of fragmentation on ecological communities.

#### Fragment and Landscape Analysis

Aerial photographs (1:20,000) taken in February 1998 were obtained from the Office of Photogrammetry at the Puerto Rico Highway and Transportation Authority. Photointerpretation and delineation of polygons to determine the distribution of land cover types surrounding each of the 12 fragments was the first step in constructing a geographic information system (GIS) database. Land use and cover types were delineated using the classification scheme of Lugo et al. (1996). Photointerpreted polygons were digitized into ARC/INFO (ESRI, Redlands, CA) and topology was constructed. The coverages were then georeferenced and transformed into Universal Transverse Mercator (UTM) grid coordinates (zone 19). Adjacent coverages were aligned, edgematched, and then joined into a final useable coverage of the 12 fragment study sites, Guánica Forest, and surrounding land use types for further analyses. Additional spatial data (hypsography, road networks) were provided by the International Institute of Tropical Forestry (IITF, Rio Piedras, Puerto Rico) for the GIS analysis.

To evaluate spatial patterns of lizard species richness and abundance, several fragment and landscape characteristics were determined from the GIS database. Fragment characteristics investigated in this study included area, perimeter, and compactness (Table 2.1). Compactness ( $K_1 = 2\sqrt{\pi area/perimeter}$ ; Bosch 1978, Davis 1986) describes the shape of a fragment and provides an indication of the amount of edge habitat; edge effects can be very important in structuring some communities (Saunders *et al.* 1991). Compact forms are

Site ID <sup>†</sup>	Area	Perimeter	Patch	Distance to nearest	Primary
	(ha)	(m)	Compactness	Forest Fragment (m)	Aspect
Small:			•		
40	0.01	27	0.99	392	S
36	0.06	93	0.90	110	S
30	0.26	227	0.79	364	E
27	0.69	409	0.72	10	W
Medium:					
28	2.0	836	0.60	8	Е
13	3.1	920	0.68	20	Flat
16	3.4	8320	0.79	278	E + S
10	6.4	1723	0.52	15	N
Large:					
7	34	3517	0.58	10	All
5	97	5258	0.66	30	All
4	137	7563	0.55	10	All
2	854	23277	0.45	20	All
Ref. Site <sup>‡</sup>	3725	47885	0.45		All

Table 2.1Characteristics of forest fragments and reference site (Guánica<br/>Forest) selected as study sites

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<sup>†</sup> from Ramjohn *et al.* (*unpubl. data*)

<sup>+</sup> area and perimeter measurements are for the entire tract of continuous forest in which the eastern portion of Guánica Forest lies. effective in conserving resources, while convoluted forms have enhanced interface and interaction with the surrounding landscape (Portmann 1967, Harris and Kangas 1979).

To investigate the isolation of fragments and their relationships with the surrounding landscape, ARC/INFO was used to create a 1000 m buffer around each of the study sites (Appendix B, Figure B.1). The 1000m buffer was used to characterize the fragment in a landscape context. Buffer coverages were imported into ArcView 3.1 (ESRI, Redlands, CA), and the following landscape variables were measured within the buffer zone: (1) number of closed canopy forest fragments, (2) distance to nearest closed canopy fragment, (3) percentage of closed canopy forest, (4) percentage of open canopy forest, (5) percentage of total forest, (6) percentage of agriculture, and (7) percentage of urban land use.

The land use in the area directly adjacent to the perimeter of each study site may affect the lizards by inhibiting patch-to-patch dispersal. The influence of adjacent land use was evaluated by calculating the percentage of fragment perimeter comprised by each major land use category (open forest, closed forest, agriculture, and urban). If a fragment was separated from other closed canopy forest only by a road, it was considered adjacent. Other types of land use and cover (i.e., water, wetland, barren land) were directly adjacent to very few sites and were not included in the analysis.

# Lizard Community Sampling

Quantitative surveys of the lizard communities in the 12 fragments and reference sites were conducted in the summers of 1997 (May-July) and 1998 (July-August). Nine fragments were sampled in 1997; in 1998, five of these were resampled and three additional fragments were added to the study. Due to differences in the biology and activity patterns of the 10 commonly encountered dry forest lizard species, two distinct survey strategies were required to obtain accurate estimates of diversity and abundance (described in Chapter 1). Abundant and visually conspicuous arboreal and free-ranging lizards (Anolis spp. and Ameiva spp.) were censused along 100 m transects of fixed area. Three members of the genera Sphaerodactylus and Phyllodactylus are primarily nocturnal and/or fossorial, making it unrealistic for transect surveys to obtain accurate diversity and abundance measures. These species were sampled by exhaustively searching randomly selected 2 x 2m subplots nested within 10 x 10m plots located at the beginning of each transect (see previous chapter for a detailed description of transect and plot sampling).

The number of transects and plots was scaled to the area of each site (Table 2.2) and represented considerations of adequate sampling efficiency coupled with time constraints. When site area and topography allowed (i.e., in large fragments), selection of sampling locations was stratified using four aspect categories (N-, S-, E-, and W-facing slopes). Sampling effort in each of these categories was determined by the proportion of total fragment area comprised by each aspect category.

In addition to the quantitative transect and plot sampling methods described above, qualitative focal searches (site walks) of study sites sampled in 1997 were made during the summer of 1998 to make certain that the species lists for each site were complete and accurate. Some of the large fragments encompassed areas that were too large to make quantitative sampling of the entire site feasible. A species list was compiled for each site and considered complete if all ten species found in the reference site were present in any given fragment. Site walks yielded only qualitative presence/absence data, and were conducted only at sites with incomplete species lists. Data from the five sites sampled in both 1997 and 1998 were used to test for temporal differences in lizard community composition and abundance. Sampling efficiency was assessed for each fragment, and species-area curves are provided in Appendix B.

Site ID # <sup>†</sup>	Area (ha)	Total Area of Transects (m <sup>2</sup> ) (No. of transects)	No. of 10m x 10m plots <sup>‡</sup>	No. of 2m x 2m plots	Site Walk*
Small	1				
40 <sup>§</sup>	0.01	entire fragment	-	4	Νο
		searched			
36 <sup>§</sup>	0.06	236 (2)	-	4	No
30 <sup>§</sup>	0.26	511 (2)	-	5	Yes
27	0.69	825 (2)	4	12	Νο
Mediu	J <b>m</b>				
28	2.0	825 (2)	4	12	Yes
13	3.1	825 (2)	4	12	No
16	3.4	825 (2)	4	12	Yes
10	6.4	825 (2)	4	12	Yes
Large	<del>)</del>				
7	34	2520 (6)	8	24	Yes
5	97	3360 (8)	12	36	Yes
4	137	3360 (8)	12	36	Yes
2	854	3360 (8)	12	36	Yes

# Table 2.2 Summary of sampling design in forest fragment study sites

<sup>†</sup> From Ramjohn *et al.* (*unpubl. data*).

<sup>‡</sup> Located at the beginning of each transect and additional randomly located plots (see text).

\* Presence/absence data only.

<sup>S</sup> Sites were not large enough to establish complete 100 m transects; instead the entire fragment was searched (site 40) or transects were established along the long and short axes of the fragment (sites 36 and 30).

#### Statistical Analyses

Sites were compared using a one-way analysis of variance (ANOVA) to determine if the three size classes of fragments differed in lizard community composition (both species richness and individual species abundances) from the reference site. As a result of low sample size, it was difficult to determine whether the data were normally distributed. Both parametric and nonparametric methods were used (ANOVA and Kruskal-Wallis ANOVA, respectively), and results are reported for both analyses.

Pearson correlation analysis was used to investigate associations of lizard diversity and abundance with fragment and landscape characteristics. Additionally, potential relationships between lizard variables and termite or plant species richness were also investigated with correlation analysis. Data were transformed to better approximate the normal distribution (Zar 1984); fragment area was log transformed, and percentage data (adjacent and surrounding land use) were arcsine transformed. Multiple regression models were used to identify relationships between lizard variables (species richness and individual abundances) and combinations of fragment and landscape variables. All univariate statistical analyses were performed using Systat (version 5.0, Evanston, IL).

Principal components analysis (PCA) was used to summarize the variation in the fragment and landscape variables (Morrison 1990); a reduced number of independent variables (principal components) were then used to investigate patterns among fragment and landscape characteristics of the 12

fragment study sites. Since variables were not commensurable and a single variable (fragment perimeter) dominated the covariance matrix, PCA was performed using the correlation matrix (Joliffe 1986).

Correspondence analysis (Greenacre 1993) was performed using lizard densities (#/ha) at 12 fragments and four sites within Guánica Forest to reveal possible patterns of associations and differences among species and sites that may be ordered along an underlying environmental gradient. Lizard densities were used instead of raw counts for two reasons: (1) to ameliorate differences in sampling methods (transect vs. plot), and (2) to weight the fragments in proportion to their total frequency of lizards per unit surface area (Greenacre and Vrba 1984). All multivariate statistical analyses were performed using SAS (version 6.12, Cary, NC).

# Results

The survey of lizard communities in dry forest fragments in southwestern Puerto Rico revealed a total of 10 species representing three families and four genera (Table 2.3); the same species were also encountered in the reference site (see Chapter 1, Table 1.2). Three of these species (*A. cooki, A. poncensis,* and *S. roosevelti*) were not found in the smallest fragments (<1 ha). All other species were represented in at least one fragment of each size class. Occurrence of lizard species in the 12 forest fragments and the reference site (Guánica Forest). X = species detected by quantitative transect and plot sampling methods. P = present, detected during a qualitative search (site walk). Table 2.3

		1 V	a B			1-10	na La			10	a			Ref. S	ite <sup>†</sup>			# sites
Species	<del>6</del>	36	ဓ	27	28	13	16	10	2	2	4	2	ပိ	e C	z	۲	⊢	present
<sup>-</sup> amily Polychridae																		
Anolis cristatellus		×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	15
A. cooki							×					×	×			×	×	ო
A. stratulus			×	×	٩		×			×	×	×		×	×	×	×	10
A. pulchellus			٩	×	٩					×	×	×	٩.	٩	م		×	ი
A. poncensis								٩		×	×	×	×	۵.			×	S
<sup>-</sup> amily Teiidae																		
Ameiva exsul		×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	15
A. wetmorei				×	×		×			×	×	×	×	×	×	×	×	10
<sup>-</sup> amily Gekkonidae																		
Sphaerodactylus nicholsi			×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	14
S. roosevelti					×		٩				٩	×	×	×	۵.		×	9
<sup>D</sup> hyllodactylus wirshingi			٩	×	×	×	×		×	٩	٩	٩	×		×	×	×	12
Site species richness	0	2	9	7	ω	4	ω	4	4	œ	ი	10	თ	œ	œ	2	10	

<sup>†</sup> Sites within Guánica Forest, the reference site. Co = coastal scrub, Ce = central, deciduous forest with south-facing aspect, N = north, deciduous forest with north-facing aspect, R = ravines, T = cumulative total of all sites within Guánica Forest.

#### Fragment and Landscape Characteristics

Lizard species richness and abundance of each species did not differ significantly among fragment size classes or between fragments and the reference site (ANOVA, p>0.05; Kruskal-Wallis ANOVA, p>0.05; see Appendix B, Tables B.1-3 for species densities in small, medium, and large fragments, respectively), although there appeared to be a trend of increasing species richness with increasing fragment area (Figure 2.2). Indeed, there were significant correlations between species richness and fragment characteristics (Table 2.4). Only 4 of 33 correlations (~12%) with fragment characteristics were significant (Table 2.4), however, it should be noted that fragment area and compactness are very strongly correlated (r = -0.886, p < 0.001), and perhaps should be treated as a single variable.

Land use immediately adjacent to fragments did not appear to greatly affect lizard community composition; only four of 55 correlations (~7%) were significant (Table 2.5). Multiple regression analyses using backward selection (p<0.05) yielded no models for species richness and density of the most abundant species within each family (*A. cristatellus, A. exsul,* and *S. nicholsi*) that contained more than one significant fragment or landscape predictor variable. The number of lizard species in forest fragment study sites was significantly correlated with the number of termite and tree species, and both of these variables were significantly correlated with fragment area (Table 2.6). Additionally, certain individual lizard species were significantly correlated with

variables describing vegetation structure and diversity and number of termite species in each fragment (Table 2.6).



Figure 2.2 Number of lizard species (mean  $\pm$  SE) for fragment size classes and reference site. Differences were not significantly different (ANOVA, p=0.102; Kruskal-Wallis ANOVA, p=0.095).

