ECOMORPHOLOGY, LOCOMOTION, AND MICROHABITAT STRUCTURE:
PATTERNS IN A TROPICAL MAINLAND ANOLIS COMMUNITY

By

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TABLE OF CONTENTS

	<u>Page</u>
ACKNOWLEDGMENTS.....	ii
ABSTRACT.....	vi
INTRODUCTION.....	1
THE HABITAT-MATRIX MODEL.....	3
Locomotor Behavior.....	3
Functional Morphology.....	4
STUDY SYSTEM AND METHODS.....	9
The System.....	9
Approach for Testing the Model.....	10
Experiment I. Proximate Effects of Microhabitat Structure on Locomotor Behavior.....	11
Field Test of Predictions Concerning Locomotor Behavior.....	14
Experiment II. Interspecific Differences in Locomotor Propensities.....	22
Morphometrics.....	23
RESULTS.....	26
Experiment I. Proximate Effects of Microhabitat Structure on Locomotor Behavior.....	26
Field Test of Predictions Concerning Locomotor Behavior.....	32
Experiment II. Interspecific Differences in Locomotor Propensities.....	50
Morphometrics.....	53

DISCUSSION.....	66
Microhabitat Structure and Locomotor Behavior:	
Proximate Influences.....	66
Microhabitat Structure and Locomotor Behavior in	
the Field.....	67
Interspecific Differences in Locomotor Behavior:	
Proximate Responses Or Evolved Propensities?.....	69
Microhabitat Structure and Morphology: Patterns	
and Predictions.....	71
Body Size and the Habitat-matrix Model.....	74
Are Differences in Proportions Among Species an	
Allometric Consequence of Size?.....	81
Mass-length Relationships.....	82
What Measure of Locomotor Performance Do Anoles Maximize?....	85
Adaptation Versus "Phylogenetic Inertia".....	87
Locomotor or Microhabitat Specialization?.....	88
Habitat Structure and Community Structure.....	89
LITERATURE CITED.....	95
BIOGRAPHICAL SKETCH.....	107

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ECOMORPHOLOGY, LOCOMOTION, AND MICROHABITAT STRUCTURE:
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By

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At a lower montane site in northwestern Costa Rica, I studied the locomotor behavior and functional morphology of six species of Anolis lizards in relation to structural features of their microhabitats in an attempt to understand better the phenotypic structure of this community. I tested the habitat-matrix model, which was formulated to explain patterns of morphological convergence among Anolis faunas on islands of the Greater Antilles. According to this model, the relative importance of various patterns of locomotion (running, jumping, and crawling) for each species depends on two structural-microhabitat features--support sizes and support-matrix density; each species adapts behaviorally and morphologically to these features.

To study locomotor behavior, I employed field observation and