Table 2.4Pearson correlation coefficients (r) of species abundance<br/>(# individuals/ha) and species richness with fragment<br/>characteristics. \*p<0.05, \*\*p<0.01</th>

Lizard Variables	Area	Perimeter	Compactness
Anolis cristatellus	0.312	0.039	-0.561*
Anolis cooki	0.099	0.010	0.069
Anolis stratulus	0.035	-0.108	0.146
Anolis pulchellus	0.021	-0.078	-0.014
Anolis poncensis	0.572*	0.401	-0.486
Ameiva exsul	-0.130	-0.246	-0.007
Ameiva wetmorei	-0.047	-0.094	-0.133
Sphaerodactylus nicholsi	0.134	-0.058	-0.155
Sphaerodactylus roosevelti	0.314	0.368	-0.458
Phyllodactylus wirshingi	-0.082	-0.147	0.081
Number of lizard species	0.756**	0.565	-0.654*

Table 2.5Pearson correlation coefficients (r) of species abundance<br/>(# individuals/ha) and species richness with immediately<br/>adjacent land use types around fragment perimeter<br/>\*p<0.05, \*\*p<0.01</th>

Lizard		Adja	cent Land U	se	
Variables	<b>Open Forest</b>	<b>Closed Forest</b>	<b>Total Forest</b>	Agriculture	Urban
A. cristatellus	0.377	0.509	0.552	-0.538	0.242
A. cooki	-0.302	-0.239	-0.317	-0.269	0.266
A. stratulus	-0.213	-0.099	-0.205	0.011	0.168
A. pulchellus	0.544	0.712**	0.768**	-0.395	-0.102
A. poncensis	0.060	0.201	0.045	-0.146	0.249
A. exsul	-0.320	-0.372	-0.343	0.366	0.181
A. wetmorei	0.515	0.328	0.581*	-0.476	-0.296
S. nicholsi	0.140	-0.155	0.048	0.120	0.010
S. roosevelti	0.206	-0.183	0.024	-0.240	-0.211
P. wirshingi	0.371	0.248	0.431	-0.485	-0.186
Species richness	0.288	0.266	0.276	-0.650*	0.348

Lizard	# Plant <sup>†</sup>	# Tree <sup>†</sup>	# Stems	# Stems	# Stems	Basal	#
Variables	Species	Species	≥ 1cm DBH <sup>†</sup>	<u>≥</u> 2.5cm DBH <sup>†</sup>	≥ 5cm DBH <sup>†</sup>	<b>Area</b> (m²/ha) <sup>†</sup>	Termite <sup>‡</sup> Species
A. cristatellus	0.346	0.249	0.242	0.447	0.193	0.232	0.505
A. cooki	-0.105	-0.029	-0.075	-0.310	-0.270	-0.356	-0.058
A. stratulus	0.167	0.245	-0.219	-0.373	-0.286	-0.044	0.273
A. pulchellus	0.088	0.059	0.333	0.624*	0.781**	0.744**	0.205
A. poncensis	0.523	0.634*	0.368	0.254	-0.055	0.068	0.248
A. exsul	0.273	0.154	-0.041	-0.258	-0.370	0.022	0.133
A. wetmorei	-0.158	-0.182	0.284	0.693*	0.691*	0.386	0.331
S. nicholsi	0.390	0.301	0.247	0.153	0.009	0.272	0.676*
S. roosevelti	-0.020	0.044	0.264	0.390	0.081	-0.146	0.274
P. wirshingi	-0.326	-0.359	0.137	0.266	0.356	0.036	0.079
Species	0.539	0.621*	0.408	0.322	-0.023	0.070	0.701*
richness							

Table 2.6Pearson correlation coefficients (r) describing associations<br/>between lizard, termite, and vegetation variables.<br/>\* p<0.05, \*\*p<0.01</th>

<sup>†</sup>Ramjohn *et al. (unpubl. data)* 

<sup>+</sup> J. Genet (*unpubl. data*)

# Minimum Fragment Area

The minimum fragment area required to support 50% and 75% of the

lizard community of Guánica Forest was 0.26 ha (site 30) and 2.0 ha (site 28),

respectively (Figure 2.3). The threshold of fragment area required to support

both 50% and 75% of the reference lizard community was 97 ha. When

fragments sampled only in 1998 (sites 7, 10, and 13) were omitted, the threshold

to support 50% and 75% of the reference lizard community was reduced to 0.26

ha and 2.0 ha, respectively (Figure 2.4).



Figure 2.3 Relationship between fragment area (log transformed for analysis and graphical display) and proportion of reference lizard community supported by fragments.



Figure 2.4 Proportion of reference lizard community supported by fragments. Sites 7, 10, and 13 (sampled only in 1998) omitted from display.

# Principal Components Analysis

Principal components analysis (PCA) of fragment and landscape characteristics was performed twice, once with all fragment and landscape variables, and subsequently without the variables describing the percentage of land in the 1000 m buffer comprised of forest, agriculture, and urban land use. PCA with the three buffer landscape variables indicated that they were correlated with and very similar to the land use directly adjacent to the fragments; interpretations were therefore based on the PCA of the reduced data set containing seven variables (fragment area, fragment perimeter, nearest fragment distance, number of fragments in 1000 m buffer, and percentage of land adjacent to fragment perimeter comprised of forest, agriculture, and urban development). This analysis reduced the dimensionality of the data set to three principal components which accounted for >88% of the total variation (Table 2.7, Figure 2.5).

The first principal component separated out the fragments which were most isolated (in terms of distance to the nearest forest fragment and number of neighboring closed canopy forest fragments) and surrounded by agriculture (sites 30, 36, and 40) from all other sites (Figure 2.5). Surrounding land use was also important for the interpretation of the second principal component; fragments that were less isolated (sites 13, 27, and 28) were distinguished from those fragments that are embedded in more urban areas (sites 10 and 16). The third principal component contrasted those sites which had the greatest perimeter, were surrounded predominantly by agricultural land yet not very

isolated from other forest fragments with sites surrounded by forest and urban

land use.

Table 2.7Eigenvalues and eigenvectors from PCA of fragment and<br/>landscape characteristics. Additional principal components<br/>accounted for  $\leq 5\%$  of the variation in the data set.

	PC 1	PC 2	PC 3
Eigenvalue	3.45	1.46	1.27
% Variation	49.24	20.79	18.19
Cumulative % Variation	49.24	70.03	88.22
Eigenvectors:			
Fragment Area	0.47	0.28	0.10
Fragment Perimeter	0.34	0.17	0.64
Nearest Fragment Distance	-0.46	0.19	0.15
# Fragments in 1 km Buffer	0.32	-0.39	0.47
% Adjacent Forest	0.32	-0.53	-0.33
% Adjacent Agriculture	-0.42	-0.04	0.43
% Adjacent Urban Land	0.27	0.65	-0.21


Figure 2.5 PCA results of fragment ordination, see text for fragment identification numbers. (A) PC 1 vs. PC 2, (B) PC 1 vs. PC 3 Eigenvectors scaled by a factor of 5 for plotting purposes.

# Correspondence Analysis

Correspondence analysis (CA) of the ten dry forest lizard species in 12 fragments and four sites within Guánica Forest produced an ordination in which ~93% of the total inertia was explained in the first four dimensions (Appendix B, Figure B.5, Tables B.4-6). From this analysis, *A. cooki* was identified as a rare species which was highly influential on the analysis; this species was then omitted and CA was performed again to identify patterns among the nine more common species. More than 94% of the total inertia was accounted for in the first four dimensions (Table 2.8, Figure 2.6). Sites 30, 16, 36, and 16 contributed the most to the row ordinations of the first four dimensions, respectively, while *S. nicholsi, P. wirshingi, S. roosevelti,* and *A. exsul* had the greatest respective contributions to the column ordinations (Table 2.9). All sites are represented relatively well in these four dimensions, but *A. stratulus, A. pulchellus, A. poncensis,* and *A. wetmorei* are very poorly depicted (Table 2.10).

Table 2.8Correspondence analysis of lizard abundance in dry forest<br/>fragments (A. cooki omitted from analysis). Total inertia was 0.50;<br/>each additional dimension explained <1% of the total variability.</th>

Dimensio n	Principal Inertia	% Total Inertia	Cum. % Total Inertia
1	0.20	39.24	39.24
2	0.14	27.79	67.03
3	0.11	21.25	88.28
4	0.03	6.44	94.72
5	0.01	2.65	97.37
6	<0.01	1.64	99.01

Table 2.9Partial contributions of row (sites) and column (species) points<br/>to inertia of first four CA dimensions. Anolis cooki omitted from<br/>analysis.

	<b>Dimension 1</b>	<b>Dimension 2</b>	Dimension 3	Dimension 4
Site 36	0.11	0.14	0.26	0.08
Site 30	0.29	<0.01	<0.01	0.05
Site 27	0.02	0.13	<0.01	0.13
Site 28	0.06	<0.01	0.14	<0.01
Site 13	0.10	0.04	0.02	0.01
Site 16	0.04	0.36	<0.01	0.25
Site 10	0.04	0.09	0.15	<0.01
Site 7	0.11	<0.01	0.02	0.10
Site 5	0.03	<0.01	<0.01	0.09
Site 4	0.01	0.01	0.01	0.14
Site 2	0.05	0.09	0.09	<0.01
GF coastal	<0.01	<0.01	0.01	0.06
GF central	0.02	0.09	0.24	0.01
GF north	0.08	0.04	0.01	0.04
GF ravines	0.04	<0.01	<0.01	0.04
A. cristatellus	0.32	0.05	0.06	0.19
A. stratulus	0.01	0.01	<0.01	<0.01
A. pulchellus	<0.01	0.01	<0.01	0.15
A. poncensis	<0.01	<0.01	<0.01	0.01
A. exsul	0.01	0.15	0.25	0.42
A. wetmorei	0.01	<0.01	0.02	0.02
S. nicholsi	0.42	<0.01	0.01	<0.01
S. roosevelti	0.08	0.13	0.65	0.08
P. wirshingi	0.15	0.64	<0.01	0.13

Table 2.10Squared cosines of row (sites) and column (species) points<br/>for the first four CA dimensions. Cumulative total represent the<br/>total quality of the display of each site or species in four-<br/>dimensional space. Anolis cooki omitted from analysis.

	Dim. 1	Dim. 2	Dim. 3	Dim. 4	Cumulative
Site 36	0.30	0.27	0.38	0.03	0.98
Site 30	0.97	<0.01	<0.01	0.02	0.99
Site 27	0.11	0.55	<0.01	0.13	0.79
Site 28	0.41	0.01	0.51	<0.01	0.93
Site 13	0.67	0.18	0.07	0.01	0.93
Site 16	0.11	0.75	<0.01	0.12	0.98
Site 10	0.22	0.35	0.44	<0.01	1.0
Site 7	0.76	0.01	0.06	0.11	0.94
Site 5	0.51	0.01	0.01	0.26	0.79
Site 4	0.23	0.14	0.09	0.48	0.94
Site 2	0.29	0.35	0.27	<0.01	0.91
GF coastal	0.04	0.01	0.71	0.21	0.97
GF central	0.10	0.29	0.58	0.01	0.98
GF north	0.61	0.21	0.05	0.05	0.92
GF ravines	0.68	0.05	<0.01	0.11	0.84
A. cristatellus	0.76	0.09	0.07	0.07	0.99
A. stratulus	0.12	0.18	<0.01	<0.01	0.30
A. pulchellus	0.01	0.07	<0.01	0.34	0.42
A. poncensis	0.03	0.11	0.08	0.05	0.27
A. exsul	0.03	0.33	0.41	0.21	0.98
A. wetmorei	0.18	0.04	0.23	0.06	0.51
S. nicholsi	0.97	0.01	0.02	<0.01	1.0
S. roosevelti	0.15	0.17	0.66	0.03	1.0
P. wirshingi	0.24	0.72	<0.01	0.03	0.99





### Discussion

### Lizard Community Response to Fragmentation

Dry forest lizards of southwestern Puerto Rico appeared to be relatively resilient to the effects of habitat fragmentation, including reductions in available habitat and isolation from other forested areas. Species richness and composition of lizard communities did not significantly differ among fragments of varying sizes and the continuous forest reference site, although there was a definite trend of increasing species richness with increasing fragment area (Figure 2.2). *Anolis cristatellus* and *S. nicholsi* were the dominant species in Guánica Forest, comprising more than 75% of the lizard community. These two species also comprised the majority of the lizard community in all fragment study sites (Appendix B, Tables B.1-3).

A number of potential mechanisms may explain why lizard communities were not found to be as susceptible to the consequences of habitat fragmentation as other vertebrate groups such as birds and large carnivorous mammals (Soulé *et al.* 1979, Schaller and Crawshaw 1980, Newmark 1987, Laurance and Bierregard 1997). Lizards may be better equipped to cope with altered microhabitats than other vertebrates (e.g., mammals and birds) as a result of comparatively lower energy and space requirements (Turner *et al.* 1969, Nagy 1987). Forest fragments, especially if very small, are likely to have reduced resources compared to large expanses of forested habitat. Lizards are able to maintain higher populations in fragmented habitats than animals with greater energy and space requirements (Smith *et al.* 1996).

Fahrig and Merriam (1994) proposed that spatial structure of the landscape must be considered in management programs if the goal is species conservation. The potential importance of biogeographic and habitat variables for species persistence in small fragments has been considered in many previous studies (i.e., Lord and Norton 1990, Cutler 1991, Smith *et al.* 1996). The landscape of southwestern Puerto Rico has undergone many changes over the past century, and organisms have been forced to tolerate and adapt to the resulting landscape structure. In general, the distance to the nearest fragment and the number of fragments within 1 km of each study site were independent of urban land use directly adjacent to the fragment. Percentage of forest directly adjacent to the fragments and the number of nearby closed canopy fragments were unrelated to fragment area and perimeter; however, as perimeter increased, more forest fragments were located within the buffer (a function of greater area contained in the buffer region of a larger fragment).

Very few of the correlations between lizard abundance or species richness and fragment and landscape variables were significant (Tables 2.4, 2.5). Lizard species richness was significantly correlated with fragment area (Table 2.4), as were termite and tree species richness (J. Genet, I. Ramjohn, *pers. comm.*). Fragment area most likely explains these observed associations between species richness of lizard, termite, and plant communities. Lizards in the Australian wheatbelt region are also associated with available habitat area (Kitchener *et al.* 1980, Smith *et al.* 1996), although this relationship is perhaps confounded with the larger body size and area requirements of some species in

these studies. Anolis pulchellus was somewhat suprisingly significantly positively correlated with the number of stems  $\geq 2.5$  cm DBH and basal area; this grass-bush ecomorph was expected to be negatively correlated with stem density of larger trees, if associated with any woody vegetation variables at all. However, stems  $\geq 2.5$  cm DBH are predominantly comprised of stems skewed towards the smallest measurements; dry forests of southwestern Puerto Rico are typified by a high density of small stems (Murphy and Lugo 1986a, Ramjohn *et al. unpubl. data*). On the other hand, *A. stratulus* abundance was expected to be positively correlated with stem density (especially  $\geq 5$  cm DBH) and basal area, since this trunk-crown ecomorph prefers perching higher on larger mature trees (Rivero 1978, Schwartz and Henderson 1991, Reagan 1986, 1992).

Distance between fragments (isolation) has implications for dispersal abilities of some lizards, and previous studies have found that species richness has a significant negative relationship with isolation, indicating that dispersal and colonization of other fragments is a limited phenomenon in some ecosystems (Sarre 1995, Sarre *et al.* 1995, Smith *et al.* 1996). Only *A. cristatellus* was significantly (negatively) correlated with fragment isolation, which implies that its dispersal and colonizing ability is restricted, while other dry forest lizard species may not be so hindered. This was a somewhat surprising result, given that this species is the most widespread and common lizard throughout Puerto Rico, and is observed in many types of habitats, whether forested, agricultural, or residential (Rivero 1978, Schwartz and Henderson 1991, *pers. obs.*). The lack of significant relationships between lizard and

biogeographic variables indicates that these species are predominantly generalists, or if they have specialist habitat requirements, these are met in the fragments. Also, the dry forest fragments in this study may not be truly isolated to the degree that would negatively affect the lizard communities. The 12 fragments in this study were separated by no more than 400 m from other patches of closed canopy forest, and many were isolated from other forested areas only by roads or short expanses of non-forested land. However, the low occurrence of the less common lizard species may have precluded the detection of significant associations.

If fragment and landscape characteristics are not very influential, what are the important factors in structuring dry forest lizard communities? Based on the correspondence analysis of fragments and species, it appears that environmental and habitat characteristics within the fragment were more influential than those in the surrounding landscape. Ordination along the first four axes primarily described differences among sites attributable to vegetation characteristics; sites with denser and more complex vegetation contrasted with sites that have open and scrubby vegetation. Lizard species ordinated along a similar gradient; *S. nicholsi* and *A. stratulus*, both of which prefer a shaded and protected environment, contrasted with other species that are better adapted to open, xeric, and rocky conditions. *Phyllodactylus wirshingi* and *S. roosevelti* emerged as distinctly different from all other species along the second and third axes, respectively. These two species, while relatively common to most sites, were not frequently encountered during quantitative sampling. They were

recorded at a number of sites during qualitative searches, but were not well represented in the density estimates used in the correspondence analysis. A similar argument could be posed for *A. pulchellus* and *A. poncensis*; both species were frequently encountered during site walks, but density estimates for all sites at which they were present were also lacking for these species. *Anolis pulchellus* and *A. poncensis* were also quite poorly represented in this analysis (Table 2.10).

Most lizards were present even in small (< 1 ha) fragments, with the exception of A. cooki, A. poncensis, and S. roosevelti, which were only represented in the medium and large fragments. Anolis cooki has a very limited and discontinuous distribution which is restricted to very few areas, all within 1 km of the coast (Marcellini et al. 1985, Jenssen 1990). Sphaerodactylus roosevelti, like A. cooki, is restricted to coastal habitats and relatively uncommon in forested habitat farther inland (Schwartz and Henderson 1991). Since the four small fragments were located further inland than some of the other sites, none were within the range of these two species, although I would expect these species to be able to maintain populations within small fragments that are within their range. Anolis poncensis is found in exposed grassy or shrubby areas (Schwartz and Henderson 1991); this species was encountered most frequently along fragment margins or in grassy clearings within larger fragments. It is likely that this species is indeed present along the edges of small fragments, but was not detected during this study. Another species very similar in appearance and ecology to A. poncensis, A. pulchellus, was represented in small fragments.

Additional investigations into the natural history and ecology of individual species (i.e., Kitchener *et al.* 1988, Fobes *et al.* 1992) would be valuable contributions to understanding species-level responses to habitat fragmentation and other disturbance phenomena.

It is possible that species not encountered during this study in various fragments are indeed present, but perhaps at low densities or in atypical (and therefore not sampled) microhabitats (e.g., old quarry in site 4). Lizards were more likely to be detected and added to species lists at sites which were both quantitatively and qualitatively resampled in 1998 (Sites 30, 28, 16, 5, 4, and 2). Unequal sampling effort at sites sampled only in 1997 or 1998 may mean that the species richness in these fragments was underestimated, although the fragments sampled in both years did not show any significant temporal differences (paired *t* test, p>0.05). Sites 13, 10 and 7 were added to the study in 1998, and all three of these sites had lower species richness than expected, given their size and habitat quality (s = 4 for all three sites). The trend of increasing species richness with increasing fragment area (Figure 2.3) was not as strong when these three sites were added to the study in 1998.

A common tool for characterizing the species composition of isolated fragments is the nested subset model, which assumes that the species present in small fragments are subsets of those present in larger areas (Patterson and Atmar 1986, Cutler 1991). In the Bahamas, the presence of a given lizard species and total species richness can be predicted from habitat area (Schoener and Schoener 1983a, b). In southwestern Puerto Rico, *A. cristatellus* and *A*.

*exsul* were present in virtually all fragments (except site 40), and as fragment area increased, *S. nicholsi* was added to the community. Occurrences of other species were determined more by habitat heterogeneity and availability of suitable microhabitats than fragment area. For example, grass-bush anoles were only found at edges or in fragments with interior grassy clearings.

Although little is known about dispersal behavior in these groups of lizards (T.A. Jenssen, pers. comm.), existing data suggest that Anolis spp. show little vagility (Gorman and Harwood 1977, Andrews and Rand 1983). Nonforested land surrounding fragments may be dispersal barriers for some species, but this would be ameliorated if lizards were able to live and maintain populations in these alternative habitats. Anolis cristatellus is very common in open areas and along roadsides where fence posts provide suitable perches (pers. obs., Schwartz and Henderson 1991). This species has also become adapted to take advantage of novel feeding opportunities at night where insects aggregate around lights in residential areas (Garber 1978). Ameiva exsul is also well adapted to anthropogenic habitat disturbance, and is frequently seen in urban areas (pers. obs., Heatwole and Torres 1967). The wide variety of food types consumed by A. exsul includes items such as garbage scraps, indicating that this generalized omnivore prospers in the midst of human disturbance (Grant 1931, Heatwole and Torres 1967, Lewis 1986). Other species, such as the grass-bush ecomorphs A. pulchellus and A. poncensis, are also able to maintain populations in non-forested habitats. Gorman and Harwood (1977)

reported extremely high population densities of *A. pulchellus* along roadsides and in open grassy areas (up to 20,000 individuals/ha).

Lizard population dynamics are important to consider when assessing the long term effects of habitat fragmentation. The small-bodied dry forest lizards are relatively short-lived, and complete population turnover could potentially occur over short time scales. Lizard populations fluctuate dramatically over time, and annual changes can be as great as 50% (Turner 1977), however, although year to year variability may be great, lizard populations remain relatively constant over ecological time (Schoener 1985, 1994). Survival is influenced by many factors; the presence of a greater number of bird species in dry forests as compared to wet forests in Puerto Rico (Kepler and Kepler 1970) may lead to lower survivorship in lizards (Schoener and Schoener 1978, 1982). Some dry forest bird species, most notably the Puerto Rican lizard cuckoo (Saurothera vieilloti) feed primarily on small lizards (Raffaele 1989). Although it is not known how this particular species responds to habitat fragmentation, most native bird populations suffer severe reductions following disturbance and fragmentation (Robbins et al. 1989, Faaborg and Arendt 1990).

After a fragment becomes isolated, there is a lag before a new equilibrium of extinction and colonization rates is reached (Diamond 1972, 1973, Corlett and Turner 1997). The relatively rapid and unpredictable pace of lizard population dynamics suggests that there has probably been sufficient time for faunal relaxation in the 12 dry forest fragments studied, given that the majority of the fragments have been isolated for at least 20 years and others for more than 60

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years (Lugo *et al.* 1996). Another component of lizard population dynamics is that density fluctuations are correlated with timing and amount of precipitation (Andrews and Wright 1994). In the harsh and often drought-stricken dry forest life zone, water limitation may lead to reduced population sizes in fragments that are even more susceptible to local extinction than under natural conditions.

The primary mechanisms for the maintenance of lizard communities in dry forest fragments in southwestern Puerto Rico may be related to: (1) lower energy and space requirements than other vertebrates (e.g., mammals or birds), (2) generalist habitat requirements, (3) ability to move through intermittent nonforested habitats, and (4) ability to successfully establish and maintain populations in non-forested habitats. Any of these mechanisms will increase the probability of lizard survival and persistence in a fragmented landscape. The true explanation for lizard persistence in forest fragments is most likely a combination of the above factors, and may vary with the species or group of species considered.

## Conservation of Dry Forest Fragments

Overall, lizard species richness was positively related to fragment area, suggesting that larger fragments should receive the highest conservation priority in management programs. Greater heterogeneity inherent in larger expanses of habitat increases the probability of supporting a rich and diverse ecological community. However, fragments as small as 2 ha were able to support a diverse

lizard community, indicating that these habitats also deserve attention in management and conservation activities at the landscape level.

Characteristics of the surrounding landscape were generally not related to fragment lizard community composition and abundance, although it would be very useful to examine the influence of surrounding land use in buffers of various sizes (e.g., 100 m, 500 m). If lizards are not hindered by nonforested land uses, they will likely be resilient to the negative consequences of habitat fragmentation. If the trend of increasing forest cover throughout Puerto Rico continues, lizards in existing forest fragments should be able to serve as colonizers once additional patches of secondary forest become available in the landscape. This study represents a preliminary investigation into the complex effects of habitat fragmentation on lizards in a landscape that is dominated by anthropogenic influences. Although more than 300 patches of forested habitat are scattered throughout the dry forest life zone (Ramjohn et al. unpubl. data), only 12 fragments were considered in this study. Because of the number of sites and lack of variation in the surrounding landscape (three of the fragments were entirely enclosed by agricultural land), additional studies investigating a greater number of fragments are warranted to further investigate the implications of the surrounding landscape for the persistence of ecological communities in subtropical dry forest fragments. However, conclusions based on this study point very strongly to the conservation potential of fragments in this region, at least if lizards are the focal taxa.

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This study has shown that even forest fragments as small as 2 ha contain suitable habitat to support a diverse dry forest lizard community. Although it is true that some vertebrates (e.g., birds) require substantial areas for habitat preservation, other vertebrates (e.g., lizards) have much smaller area requirements. Given the already fragmented nature of the dry forest landscape in southwestern Puerto Rico, preservation of the remaining small habitat fragments should receive conservation priority. Fragments containing the few remaining populations of the endangered *A. cooki* should receive top and highest priority; if these patches of habitat are lost, this species will inevitably slip towards extinction. If forest fragments in the dry forest life zone of Puerto Rico were integrated into local management and conservation efforts, the threats of anthropogenic disturbance on natural communities may begin to be ameliorated.

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# Chapter 3

# Structural Habitats of Dry Forest Trunk-Ground Ecomorphs: <u>Anolis cristatellus</u> and <u>Anolis cooki</u>

# Introduction

Anolis cristatellus and A. cooki are morphologically and ecologically similar anoles found in the dry forest region of southwestern Puerto Rico. Where these two species coexist, few characters can be used to distinguish them in the field (Marcellini and Jenssen 1983); they are osteologically identical (Pregill 1981) and have only recently been recognized as separate species based on karyotypic differences (Gorman *et al.* 1968, 1980, 1983). Both are medium sized anoles that are classified as trunk-ground ecomorphs (Williams 1983), although they differ in their distribution, species status, and biotic interactions.

While *A. cristatellus* is a widespread and abundant anole throughout Puerto Rico (Heatwole 1976, Rivero 1978, Schwartz and Henderson 1991), *A. cooki* is restricted to a limited number of discontinuous coastal scrub habitat patches within 1 km of the coast in the extreme southwestern portion of the island (Marcellini *et al.* 1985, Jenssen 1990). Although previous studies have documented small allopatric populations of *A. cooki* (Jenssen *et al.* 1984, Marcellini *et al.* 1985), virtually the entire distribution of this species overlaps with that of *A. cristatellus*. *Anolis cooki* populations may be diminishing towards eventual extinction (Williams 1972), and the current and future status of this species requires not only immediate, but also continual conservation attention.

Rand (1964) introduced the concept of structural habitat for *Anolis* lizards; the spatial niche occupied by an anole can best be described by the height and diameter of the perch site. Other perch characteristics such as texture, color, and thermal microhabitat (sun vs. shade) may also be used to describe structural habitat (Heatwole 1968, Scott *et al.* 1976), but the most powerful variables to discriminate between species or age classes within a species are perch height and diameter (Schoener 1968). Structural habitat represents one of the primary resource axes which are partitioned by sympatric anoles; thermal habitat and prey size comprise the remainder of the ecological niche (Schoener and Schoener 1971a, b, Williams 1972, Schoener 1977).

The structural habitat of an anole has implications for a multitude of activities including foraging, courtship, aggression, and thermoregulatory behaviors. Perch substrate has also been found to be important in anole movement through their three-dimensional habitat; perch diameter influences sprint speed, clinging ability and agility (Losos and Sinervo 1989). Intra- and interspecific interactions often elicit escape behaviors, which can be predicted from the relationships among perch diameter and the locomotion characteristics mentioned above (Losos and Irschick 1996). However, Moermond (1979) suggested that distribution of perches, rather than perch characteristics themselves, were more influential for anole movement through a habitat.

In sympatry, similar species must differ from one another along at least one of the primary resource axes to coexist in stable equilibrium (Schoener and Schoener 1971a, b). In response to competitive interactions, Anolis lizards have been found to alter selection of perches and perch position (e.g., Jenssen 1973. Schoener 1975, Lister 1976, Campbell 1999). Shifts in structural habitat among sympatric species have been documented in response to seasonal variation in food availability and reproductive condition (Lister 1981) and the co-occurrence of direct competitors (Salzburg 1984, Losos et al. 1993, Losos and Spiller 1999). Jenssen et al. (1984) found that where A. cristatellus and A. cooki are allopatric, their structural habitats are not significantly different. Ortiz and Jenssen (1982) found that intense aggressive encounters between these two species had implications for ecological displacement; indeed, when they are sympatric, A. cooki is driven via intense competitive interference with A. cristatellus to less desirable and less complex microhabitats including small bushes and standing dead vegetation (Jenssen et al. 1984).

While many studies have approached competitive interactions from the interspecific competitive interference perspective, these studies have also shown that intraspecific interactions often overshadowed interspecific competition (e.g., Tokarz and Beck 1987, Brown and Echternacht 1991). Indeed, anoles of both Jamaica and Puerto Rico partition their structural habitat in response to intraspecific competition among age and size classes (Schoener and Schoener 1971a, b). Stamps (1977) found that within a species, males are more likely to engage in intense competitive interactions for mates, while

d p ٧a fo Sų fra tra thr Siz des females compete for food. The implications for intraspecific interactions may affect the outcome of competition between *A. cristatellus* and *A. cooki*, both interand intraspecifically.

Given the tenuous existence of *A. cooki* in southwestern Puerto Rico, it is important to re-evaluate its structural habitat in the presence of *A. cristatellus*, a direct and apparently superior competitor. The objectives of this chapter are to compare the structural habitats of these two species in areas where they cooccur in the highly fragmented dry forest landscape in order to assess the current status of *A. cooki* and conservation implications of both inter- and intraspecific interactions. *Anolis cooki* presently has a limited and patchy distribution, and habitat fragmentation may further increase the chance of local population extinctions and eventual species extirpation.

## **Materials and Methods**

Anolis cristatellus and A. cooki were surveyed in forest fragments of varying sizes and a reference site (Guánica Commonwealth Forest) in the dry forest zone (*sensu* Holdridge 1967) of southwestern Puerto Rico during the summers of 1997 and 1998. A complete description of the reference site and fragments can be found in chapters 1 and 2, respectively. At each site, 100 m transects of fixed area (see Chapter 1, Figure 1.2) were randomly located throughout the study area; the number of transects was scaled according to the size class of each site (see Chapter 2 for a complete summary of the sampling design).

Transect sampling involved surveying lizards at 5 m intervals along the length of the transect. At each interval, the following data were recorded for all *A. cristatellus* and *A. cooki* individuals within a 2.5 m radius of the transect sampling interval: (1) species identification, (2) age/size class, (3) perch height, (4) perch diameter, and (5) perch species (identification of the tree species used as a perch). *Anolis cristatellus* and *A. cooki* were distinguished in the field by estimating the ratio of tail length (TL) to snout-vent length (SVL) (Marcellini and Jenssen 1983). Each individual was assigned to an age/size class upon visual estimation of TL and SVL (Schwartz and Henserson 1991, Table 3.1). Individuals were periodically captured (every 10-15 individuals) and measured to ensure that visual estimation of TL and SVL was accurate and specimens were correctly identified and assigned to the proper age/size class.

Perch height was visually estimated to the nearest 0.1 m using reference points on the observer's body; during the 1998 field season, perch diameter was visually estimated to the nearest 0.5 cm, and subsequently measured with calipers. A single observer conducted all surveys to avoid any bias introduced by observer error.

	A. cristatellus	A. cooki
adult male	>70 mm	> 60 mm
adult female/sub-adult male	55 - 69 mm	50 - 59 mm
juvenile	< 55 mm	< 50 mm

Table 3.1Age/size classes for A. cristatellus and A. cooki based on SVL<br/>(Schwartz and Henderson 1991)

Structural habitats and density estimates were analyzed to determine whether inter- or intraspecific differences existed between species and/or age/size classes. *Anolis cristatel/us* structural habitat was evaluated under both allopatric and sympatric conditions. All statistical analyses were performed using Systat (version 5.0). Non-parametric statistics were utilized on untransformed data throughout, as perch height, perch diameter, and density data are not normally distributed, nor did transformation improve the distribution. Significance level for all tests was set to  $\alpha = 0.05$ . Perch height data from 1997 and 1998 were pooled; there were no significant differences between years (Wilcoxon paired sample test; p>0.05). Density estimates for both species from 1997 and 1998 were also pooled, as there were no significant differences in abundance between years (Wilcoxon paired sample test, p>0.05).

### Results

The total number of lizards sampled in this study was dramatically biased towards *A. cristatellus*, the more common and widespread species (*A. cristatellus*, n = 2413; *A. cooki*, n = 76). Of these individuals, the distribution among age/size classes exhibited a striking pattern (Figure 3.1). A large proportion of the *A. cristatellus* individuals sampled were juveniles (0.44, n=1132), with the remainder comprised of adult females/sub-adult males and adult males(0.41, n=936; 0.15, n=345; respectively). The age distribution of *A. cooki* seems to be the inverse pattern; adult males comprise the largest proportion of sampled individuals (0.52, n=40) while adult females/sub-adult

males and juveniles represent proportionally smaller age classes for this species (0.26, n=20 for females/sub-adult males and 0.22, n=16 for juveniles, respectively).



Figure 3.1 Age distribution of *A. cristatellus* (n=2413) and *A. cooki* (n=76) in 1997-1998. Sample sizes for age/size classes are given in the text.

Anolis cristatellus was found at all but one study site, while A. cooki was found in only 2 fragments and two isolated areas in the reference site (Table 3.2). Over the entire distributions of these two species, the differences in structural habitat were not statistically significant between A. cristatellus and A. cooki. (Table 3.3, Mann-Whitney U Test: perch height, p=0.09; perch diameter, p=0.239). Adult anoles showed a tendency to perch higher than juveniles in both species; adult male *A. cristatellus* perched significantly higher and on larger stems than adult male *A. cooki* (Figure 3.2; Kruskal-Wallis ANOVA, p<0.05). No other differences among age/size classes or species were statistically significant when the entire habitat range of each species was considered.

Although allopatric populations of A. cristatellus did not perch significantly higher, they selected significantly larger stems than when they co-occur with A. cooki (Mann-Whitney U Test, p<0.01; Figure 3.3). When the two species were sympatric, they occupy virtually the identical structural habitat; an overall comparison of perch height and diameter showed that there were no significant differences between A. cristatellus and A. cooki perch dimensions (Mann-Whitney U Test, p>0.05; Table 3.4). Intraspecifically, there were no significant differences in perch height or diameter for A. cooki (Kolmogorov-Smirnov two sample test, p>0.05, Figure 3.4). However, adult males and females (considered together with sub-adult males) A. cristatellus perch significantly higher than juveniles (Kolmogorov-Smirnov two sample test, p<0.001; Figure 3.4); low sample size precluded intraspecific comparisons of *A. cristatellus* perch diameters in sympatry with A. cooki. Regression analysis indicated that neither A. cristatellus nor A. cooki adult males showed a significant relationship between SVL and perch height (p>0.05, Figure 3.5). Low sample size precluded testing for significant relationships between adult male lizard SVL and perch diameter.

At sites where *A. cristatellus* and *A. cooki* are sympatric, *A. cristatellus* is significantly more abundant than *A. cooki* (Mann-Whitney U Test, p<0.001),

although abundance of both species did not differ significantly among study sites
(Kruskal-Wallis ANOVA, p>0.05). Intraspecifically, A. cooki density did not differ
significantly among age/size classes (Kruskal-Wallis ANOVA, p=0.514), but A.
cristatellus differed significantly among age/size classes (Kruskal-Wallis
ANOVA, p=0.035). Interspecifically, density of adult males did not differ
between species (Mann-Whitney U Test, p=0.613), but A. cristatellus adult
female/sub-adult males and juveniles were significantly more abundant than
their <i>A. cooki</i> counterparts (Mann-Whitney U Test, P < 0.01; Figure 3.6).

Table 3.2Distribution of A. cristatellus and A. cooki among study sites1 = presence of A. cristatellus, 2 = presence of A. cookiRefer to text and Figure 2.1 in Chapter 2 for a complete descriptionof fragment study sites.

Small F	ragments	Medium	n Fragments	Large Frag	ments	Referen	ce Site
Site 40		Site 28	1	Site 7	1	Coastal	1, 2
Site 36	. 1	Site 13	1	Site 5	1	Central	1
Site 30	1	Site 16	1, 2	Site 4	1	North	1
Site 27	1	Site 10	1	Site 2	1, 2	Ravines	1, 2*

\* only a single A. cooki was found in a ravine that was in close proximity to the coast

.

Table 3.3Overall perch height (SE) and perch diameter (SE) for A.<br/>cristatellus and A. cooki; all sites and age/size classes combined.<br/>Differences in perch height or diameter were not significantly<br/>different between species.

Structural Habitat	A. cristatellus	A. cooki
Perch height (m)	0.818 (0.013) n=2413	0.774 (0.06) n=76
Perch diameter (cm)	6.234 (0.194) n=728	5.339 (0.577) n=31



Figure 3.2 (A) Mean perch height (A. cristatellus, n=2413; A. cooki, n=76) and (B) mean perch diameter (A. cristatellus, n=728; A. cooki, n=31) for A. cristatellus and A. cooki age/size classes at all study sites. Error bars represent standard error of the mean. Mean perch size selection (height and diameter) was significantly different between adult males of the two species (Mann-Whitney U Test, p<0.05), but females and juveniles did not differ significantly in structural habitat characteristics (Mann-Whitney U Test, p>0.05).



Figure 3.3 (A) Mean perch height and (B) mean perch diameter of Anolis cristatellus in allopatry (n=1872) and sympatry (n=289) with A. cooki. Error bars represent standard error of the mean. Perch diameter was significantly less in sympatry with A.cooki (Mann Whitney U Test, p=0.001), but perch height was not significantly different (Mann-Whitney U Test, p=0.632)).

Table 3.4 Perch height (SE) and perch diameter (SE) for A. cristatellus and A. cooki at sites where they are in sympatry; age/size classes combined. Differences between species in perch height or diameter were not significant (Mann-Whitney U Test, p>0.05).

Structural Habitat	A. cristatellus	A. cooki
Perch height (m)	0.76 (0.03) n=289	0.77 (0.06) n=76
Perch diameter (cm)	4.78 (0.39) n=728	5.34 (0.58) n=31



Figure 3.4 Mean (<u>+</u> SE) perch height for *A. cristatellus* (n=289) and *A. cooki* (n=76) where they occur in sympatry. Within age/size classes, differences between species were not significant (Mann-Whitney U Test, p>0.05).

Structural habitat of *A. cristatellus* differed significantly among study site size classes (Kruskal-Wallis ANOVA, P < 0.001; Figure 3.7). *Anolis cooki* was found in only 2 of 12 fragments (site 2 and 16) and 2 of 4 reference site habitats sampled (coastal and ravine), precluding any statistical evaluation of potential effects of habitat fragmentation on this species. Neither species exhibited a perch preference for a particular plant species. Both *A. cristatellus* and *A. cooki* perched most often on standing dead vegetation (16% and 17%, of perch sites, respectively). The remainder of perch sites were comprised of many different species, each comprising less than 10% of the total perch sites. A complete summary of perch sites for *A. cristatellus* and *A. cooki* can be found in Appendix C.



Figure 3.5 Relationship between SVL and perch height for adult male (A) *A. cristatellus* (n=47) and (B) *A. cooki* (n=39) at sympatric sites. Neither species showed a significant association between the characters (Spearman rank correlation, P > 0.05)



Figure 3.6 Density (mean <u>+</u> SE) of *A cristatellus* (n=289) and *A. cooki* (n=76) where they occur in sympatry. *Anolis cristatellus* adult females/sub-adult males and juveniles were significantly more abundant than the same *A. cooki* age/size classes (Mann-Whitney U Test, p<0.05).



**Study Site Size Classes** 

Figure 3.7 Structural Habitat (mean <u>+</u> SE) perch height and perch diameter of *A. cristatellus* (n=2413) among study site size classes. Perch height and diameter are both significantly different among site size classes (Kruskal-Wallis ANOVA, p<0.05).

### Discussion

Anolis cristatellus is one of the most conspicuous and widespread anoles on the island of Puerto Rico (Rivero 1978, Schwartz and Henderson 1991). It occured in all habitat types, with the possible exception of mesic and montane forest interior (Rand 1964, Schoener and Schoener 1971b). *Anolis cooki* was significantly less common; its extremely restricted and patchy distribution have made it a species of special concern for management and conservation officials in southwestern Puerto Rico (Ortiz 1990, M. Canals Mora, *pers. comm.*). The implications of both inter- and intraspecific competitive interference interactions between these two species for the survival of *A. cooki* reinforces the need to monitor and document any changes in the ecological status of *A. cooki* in the interest of developing management and conservation strategies for the protection of this species.

The age distribution of *A. cooki* populations sampled in this study suggested that the future of this species is uncertain. The vast majority of the individuals sampled were adults and sub-adult males (78%), with very few juveniles to replace the adults as they mature, senesce, and die. The age distribution of *A. cristatellus* was more stable and indicative of adequate replacement and persistence of populations through time; a sizable proportion of individuals sampled were juveniles (44%). Another Puerto Rican anole, *A. stratulus*, had a healthy population comprised of 57% adults and 43% juveniles (sex ratio 1 male: 1 female) in the Luquillo rain forest (Reagan 1996). It appeared that the reproductive rates of these two species were quite different; if

*A. cooki* is not reproducing at a rate to replace the current populations, the species is likely to be on the trajectory of natural extinction. However, the possibility also exists that the sex ratio and age distribution of the population were closer to stability. *Anolis* males often "hide" in the vicinity of dominant males' territories, ready to overtake the territory if predation or some other circumstance renders the territory unoccupied and undefended (T. Campbell, *pers. comm.*).

When the data for all age/size classes and sites were pooled (including both allopatric and sympatric populations of *A. cristatellus*, but only sympatric populations of A. cooki), there were no significant differences in structural habitat characteristics between A. cristatellus and A. cooki. This supported the contention that these species occupy similar niches and are virtual ecological equivalents. In both species, there was a tendency for adults to perch higher than juveniles. Within adults, males of both species perched higher than females; Lister (1981) also found that male anoles in the Luquillo rain forest of northeastern Puerto Rico perched higher than females. Adult male A. cristatellus also occupied larger stems than females and juveniles, but no significant trends were apparent for A. cooki. While some studies have found a general trend of larger lizards occupying perches of greater diameter (Schoener 1968, Schoener and Schoener 1971a), Lister (1981) found that mean perch diameters were generally similar both between and within species of Puerto Rican anoles. Differences in perch diameter between and within species may reflect the degree of potential competitive interference; species and age/size
classes which are ecologically less similar should show little difference in perch size preference, thereby limiting competition to lizards of presumably differing size and energetic requirements. The tendency for larger anoles to be found on higher and larger perches than smaller lizards results in reduced intraspecific spatial overlap (Schoener and Schoener 1971a).

Neither *A. cristatellus* nor *A. cooki* showed a significant relationship between adult male SVL and perch height. Such a relationship would indicate intraspecific competition among males, with larger males predominating in larger and more complex habitats. Jenssen *et al.* (1984) found that with the exception of sympatric *A. cooki*, adult males in both allopatric and sympatric habitats showed a significant positive relationship between SVL and the relative complexity and height of their microhabitat. The lack of a significant relationship between adult male size and perch height in either species (absence of intraspecific competition?) as well as the lack of a significant difference in perch height between the two species indicated that extensive structural habitat overlap and predominantly interspecific competitive interactions may be the driving forces shaping *A. cristatellus* and *A. cooki* community dynamics.

Although adult males of the two species differed significantly in perch height and diameter when all populations of *A. cristatellus* (allopatric and sympatric) were considered, there were no significant differences in structural habitat of *A. cristatellus* in sympatry with *A. cooki*. In anoline lizards, the greatest potential for competition and aggression interactions is between males (Ortiz and Jenssen 1982), and differences in structural habitat serve to segregate

congeneric species spatially and reduce interspecific competition. Competitive interactions are less frequent in juveniles, and their selection of lower and smaller structural habitats probably reflects an active choice rather than the results of an intraspecific aggressive encounter (Kiester *et al.* 1975).

Allopatric A. cristatellus populations perched at similar heights and on larger stems than those sympatric with A. cooki. These two species have virtually identical habitat requirements, and shifts in structural habitat function to minimize competitive interference where they co-occur. The ability to shift and modify structural habitats in response to competitive interactions has been documented for many Anolis species in many areas throughout the West Indies and the southeastern United States (e.g., Jenssen 1973, Schoener 1975, Lister 1976, Campbell 1999, Echternacht 1999). Jenssen et al. (1984) found that there were no interspecific differences in structural habitat in allopatric areas of southwestern Puerto Rico, but in sympatry, A. cooki perched on significantly lower and thinner vegetation while A. cristatellus maintained the same structural habitat characteristics in sympatric and allopatric populations. The results of this study indicated that these two species may have altered their ecological roles to some extent in these habitats; although A. cristatellus did not significantly alter perch height in sympatry with A. cooki, they selected significantly smaller stems for perches. Based on these data, structural habitats of these two species do not differ significantly under sympatric conditions. Although A. cooki presently appears to be maintaining relatively high quality perch sites in sympatry with A. cristatellus, population density and age

distribution of this species do not indicate a state of stable equilibrium with its congeneric competitor.

At every study site where both species occur, *A. cristatellus* is present in significantly higher densities than *A. cooki*. Low population densities of *A. cooki* do not bode well for the persistence of these populations over ecological, much less evolutionary time. Adult males were present in similar densities at sympatric sites, but *A. cristatellus* adult females/sub-adult males and juveniles were significantly more abundant than *A. cooki* females and juveniles. Lower densities of females and juveniles will probably lead to declining populations and eventual local extinctions, depending on fecundity and recruitment within the population.

Neither *A. cristatellus* nor *A. cooki* showed a perch preference for a particular vegetation type or species. Standing dead vegetation comprised the largest percentage of perch sites for both species ( $\leq 17\%$ ), although the vast majority of perches were distributed relatively evenly among dozens of dry forest trees, shrubs, and vines (Appendix C). Standing dead stems comprise 13% of total stem density in Guánica Forest (Murphy and Lugo 1986a); dead stem density may be even higher in forest fragments, constituting a sizable proportion of available perching habitat for anoles (*pers. obs.*). Lister (1976) indicated that some arboreal anoles may be generalists with respect to structural habitat, and this seems to be the case for perch substrate selection by *A. cristatellus* and *A. cooki*. Other investigators have also stated that plant species is not an important criterion for anoles in selecting perch sites, and have characterized the substrate

component of structural habitat by vegetation physiognomy (Jenssen *et al.* 1984). These studies have found that open areas comprise a large proportion of the habitat of *A. cristatellus* and *A. cooki*, both in allopatry and sympatry, and that *A. cooki* perches were strongly skewed to standing dead vegetation and small shrubs in the presence of *A. cristatellus* (Jenssen *et al.* 1984, Marcellini *et al.* 1985). The results of the current study do not strongly support these previous conclusions, as shrubby and standing dead vegetation constitute approximately equal proportions of perch sites for both species. However, explicit vegetation data necessary to evaluate differences in microhabitat complexity between species and among age/size classes were not available for this study, limiting the conclusions strictly to structural perch characteristics.

### Current and Projected Future Status of <u>A. cooki</u>

Past studies have indicated that *A. cristatellus* is the dominant species and superior competitor in habitats where it coexists with *A. cooki* (Jenssen *et al.* 1984). This study suggests that although *A. cooki* appears to have altered perch site selection in areas of sympatry with *A. cristatellus* over the past two decades, other natural history characteristics of this species imply that it is far from coexisting in stable equilibrium. *Anolis cooki* did not appear to be driven to lower and thinner perches as found in Jenssen *et al.* (1984), however, low population density and potentially low recruitment (few juveniles in populations) indicated that *A. cooki* is likely in decline. Earlier assertions that *A. cooki* may be on the pathway to natural extinction driven by competitive interactions with *A.* 

*cristatellus* (Williams 1972, Marcellini *et al.* 1985, Ortiz 1990) cannot be rejected based on this study; the long-term persistence of this species remains questionable, and continual monitoring of remaining *A. cooki* populations will be critical to the long-term survival of the species.

Differences in structural habitat and abundance between these two species also have implications for food consumption, courtship, thermoregulation, and relative risk of predation. Anoles are opportunistic predators and are able to consume a wide variety of prey (Reagan 1996); perhaps a perch position lower to the ground confers an advantage to *A. cristatellus* when feeding on leaf litter arthropods. The coastal scrub habitats where *A. cooki* is found are exposed to harsh wind and sea spray conditions which account for the open and wind-pruned vegetation in these areas (Ewel and Whitmore 1973). Perch positions slightly lower on trees and shrubs in these habitats may provide more protection and control over active thermoregulatory behaviors. *Anolis cooki* may be at a disadvantage on higher perches both because the microhabitat may be harsher and also more exposed to predation risks from birds such as red-tailed hawks (*Buteo jamaicensis*) and the Puerto Rican lizard cuckoo (*Saurothera vieilloti*).

Competitive interference and habitat partitioning between *A. cristatellus* and *A. cooki* appears to be a dynamic interaction through time, and the evolutionary outcome depends on the ability of *A. cooki* to persist and reproduce *ur*der the inhospitable conditions inherent in the coastal scrub habitats where it is found, coupled with the ability to compete effectively with *A. cristatellus*. The

few remaining patches within the range of *A. cooki* need to be preserved and protected; it is unlikely that this species could successfully cope with the intense pressures of anthropogenic habitat modification combined with the natural competitive pressures already present.

## SUMMARY

In this study, dry forest fragments in southwestern Puerto Rico were able to support relatively rich and diverse lizard communities. When fragments were viewed collectively, they supported the same species composition as Guánica Commonwealth Forest, the largest continuous tract of protected dry forest in Puerto Rico. Abundances of the 10 lizard species in the fragments and in the reference site are provided in Appendix B (Tables B.2-4) and Table 1.7, respectively. The 12 fragments in this study contained a wide variety of habitat types, and ranged in size from 0.01 to >800 hectares. Some of these fragments may be sheltered from excessive anthropogenic disturbances due to their harsh topography and relative inaccessibility. Other fragments were located in areas where the potential for human disturbance was much greater. For instance, one of the study sites was previously part of a golf course and is located along a heavily traveled road which receives a substantial amount of trash from passing vehicles (*pers. obs.*).

These fragments varied greatly in the type and quality of habitats. Two species, *A. cristatellus* and *A. exsul*, were present in all fragments except the very smallest one (0.01 ha). *Sphaerodactylus nicholsi* was present in all fragments larger than 0.25 ha. The occurrence of the remaining dry forest species depended on the habitat heterogeneity of the fragment. The diversity of lizards was hypothesized to increase as the total area of the fragment increased; the number of lizard species was indeed significantly (positively) correlated with

fragment area. There were no patterns of abundance among species and fragment or landscape characteristics.

The fragment area required to support the lizard community found in the reference site was >800 ha. Other large fragments would also be able to support the reference community if suitable habitat were provided and the site were located within the range of all 10 dry forest lizard species. Nine species were recorded at site 4 (137 ha); *A. cooki* was the only species not encountered because the fragment was outside that species' distribution. The minimum fragment area required to support 50% and 75% of the lizard community of Guánica Forest was 0.26 ha (site 30) and 2 ha (site 28), respectively. Fragments greater than 97 ha consistently supported lizard communities with 75% of the species found in the reference site, although when sites sampled only one year were excluded, fragments greater than 2 ha consistently supported >75% of the reference lizard community.

Analysis of landscape level phenomena using GIS combined with statistical techniques indicated that patterns of land use surrounding the forest fragments had little, if any, influence on species richness and the distribution of lizard communities. Although no generalizations could be made from the results of this study, landscape characteristics may be important for certain individual species requirements. Further studies of the landscape ecology of the fragmented dry forest life zone with a greater number of study sites and increased variability in landscape characteristics (as well as investigating the influence of surrounding land use in buffers of various sizes) are necessary before any firm conclusions can be reached.

Habitat characteristics were important for the distribution and abundance of some dry forest lizards. Sphaerodactylus nicholsi was found at higher densities when the litter layer was relatively deep, providing a mesic environment. This may represent a tradeoff between preference for a xeric habitat (Schwartz and Henderson 1991) and a need for the abundant and stable arthropod food supply found in the moist substrate. Structural habitats of A. cristatellus and A. cooki were also investigated in this study. While the rarity of A. cooki precluded comparisons among fragments or size classes, comparisons of the two species in allopatry and sympatry yielded provocative results. Overall, there were no significant differences in structural habitat between A. cristatellus and A. cooki. In general, adults perched higher than juveniles, and adult males perched higher than adult females. Allopatric A. cristatellus perched higher than when they are found in sympatry with A. cooki. Jenssen et al. (1984) found the reverse to be true; A. cooki was forced to lower and poorer quality perch sites when sympatric with A. cristatellus than when allopatric.

Although the number of fragments was limited and variation in surrounding landscape characteristics was low in this study, these results allow for some conservation and management recommendations. Large fragments which contain a variety of habitat types and support rich and diverse lizard communities should receive highest conservation priority, but fragments as small as 2 ha also supported a large proportion of the reference lizard community and

warrant management and conservation efforts. Fragments  $\geq$  2 ha typically support a rich lizard fauna and should also be integrated into management and conservation strategies. Characteristics of the vegetation and substrate are potentially very important to the organisms living in the fragments; quantification of these factors is also necessary in preparing recommendations and guidelines for conservation biologists and natural resource managers. Additionally, protection of fragments containing populations of *A. cooki* is also mandatory for the preservation of the few remaining populations of this endangered species.

The results of this study corroborated previous investigations of lizard communities of the highly fragmented wheatbelt region of western Australia (Kitchener et al. 1980, Kitchener and How 1982, Smith et al. 1996). Among the vertebrates in this ecosystem, lizards have endured the best despite habitat fragmentation. This can be attributed to a number of life history characteristics that make lizards in essence preadapted to coping with the consequences of habitat fragmentation such as low metabolic and area needs and generalist habitat requirements. These life history traits are presumably more important for lizards in fragmented habitats than habitat and biogeographic characteristics; there were few significant relationships between lizard taxa and either habitat or biogeographic variables (Smith et al. 1996). Dry forest lizards in southwestern Puerto Rico also appear to be resilient to the consequences of habitat fragmentation compared to other faunal groups, although additional studies are needed to assess the ecological status of lizards before broad generalizations can be made concerning their sensitivity to the effects of fragmentation.

These investigations concerning lizard community ecology in the fragmented dry forest life zone of southwestern Puerto Rico will be most robust when combined with concurrent investigations of termite (J. Genet, *unpubl. data*) and plant communities (Ramjohn *et al. unpibl. data*). Without a doubt, responses of representative vertebrate (lizards), invertebrate (termites), and plant communities will provide a thorough indication of the ecological status of these groups of organisms in a fragmented landscape and lead to conservation and management recommendations such that natural communities will be able to persist in the face of inevitable anthropogenic disturbance.

APPENDICES

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Figure A.1 Species-area curves for transect sampling at Guánica Forest sites.
(A) Coastal site: A. pulchellus added via qualtitative sampling, S. nicholsi, S. roosevelti, and P. wirshingi added via plot sampling;
(B) Central site: A. pulchellus and A. poncensis added via qualitative sampling, S. nicholsi and S. roosevelti added via plot sampling;
(C) North site: A. pulchellus added via qualitative sampling;
(D) North site: A. pulchellus added via qualitative sampling;
(C) North site: A. pulchellus added via qualitative sampling;
(D) Ravines: S. nicholsi and P. wirshingi added via plot sampling.

#### APPENDIX B





Figure B.1 Land use map of site 5 and vicinity, illustrating the delineation of the 1000 m buffer around study sites.



Figure B.2 Species-area curves for transect sampling at small fragment sites; no species were present at site 40. (A) Site 36: no additional species added by qualitative or plot sampling; (B) Site 30: A. *pulchellus* added via qualitative sampling, S. *nicholsi* and P. *wirshingi* added via plot sampling; (C) Site 27: S. *nicholsi* and P. *wirshingi* added via plot sampling.



Figure B.3 Species-area curves for transect sampling at medium fragment sites. (A) Site 28: *A. stratulus* and *A. pulchellus* added via qualitative sampling, *S. nicholsi*, *S. roosevelti*, and *P. wirshingi* added via plot sampling; (B) Site 13: *S. nicholsi* and *P. wirshingi* added via plot sampling; (C) Site 16: *S. nicholsi*, *S. roosevelti*, and *P. wirshingi* added via plot sampling, (D) Site 10: *A. poncensis* added via qualitative sampling, *S. nicholsi* added via plot sampling.



Figure B.4 Species-area curves for transect sampling at large fragment sites. (A) Site 7: S. nicholsi and P. wirshingi added via plot sampling; (B) Site 5: P. wirshingi added via plot sampling; (C) Site 4: S. nicholsi, S. roosevelti, and P. wirshingi added via plot sampling, (D) Site 2: S. nicholsi, S. roosevelti and P. wirshingi added via plot sampling.

(# individuals/ha	), n = total number	of individuals per s	ite.	
Species	Site 40	Site 36	Site 30	Site 27
Anolis cristatellus	0	594 (164)	274 (76)	909 (159)
	0=u	n=14	n=23	n=75
Anolis cooki	0	0	0	0
	0=u	0=u	n=0	0=u
Anolis stratulus	0	0	59 (33)	12 (12)
	0=u	n=0	n=3	n=1
Anolis pulchellus	0	0	*	61
	0=u	0=u		n=6
Anolis poncensis	0	0	0	0
	0=u	0=U	0=U	n=0
Ameiva exsul	0	223 (150)	170 (28)	6 (6)
	0=u	n=4	n=15	n=1
Ameiva wetmorei	0	0	0	48.5 (26.2)
	0=u	0=U	0=U	n=4
Sphaerodactylus nicholsi	0	0	3000 (1225)	1250 (487)
	0=u	0=u	n=8	n=6
Sphaerodactylus roosevelti	0	0	0	0
	0=u	0=u	0=u	0=u
Phyllodactylus wirshingi	0	0	*	417 (281)
	n=0	n=0		n=2
* species that were recorded a	at a site but not duri	ng quantitative sam	pling, precluding der	sity estimation.

Densities of dry forest lizards in small fragments (< 1 ha). Numbers represent mean (SE) densities Table B.1

Species	Site 28	Site 13	Site 16	Site 10
Anolis cristatellus	800 (133)	582 (86)	218 (52)	825 (83)
	n=66	n=48	n=18	n=68
Anolis cooki	0	0	146 (40)	
	0=u	n=0	n=12	0=u
Anolis stratulus	*	0	36 (20)	0
		0=u	n=3	0=u
Anolis pulchellus	ŧ	0	0	0
		0=u	0=u	0=U
Anolis poncensis	0	0	0	*
	0=u	0=u	0=u	
lmeiva exsul	30 (6)	24 (17)	24 (9)	212 (32)
	n=4	n=2	n=10	n=18
meiva wetmorei	42 (6)	0	4 (4)	2 0
	n=4	0=u	n=1	n=∩
sphaerodactylus nicholsi	833 (470)	208 (208)	417 (417)	417 (281)
	n=4	n=1	n=1	n=3
sphaerodactylus roosevelti	208 (208)	0	*	) : :
	n=1	0=u		0=U
Phyllodactylus wirshingi	208 (208)	208 (208)	417 (417)	0
	n=1	n=1	n=2	<b>U=</b> 0

Densities of dry forest lizards in medium fragments (1 - 10 ha). Numbers represent mean (SE) Table B.2

(# ILIUIVIUUAIS/ITA	ו), הו = נטנאו העודוט <del>פ</del> ר א	or individuals per si	D	
Species	Site 7	Site 5	Site 4	Site 2
Anolis cristatellus	554 (49)	388 (36)	870 (52)	476 (37)
	n=135	n=128	n=287	n=157
Anolis cooki	0	0	0	45 (13)
	0=u	0=u	0=u	n=15
Anolis stratulus	0	33 (10)	30 (10)	3 (3)
	n=0	n=11	n=10	n=1
Anolis pulchellus	0	21 (8)	12 (6)	6 (4)
	0=u	n=4	n=2	n=2
Anolis poncensis	0	3.3 (3.03)	3.03 (3.03)	9.09 (5.22)
	0=u	n=1	n=1	n=2
Ameiva exsul	257 (41)	32 (8)	62 (9)	44 (16)
	n=64	n=16	n=24	n=17
Ameiva wetmorei	0	3.03 (2.07)	9.09 (4.36)	9.7 (4.36)
	0=u	n=2	n=3	n=5
Sphaerodactylus nicholsi	2604 (697)	972 (269)	1458 (427)	278 (133)
	n=25	n=22	n=23	n=6
Sphaerodactylus roosevelti	0	0	¥	139 (97)
	0=u	0=u		n=2
Phyllodactylus wirshingi	104 (104)	*	*	*
	n=1			
* species that were recorded a	at a site but not durir	ng quantitative sam	oling, precluding der	isity estimation.

Densities of dry forest lizards in large fragments (> 10 ha). Numbers represent mean (SE) densities Table B.3



Figure B.5 Correspondence analysis of all study sites and all 10 lizard species. A.) Dimension 1 vs. Dimension 2, B.) Dimension 1 vs. Dimension 3 Species codes: ANOCRI=A.cristatellus, ANOCOO=A. cooki, ANOSTR=A. stratulus, ANOPUL=A. pulchellus, ANOPON=A. poncensis, AMEEXS=A. exsul, AMEWET=A. wetmorei, SPHNIC=S. nicholsi, SPHROO=S. roosevelti, PHYWIR=P. wirshingi. Refer to Chapters 1 and 2 for site identification.

Table B.4Correspondence analysis of lizard abundance in dry forest<br/>fragments. Total inertia was 0.57; each additional dimension<br/>explained <5% of the total variability.</th>

Dimension	Principal Inertia	% Variability	Cumulative % Variability
1	0.21	36.03	36.03
2	0.16	27.56	63.59
3	0.11	18.71	82.3
4	0.06	10.88	93.18

Table B.5Partial contributions of row (sites) and column (species) points<br/>to inertia of first four dimensions. All 10 species of lizards included<br/>in analysis.

	<b>Dimension 1</b>	<b>Dimension 2</b>	<b>Dimension 3</b>	<b>Dimension 4</b>
Site 36	0.05	0.22	0.17	0.02
Site 30	0.26	0.02	<0.01	0.01
Site 27	0.02	0.03	0.01	<0.01
Site 28	0.04	0.01	0.15	0.11
Site 13	0.09	<0.01	0.04	0.02
Site 16	0.20	0.45	<0.01	<0.01
Site 10	0.01	0.13	0.10	<0.01
Site 7	0.11	<0.01	0.01	0.15
Site 5	0.03	<0.01	<0.01	0.19
Site 4	0.02	0.01	0.01	0.19
Site 2	0.05	0.04	0.14	0.22
GF coastal	<0.01	0.01	0.07	0.06
GF central	0.01	0.07	0.29	0.01
GF north	0.07	<0.01	0.03	<0.01
GF ravines	0.04	0.01	<0.01	0.02
A. cristatellus	0.19	0.21	0.05	0.05
A. cooki	0.11	0.18	0.01	0.43
A. stratulus	<0.01	0.02	<0.01	0.01
A. pulchellus	<0.01	<0.01	<0.01	0.05
A. poncensis	<0.01	<0.01	0.01	<0.01
A. exsul	<0.01	0.14	0.15	0.36
A. wetmorei	0.01	<0.01	0.01	0.03
S. nicholsi	0.37	0.063	0.01	<0.01
S. roosevelti	0.05	0.08	0.74	0.01
P. wirshingi	0.27	0.31	0.02	0.05

Table B.6	Squared cosines of row (sites) and column (species) points
	for the first four CA dimensions. Cumulative total represent the total quality of the display of each site or species in four- dimensional space. All 10 species of lizards included in analysis.

	Dim. 1	Dim. 2	Dim. 3	Dim. 4	Cumulative
Site 36	0.14	0.49	0.26	0.10	0.98
Site 30	0.89	0.06	<0.01	0.04	0.99
Site 27	0.15	0.16	0.04	0.45	0.81
Site 28	0.30	0.07	0.45	0.08	0.90
Site 13	0.62	0.01	0.15	0.15	0.92
Site 16	0.32	0.56	<0.01	0.11	0.99
Site 10	0.06	0.58	0.29	0.06	0.99
Site 7	0.75	0.01	0.04	0.07	0.87
Site 5	0.56	<0.01	0.01	0.03	0.59
Site 4	0.38	0.11	0.06	0.05	0.60
Site 2	0.25	0.15	0.36	0.11	0.86
GF coastal	0.08	0.01	0.70	0.07	0.87
GF central	0.04	0.24	0.69	<0.01	0.97
GF north	0.56	<0.01	0.13	0.23	0.92
GF ravines	0.62	0.10	0.01	0.08	0.82
A. cristatellus	0.47	0.40	0.06	0.04	0.97
A. cooki	0.27	0.35	0.01	0.33	0.97
A. stratulus	0.03	0.34	<0.01	<b>0.06</b>	0.43
A. pulchellus	0.01	0.02	0.01	0.24	0.27
A. poncensis	0.02	0.04	0.12	0.02	0.20
A. exsul	<0.01	0.34	0.24	0.34	0.93
A. wetmorei	0.17	<0.01	0.15	0.22	0.55
S. nicholsi	0.87	0.11	0.02	<0.01	0.99
S. roosevelti	0.10	0.12	0.76	0.01	0.99
P. wirshingi	0.49	0.43	0.02	0.03	0.96

## **APPENDIX C**

Table C.1Location of Anolis cristatellus and A. cooki perches, including<br/>frequency (absolute and rounded to percentage) for each perch<br/>type selection. Type of perch also included (t = tree, s = shrub, c =<br/>cactus, v = vine).

		Frequen	су
Perch Location	Type	<u>A. cristatellus</u>	<u>A. cooki</u>
standing dead tree	t	379 (16%)	13 (17%)
Leucaena leucocephala	t	203 (8%)	
on substrate		174 (7%)	4 (5%)
Gymnanthes lucida	t	136 (6%)	1 (1%)
Pisonia albida	t	114 (5%)	6 (8%)
Exostema caribaeum	t	94 (4%)	4 (5%)
Thouinia striata	t	92 (4%)	1 (1%)
Bourreria succulenta	t	83 (3%)	
Bucida buceras	t	78 (3%)	
Amyris elemifera	t	76 (3%)	
Coccoloba diversifolia	t	73 (3%)	2 (3%)
Eugenia rhombea	t	58 (2%)	1 (1%)
Pictetia aculeata	t	54 (2%)	2(3%)
Eugenia foetida	t	50 (2%)	1 (1%)
Savia sessiliflora	t	48 (2%)	
Pithecellobium unguis-cati	t	42 (2%)	
Pilosocereus royenii	С	39 (2%)	2 (3%)
Erythroxylum rotundifolium	t	37 (2%)	6 (8%)
Krugiodendron ferreum	t	37 (2%)	
vine	V	36 (1%)	
Bursera simaruba	t	34 (1%)	4 (5%)
Capparis flexuosa	t	34 (1%)	2 (3%)
unknown	t	32 (1%)	
Tabebuia heterophylla	t	25 (1%)	2 (3%)
Guettarda elliptica	t	24 (1%)	1 (1%)
Capparis hastata	t	22 (1%)	
Coccoloba krugii-microstachya	t	22 (1%)	1 (1%)
Colubrina elliptica	t	18 (1%)	. ,
Calyptranthes pallens	t	16 (1%)	
Comocladia dodonaea	t	16 (1%)	2 (3%)
Clusia rosea	t	14 (1%)	
Prosopis pallida	t	14 (1%)	
Erythroxylum areolatum	t	13 (1%)	3 (4%)
Guaiacum sanctum	t	13 (1%)	2 (3%)
Randia aculeata	t	13 (1%)	3 (4%)

Table C.1 (cont'd)			
Leptocereus quadricostatus	С	12 (< 1%)	
Plumeria alba	t	12 (< 1%)	2 (3%)
Guaiacum officianale	t	11 (< 1%)	
Hypelate trifoliata	t	10 (< 1%)	
Jacquinia berterii	t	10 (< 1%)	1 (1%)
Antirhea acutata	t	9 (< 1%)	2 (3%)
Crossopetalum rhacoma	t	9 (< 1%)	
Swietenia mahaogani	t	9 (< 1%)	
Croton lucidus	S	9 (< 1%)	
Guettarda krugii	t	8 (< 1%)	
Capparis indica-cynophyllophora	t	7 (< 1%)	
Eugenia spp.	t	7 (< 1%)	
Erithalis fruticosa	t	6 (< 1%)	1 (1%)
Ficus citrifolia	t	6 (< 1%)	
Reynosia uncinata	t	6 (< 1%)	
Canella winterana	t	5 (< 1%)	1 (1%)
Eugenia xerophytica	t	5 (< 1%)	
Rochefortia acanthophora	t	5 (< 1%)	2 (3%)
Piscidia carthagenensis	t	4 (< 1%)	. ,
Schaefferia frutescens	t	4 (< 1%)	
Zanthoxylum flavum	t	4 (< 1%)	4 (5%)
Antirhea lucida	t	3 (< 1%)	
Celtis trinervia	t	3 (< 1%)	
Citharexylum fruticosum	t	3 (< 1%)	
Croton discolor	S	3 (< 1%)	
Eugenia lingustrina	t	3 (< 1%)	
Guapira fragrans	t	3 (< 1%)	
Meliococcus bijugatus	t	3 (< 1%)	
Picramnia pentandra	t	3 (< 1%)	
Bumelia obovata	S	2 (< 1%)	
Colubrina arborescens	t	2 (< 1%)	
Haematoxylum campechianum	t	2 (< 1%)	
Jatropha hemandifolia	S	2 (< 1%)	
Ziziphus reticulata	t	2 (< 1%)	
Acacia famesiana	t	1 (< 1%)	
Bernardia dichotoma	t	1 (< 1%)	
Croton humilis	S	1 (< 1%)	
Lantana camara	S	1 (< 1%)	
Lantana involucrata	S	1 (< 1%)	
Polygala cowelli	t	1 (< 1%)	
Reynosia guama	t	1 (< 1%)	
Rondeletia pilosa	S	1 (< 1%)	
Total		2413	76

# LITERATURE CITED

## LITERATURE CITED

- Aide, T. M., J. K. Zimmerman, M. Rosario, and H. Marcano. 1996. Forest recovery in abandoned cattle pastures along an elevational graident in Northeastern Puerto Rico. Biotropica 28(4a): 537-548
- Andrews, R. M. 1971. Structural habitat and time budget of a tropical Anolis lizard. Ecology 52: 262-270
- Andrews, R. M. and A. S. Rand. 1983. Limited dispersal of juvenile Anolis limifrons. Copeia 1983(2): 429-434
- Andrews, R. M. and S. J. Wright. 1994. Long-term population fluctuations of a tropical lizard: a test of causality. Pp. 267-285 *In:* L. J. Vitt and E. R. Pianka (eds.). Lizard ecology: historical and experimental perspectives. Princeton University Press, Princeton, NJ
- Bierregard, R. O., Jr. and V. H. Dale. 1996. Islands in an ever-changing sea: the ecological and socioeconomic dynamics of Amazonian rain forest fragments. Pp. 187-204 In: J. Schelhas and R. Greenberg (eds.). Forest patches in tropical landscapes. Island Press, Washington, D. C.
- Bierregard, R. O., Jr., W. F. Laurance, J. W. Sites, Jr., A. J. Lynam, R. K. Didham, M. Andersen, C. Gascon, M. D. Tocher, A. P. Smith, V. M. Viana, T. E. Lovejoy, K. E. Sieving, E. A. Kramer, C. Restrepo, and C. Moritz. 1997. Key Priorities for the study of fragmented tropical ecosystems. Pages 515-525 *In:* W. F. Laurance and R. O. Bierregard, Jr. (eds.). Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, IL
- Birdsey, R. A. and P. L. Weaver. 1982. The forest resources of Puerto Rico. Resource Bulletin, SO-85. USDA Forest Service Southern Experiment Station, New Orleans, LA
- Birdsey, R. A. and P. L. Weaver. 1987. Forest area trends in Puerto Rico. USDA Forest Service Research Note, SO-331. New Orleans, LA
- Bosch, W. 1978. A procedure for quantifying certain geomorphological features. Geographical Analysis 10: 241-247
- Brown, P. R. and A. C. Echternacht. 1991. Interspecific behavioral interaction of adult male *Anolis carolinensis* (Sauria: Iguanidae): A preliminary field study. Anolis Newsletter IV: 21-30

- Brown, J.H. and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 56: 987-992
- Campbell, T. 1999. Consequences of the Cuban brown anole invasion in Florida: it's not easy being green. Anolis Newsletter V: 12-21
- Castilleja, G. 1991. Seed germination and early establishment in a subtropical dry forest. Ph.D. dissertation, Yale University, New Haven, CT
- Corlett, R. T. and I. M. Turner. 1997. Long-term survival in tropical forest remnants in Singapore and Hong Kong. Pages 333-345 *In:* W. F. Laurance and R. O. Bierregard, Jr. (eds.). Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, IL
- Cutler, A. 1991. Nested faunas and extinction in fragmented habitats. Conservation Biology 5(4): 496-505
- Dale, V. H. and S. M. Pearson. 1997. Quantifying habitat fragmentation due to land use change in Amazonia. Pages 400-409 *In:* W. F. Laurance and R. O. Bierregard, Jr. (eds.). Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, IL
- Davis, J. C. 1986. Statistics and data analysis in geology, 2<sup>nd</sup> ed. John Wiley, New York, NY
- Dial, R and J. Roughgarden. 1994. Notes on the absolute abundance of canopy anoles, Anolis cuvieri, A. stratulus and A. evermanni (Lacertilia: Polychridae) in the Luquillo Forest, Puerto Rico. Caribbean Journal of Science 30(3-4): 278-279
- Diamond, J. 1972. Biogeographic kinetics: estimation of relaxation times for Avifaunas of southwest Pacific islands. Proceedings of the National Academy of Science, U.S.A. 69: 3199-3202
- Diamond, J. 1973. Distributional ecology of New Guinea birds. Science 179: 759-769
- Dietz, J. L. 1986. Economic History of Puerto Rico: Institutional Change and Capitalist Development. Princeton University Press, Princeton, NJ
- Echternacht, A. C. 1999. Possible causes for the rapid decline in population density of green anoles, *Anolis carolinensis* (Sauria: Polychrotidae) following invasion by the brown anole, *Anolis sagrei*, in the southeastern United States. Anolis Newsletter V: 22-27

- Estes, R. 1983. The fossil record and early distribution of lizards. Pp. 365-398 *in:* A. G. J. Rhodin and K. Miyata (eds.) Advances in Herpetology and Evolutionary Biology. Harvard University Press, Cambridge, MA
- Ewel, J. J. and J. L. Whitmore. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. USDA, Forest Service. International Institute of Tropical Forestry, Rio Piedras, PR. Forest Service Research Paper ITF-18
- FAO (Food and Agriculture Organization of the United Nations)/UNESCO. 1993. Forest resource assessment 1990 - tropical countries. Forestry paper no. 112. Food and Agriculture Organization of the United Nations, Rome.
- Faaborg, J. and W. J. Arendt. 1990. Long-term studies of Guánica Forest birds. Acta Científica 4(1-3): 69-80
- Fahrig, L. and G. Merriam. 1985. Habitat patch connectivity and population survival. Ecology 66: 1762-1768
- Fahrig, L. and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology 8(1): 50-59
- Farnsworth, E. J. 1993. Ecology of semi-evergreen plant assemblages in the Guánica Dry Forest, Puerto Rico. Caribbean Journal of Science 29(1-2): 106-123
- Fobes, T. M., R. Powell, J. S. Parmerlee, Jr., A. Lathrop, and D. D. Smith. 1992. Natural history of *Anolis cybotes* (Sauria: Polychridae) from an altered habitat in Barahona, Dominican Republic. Caribbean Journal of Science 28(3-4): 200-207
- Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? Ecological Applications 3(2): 202-205
- Garber, S. D. 1978. Opportunistic feeding behavior of *Anolis cristatellus* (Iguanidae: Reptilia) in Puerto Rico. Transactions of the Kansas Academy of Science 82(1): 79-80
- Gorman, G. C., D. G. Buth, M. Soulé, and S. Y. Yang. 1980. The relationships of *Anolis cristatellus* species group: electrophoretic analysis. Journal of Herpetology 14(3): 269-278
- Gorman, G. C., D. G. Buth, M. Soulé, and S. Y. Yang. 1983. The relationships of the Puerto Rican *Anolis*: electrophoretic and karyotypic studies. Pp. 626 642 *In*: G. J. Anders, Rhodin, and K. Miyata (eds.). Advances in

herpetology and evolutionary biology: essays in honor of E. E. Williams. Museum of Comparative Zoology, Harvard University, Cambridge, MA

- Gorman, G. C. and R. Harwood. 1977. Notes on population density, vagility, and activity patterns of the Puerto Rican grass lizard, *Anolis pulchellus* (Reptilia, Lacertilia, Iguanidae). Journal of Herpetology 11(3): 363-368
- Gorman, G. C., R. Thomas, and L. Atkins. 1968. Intra- and interspecific chromosome variation in the lizard *Anolis cristatellus* and its close relatives. Breviora 293: 1-13
- Goto, M. M. and M. A. Osborne. 1989. Nocturnal microhabitats of two Puerto Rican grass lizards, *Anolis pulchellus* and *Anolis krugi*. Journal of Herpetology 23(1): 79-81
- Grant, C. 1931. Notes on the ameivas of Puerto Rico. Copeia 1931: 62
- Greenacre, M. J. 1993. Correspondence analysis in practice. Academic Press, Harcourt, Brace and Company. New York, NY
- Greenacre, M. J. and E. S. Vrba. 1984. Graphical display and interpretation of antelope census data in African wildlife areas, using correspondence analysis. Ecology 65(3): 984-997
- Harris, L. D. 1984. The fragmented forest. Island biogeographic theory and the preservation of biotic diversity. University of Chicago Press, Chicago, IL
- Harris, L. D. and P. Kangas. 1979. Designing future landscapes from principles of form and function. Pp. 725-729 In: G. H. Pilsner and R. C. Smardon (eds.). Our national landscape: applied techniques for analysis and management of the visual resource. U. S. Forest Service General Technical Report PSW-34. Washington, D. C.
- Hass, C. A. 1991. Evolution and biogeography of West Indian *Sphaerodactylus* (Sauria: Gekkonidae): a molecular approach. Journal of Zoology 225: 525-561
- Heatwole, H. 1968. Relationship of escape behavior and camouflage in anoline lizards. Copeia 1968: 108-113
- Heatwole, H. 1976. Herpetolgeography of Puerto Rico. VII. Geographic variation in the Anolis cristatellus complex in Puerto Rico and the Virgin Islands. Occasional Paper for the Museum of Natural History at the University of Kansas, No. 46

- Heatwole, H. and F. Torres. 1967. Distribution and geographic variation of the Ameivas of Puerto Rico and the Virgin Islands. Studies on the Fauna of Curaçao and other Caribbean Islands 24(92): 63-111
- Heckel, D. G. and J. Roughgarden. 1979. A technique for estimating the size of lizard populations. Ecology 60(5): 966-975
- Hess, N. E. and J. B. Losos. 1991. Interspecific aggression between *Anolis cristatellus* and *A. gundlachi*: comparison of sympatric and allopatric populations. Journal of Herpetology 25(2): 256-259
- Holdridge, L. R. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica
- Janzen, D. H. 1988a. Tropical dry forests, the most endangered major tropical ecosystem. Pp. 130-137 *In:* E.O. Wilson (ed.). Biodiversity. National Academy Press, Washington, D.C.
- Janzen, D. H. 1988b. Management of habitat fragments in a tropical dry forest: growth. Annals of the Missouri Botanical Gardens 75: 105-116
- Jenssen, T. A. 1973. Shifts in the structural habitat of *Anolis opalinus* due to congeneric competition. Ecology 54: 863-869
- Jenssen, T. A. 1990. *Anolis cooki* Grant: Cook's anole. Catalogue of American Amphibians and Reptiles No. 488:1-2
- Jenssen, T. A., D. L. Marcellini, C. A. Pague, and L. A. Jenssen. 1984. -Competitive interference between the Puerto Rican lizards, *Anolis cooki* and *A. cristatellus*. Copeia 1984(4): 853-862
- Joliffe, I. T. 1986. Principal Component Analysis. Springer-Verlag, New York, NY
- Kepler, C. B. and A. K. Kepler. 1970. Preliminary comparison of bird species diversity in Luquillo and Guánica Forests. Chapter E-14; 183-191 *In:* H. T. Odum (ed.). A tropical rain forest. USAEC, Oak Ridge, TN
- Kiester, A. R., G. C. Gorman, and D. Colon Arroyo. 1975. Habitat selection behavior of three species of *Anolis* lizards. Ecology 56(1): 220-225
- Kitchener, D. J. 1982. Predictors of vertebrate species richness in nature reserves in the Western Australian wheatbelt. Australian Wildlife Research 9: 1-7

- Kitchener, D. J., A. Chapman, J. Dell, B. G. Muir and M. Palmer. 1980. Lizard assemblage and reserve size and structure in the Western Australian wheatbelt - some implications for conservation. Biological Conservation 17: 25-62
- Kitchener, D. J. and R. A. How. 1982. Lizard species in small mainland habitat isolates and islands off southwestern Western Australia. Australian Wildlife Research 9: 357-363
- Kitchener, D. J., R. A. How, and J. Dell. 1988. Biology of *Oedura reticulata* and *Gehyra variegata* (Gekkonidae) in an isolated woodland of Western Australia. Journal of Herpetology 22(4): 401-412
- Kramer, E. A. 1997. Measuring landscape changes in remnant tropical dry forests. Pp. 386-399 *In:* W. F. Laurance and R. O. Bierregard, Jr. (eds.).
   Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, IL
- Lamb, D., J. Parotta, R. Keenan, and N. Tucker. 1997. Rejoining habitat remnants: restoring degraded rainforest lands. Pages 366-385 *In:* W. F. Laurance and R. O. Bierregard, Jr. (eds.). Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, IL
- Laurance, W. F. and R. O. Bierregard, Jr. (eds.). 1997. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, IL
- Laurance, W. F., R. O. Bierregard, Jr., C. Gascon, R. K. Didham, A. P. Smith, A. J. Lynam, V. M. Viana, T. E. Lovejoy, K. E. Sieving, J. W. Sites, Jr., M. Andersen, M. D. Tocher, E. A. Kramer, C. Restrepo, and C. Moritz. 1997. Tropical forest fragmentation: synthesis of a diverse and dynamic discipline. Pages 502-514 *In:* W. F. Laurance and R. O. Bierregard, Jr. (eds.). Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, IL
- Lenart, L. A., R. Powell, J. S. Parmerlee, Jr., A. Lathrop, and D. D. Smith. 1997. Anoline diversity in three differentially altered habitats in the Sierra de Baoruco, República Dominica, Hispaniola. Biotropica 29(1): 117-123
- Lewis, A. R. 1986. Body size and growth in two populations of the Puerto Rican ground lizard (Teiidae). Journal of Herpetology 20(2): 190-195
- Lewis, A. R. 1989. Diet selection and depression of prey abundance by and intensively foraging lizard. Journal of Herpetology 23(2): 164-170

- Lewis, A. R. and J. E. Saliva. 1987. Effects of sex and size on home range, dominance, and activity budgets in *Ameiva exsul* (Lacertilia: Teiidae). Herpetologica 43(3): 374-383
- Lerdau, M., J. Whitbeck and N. M. Holbrook. 1991. Tropical deciduous forest: death of a biome. Trends in Ecology and Evolution 6(7): 201-202
- Lister, B. C. 1976. The nature of niche expansion in West Indian *Anolis* lizards. I. Ecological consequences of reduced competition. Evolution 30: 659-676
- Lister, B. C. 1981. Seasonal relationships of rainforest anoles. Ecology 62 (6): 1548-1560

- Lord, J. M. and D. A. Norton. 1990. Scale and spatial concept of fragmentation. Conservation Biology 4: 197-202
- Losos, J. B., J. C. Marks, and T. W. Schoener. 1993. Habitat use and ecological interactions of an introduced and a native species of *Anolis* lizard on Grand Cayman, with a review of the outcomes of anole introductions. Oecologia 95: 525-532
- Losos, J. B. and D. J. Irschick. 1996. The effect of perch diameter on escape behavior of *Anolis* lizards: laboratory predictions and field tests. Animal Behaviour 51:593-602
- Losos, J. B. and B. Sinervo. 1989. The effect of morphology and perch diameter on sprint performance of *Anolis* lizards. Journal of Experimental Biology 145: 23-30
- Losos, J. B. and D. A. Spiller. 1999. Differential colonization success and Assymetrical interactions between two lizard species. Ecology 80(1): 252-258
- Lugo, A. E., J. A. Gonzalez-Liboy, B. Cintron, and K. Dugger. 1978. Structure, productivity, and transpiration of a subtropical dry forest in Puerto Rico. Biotropica 10: 278-291
- Lugo, A. E., O. Ramos, S. Molina, F. N. Scatena, and L. L. Vélez Rodríguez. 1996. A fifty-three year record of land use change in the Guánica Forest Biosphere Reserve and its vicinity. USDA Forest Service, International Institute of Tropical Forestry, Rio Piedras, Puerto Rico
- MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ

- Marcellini, D. L. and T. A. Jenssen. 1983. A character for differentiating the sympatric lizards. *Anolis cooki* and *Anolis cristatellus*. Herpetological Review 14(4): 113-114
- Marcellini, D. L., T. A. Jenssen, and C. A. Pague. 1985. Distribution of the lizard *Anolis cooki*, with comments on its possible future extinction. Herpetological Review 16(4): 99-102
- Moermond, T. C. 1979. Habitat constraints on the behavior, morphology, and community structure of *Anolis* lizards. Ecology 60: 152-164
- Morales-Carrion, A. 1983. Puerto Rico, a political and social history. Norton Press, New York, NY
- Morrison, D. F. 1990. Multivariate statistical methods, 3<sup>rd</sup> ed. McGraw-Hill Publishing Company. New York, NY
- Murphy, P. G. and A. E. Lugo. 1986a. Structure and biomass of a subtropical dry forest in Puerto Rico. Biotropica 18: 89-96
- Murphy, P. G. and A. E. Lugo. 1986b. Ecology of tropical dry forest. Annual Review of Ecology and Systematics 17: 67-88
- Murphy, P. G. and A. E. Lugo. 1990. Dry forests of the tropics and subtropics: Guánica Forest in context. Acta Científica 4(1-3): 15-24
- Murphy, P. G. and A. E. Lugo. 1995. Dry forests of Central America and the Caribbean. Pp. 9-34 *In:* S. H. Bullock, H. A. Mooney, and E. Medina (eds.). Seasonally Dry Tropical Forests. Cambridge University Press, Cambridge, England
- Murphy, P.G., A. E. Lugo, A. J. Murphy, and D. C. Nepstad. 1995. The dry forest of Puerto Rico's south coast. *In:* A. E. Lugo and C. Lowe (eds.). Tropical Forests: Management and Ecology. Springer-Verlag, New York, NY
- Nagy, K. A. 1987. Field metabolic rates and food requirement scaling in mammals and birds. Ecological Monographs 57: 111-128
- Nason, J. D., P. R. Aldrich and J. L. Hamrick. 1997. Dispersal and the dynamics of genetic structure in fragmented tropical tree populations. Pp. 304-320 *In*: W. F. Laurance and R. O. Bierregard, Jr. (eds.). Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, IL

- Newmark, W. D. 1987. A land-bridge perspective on mammalian extinctions in western North American parks. Nature 325: 430-432
- Noss, R. F. 1983. A regional landscape approach to maintain diversity BioScience 33(11): 700-705
- Ortiz, P. R. 1990. Status and distribution of *Anolis cooki* (Reptilia; Sauria; Iguanidae). Acta Cientifica 4(1-3): 157-159
- Ortiz, P. R. and T. A. Jenssen. 1982. Interspecific aggression between lizard competitors, *Anolis cooki* and *Anolis cristatellus*. Zeitschrift fuer Tierpsychologie 60: 227-238
- Overton, W. S. 1971. Estimating the number of animals in wildlife populations. pp. 403-455 *in*: R. H. Giles (ed.). Wildlife management techniques. Edwards Brothers, Ann Arbor, MI
- Patterson, B. D. and W. Atmar. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. Pp. 65-82 *in:* L. R. Heany and B. D. Patterson (eds.). Island biogeography of mammals. Biological Journal of the Linnean Society. 28. Academic Press and the Linnean Society of London, England
- Philibosian, R. 1975. Territorial behavior and population regulation in the lizards, Anolis acutus and A. cristatellus. Copeia 1975(3): 428-444
- Portmann, A. 1967. Animal forms and patterns. Schocken Books, New York, NY
- Powell, G. V. N. and R. Bjork. 1995. Implications of intratropical migration on reserve design: a case study using *Pharomachrus mocinno*. Conservation Biology 9: 354-362
- Pregill, G. 1981. Late Pleistocene herpetofaunas from Puerto Rico. University of Kansas Museum of Natural History Misc. Publication. 71
- Quinn, J. F. and S. P. Harrison. 1988. Effects of habitat fragmentation and isolation on species richness: evidence from biogeographic patterns. Oecologia 75: 132-140
- Raffaele, H. A. 1989. A guide to the birds of Puerto Rico and the Virgin Islands (revised ed.). Princeton University Press, Princeton, NJ
- Ramjohn, I. A., P. G. Murphy, and T. M. Burton. Unpublished. Islands of biodiversity in altered tropical landscapes. Final project report, IITF pub. ITF-CA-94-008. Rio Piedras, Puerto Rico
- Rand, A. S. 1964. Ecological distribution in anoline lizards of Puerto Rico. Ecology 45: 745-752
- Reagan, D. P. 1986. Foraging behavior of *Anolis stratulus* in a Puerto Rican rain forest. Biotropica 18(2): 157-160
- Reagan, D. P. 1992. Congeneric species distribution and abundance in a three dimensional habitat: the rain forest anoles of Puerto Rico. Copeia 1992(2): 392-403
- Reagan, D. P. 1996. Anoline lizards. *In:* D. P. Reagan and R. B. Waide (eds.). Food web of a tropical rain forest. University of Chicago Press, Chicago, IL
- Redford, K. H., A. Taber, and J. A. Simonetti. 1990. There is more to biodiversity than the tropical rainforests. Conservation Biology 4(3): 328-330
- Rivera, L. W. and T. M. Aide. 1998. Forest recovery in the karst region of Puerto Rico. Forest Ecology and Management 108: 63-75
- Rivero, J. A. 1978. The amphibians and reptiles of Puerto Rico. University of Puerto Rico, Editorial Universitaria, Barcelona, Spain
- Robbins, C. S., D. K. Dawson, and B. A. Dowell. 1989. Habitat area Requirements of breeding forest birds of the Middle Atlantic States. Wildlife Monograph 103: 1-34
- Roughgarden, J. 1995. *Anolis* lizards of the Caribbean: ecology, evolution, and plate tectonics. Oxford University Press, New York, NY
- Salzburg, M. A. 1984. Anolis sagrei and Anolis cristatellus in southern Florida: a case study in interspecific competition. Ecology 65(1): 14-19
- Sarre, S. 1995. Size and structure of populations of Oedura retuiculata (Reptilia: Gekkonidae) in woodland remnants: implications for the future regional distribution of a currently common species. Australian Journal of Ecology 20: 288-298
- Sarre, S., G. T. Smith, and J. A. Meyers. 1995. Persistence of two species of gecko (*Oedura reticulata* and *Gehyra variegata*) in remnant habitat. Biological Conservation 71: 25-33
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5(1): 18-32

- Schaller, G. B. and P. G. Crawshaw, Jr. 1980. Movement patterns of jaguar. Biotropica 12: 161-168
- Schoener, T. W. 1968. The Anolis lizards of Bimini: Resource partitioning in a complex fauna. Ecology 49: 704-726
- Schoener, T. W. 1975. Presence and absence of habitat shift in some widespread lizard species. Ecological Monographs 45: 233-249
- Schoener, T. W. 1977. Competition and the niche. Pp. 35-136 *in:* C. Gans and D. Tinkle (eds.). Biology of the Reptilia, vol. 7. Academic Press, New York, NY
- Schoener, T. W. 1985. Are lizard populations unusually constant through time? American Naturalist 126: 633-641
- Schoener, T. W. 1994. Temporal variability in lizard numbers: what the appropriate kind of study population? American Naturalist 144(5): 868-872
- Schoener, T. W. and A. Schoener. 1971a. Structural habitats of West Indian Anolis lizards. I. Jamaican Iowlands. Breviora 368: 1-53
- Schoener, T. W. and A. Schoener. 1971b. Structural habitats of West Indian Anolis lizards. II. Puerto Rican uplands. Breviora 375: 1-39
- Schoener, T.W. and A. Schoener. 1978. Inverse correlation of survival in lizards with island size and avifaunal richness. Nature 274: 685-687
- Schoener, T.W. and A. Schoener. 1982. The ecological correlates of survival in some Bahamian *Anolis* lizards. Oikos 39: 1-16
- Schoener, T.W. and A. Schoener. 1983a. Distribution of vertebrates on some very small islands. I. Occurrence sequences of individual species. Journal of Animal Ecology 52: 209-235
- Schoener, T.W. and A. Schoener. 1983b. Distribution of vertebrates on some very small islands. II. Patterns in species numbers. Journal of Animal Ecology 52: 237-262
- Schwartz, A. and R. W. Henderson. 1991. Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history. University of Florida Press, Gainsville, FL

- Scott, N. J., Jr., D. E. Wilson, C. Jones, and R. M. Andrews. 1976. The choice of perch dimensions by lizards of the genus *Anolis* (Reptilia, Lacertilia, Iguanidae). Journal of Herpetology 10: 75-84
- Shochat, D. and H. C. Dessauer. 1981. Comparative immunological study of Albumins of *Anolis* lizards of the Caribbean Islands. Comparative Biochemical Physiology 68A: 67-73
- Smith, G. T., G. W. Arnold, S. Sarre, M. Abensperg-Traun, and D. E. Steven. 1996. The effect of habitat fragmentation and grazing on animal communities in remnants of gimlet *Eucalyptus salubris* woodland in the Western Australian wheatbelt. II. Lizards. Journal of Applied Ecology 33: 1302-1310
- Soulé, M. E., B. A. Wilcox, and C. Holtby. 1979. Benign neglect: a model of faunal collapse in the game reserves of East Africa. Biological Conservation 15: 259-272
- Stamps, J. A., 1977. The relationship between resource competition, risk, and aggression in a tropical territorial lizard. Ecology 58: 349-358
- Stohlgren, T. J., M. B. Coughenour, G. W. Chong, D. Binkley, M. A. Kalkhan, L. D. Schell, D. J. Buckley, and J. K. Berry. 1997. Landscape analysis of plant diversity. Landscape Ecology 12: 155-170
- Thomas, R. and A. Schwartz. 1966. *Sphaerodactylus* (Gekkonidae) in the Greater Puerto Rico region. Bulletin of the Florida State Museum 10(6): 193-260
- Thomlinson, J. R., M. I. Serrano, T. M. López, T. M. Aide, and J. K. Zimmerman. 1996. Land-use dynamics in a post-agricultural Puerto Rican landscape (1936-1988). Biotropica 28(4a): 525-536
- Tokarz, R. R. and J. W. Beck, Jr. 1987. Behaviour of the suspected lizard competitors *Anolis sagrei* and *Anolis carolinensis*: an experimental test For behavioural interference. Animal Behaviour 35: 722-734
- Tosi, J. A., Jr., and R. F. Voertman. 1964. Some environmental factors in the economic development of the tropics. Economic Geography 40: 189-205
- Turner, F. B. 1977. The dynamics of populations of squamates, crocodylians, and rhynchocephalians. II. Lizards. Pp. 158-201 *In:* C. Gans and D. W. Tinkle (eds.). Biology of the Reptilia, vol. 7. Academic Press, New York, NY

- Turner, F. B., R. I. Jennrich, and J. O. Weintaub. 1969. Home ranges and body size of lizards. Ecology 50: 1076-1081
- Turner, I. M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. Journal of Applied Ecology 33: 200-209
- Turner, I. M. and R. T. Corlett. 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. Trends in Ecology and Evolution 11(8): 330-333
- Vélez Rodríguez, L. L. 1995a. Land use and land cover 1936 Guánica Commonwealth Forest. USDA Forest Service, International Institute of Tropical Forestry, Rio Piedras, Puerto Rico (map)
- Vélez Rodríguez, L. L. 1995b. Land use and land cover 1950-51 Guánica Commonwealth Forest. USDA Forest Service, International Institute of Tropical Forestry, Rio Piedras, Puerto Rico (map)
- Vélez Rodríguez, L. L. 1995c. Land use and land cover 1963 Guánica Commonwealth Forest. USDA Forest Service, International Institute of Tropical Forestry, Rio Piedras, Puerto Rico (map)
- Vélez Rodríguez, L. L. 1995d. Land use and land cover 1971 Guánica Commonwealth Forest. USDA Forest Service, International Institute of Tropical Forestry, Rio Piedras, Puerto Rico (map)
- Vélez Rodríguez, L. L. 1995e. Land use and land cover 1983 Guánica Commonwealth Forest. USDA Forest Service, International Institute of Tropical Forestry, Rio Piedras, Puerto Rico (map)
- Vélez Rodríguez, L. L. 1995f. Land use and land cover 1989 Guánica Commonwealth Forest. USDA Forest Service, International Institute of Tropical Forestry, Rio Piedras, Puerto Rico (map)
- Whitmore, T. C. 1997. Tropical forest disturbance, disappearance, and species loss. Pp. 3-12 *In:* W. F. Laurance and R. O. Bierregard, Jr. (eds.).
  Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, IL
- Wilcox, B. A. and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. American Naturalist 125: 879-887
- Williams, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. Quarterly Review of Biology 44: 345 389

- Williams, E. E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. Pp. 47-89 *In:* T. Dobzhansky, M. Hecht, and W. Steere (eds.). Evolutionary Biology, 6. Appleton-Century Crofts. New York, NY
- Williams, E. E. 1976. West Indian anoles: a taxonomic and evolutionary summary. I. Introduction and a species list. Breviora 440: 1-21
- Williams, E. E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. Pages 326-370 *In*: R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.). Lizard ecology: studies of a model organism. Harvard University Press, Cambridge, MA
- Zar, J. H. 1984. Biostatistical Analysis, second edition. Prentice Hall, Englewood Cliffs, NJ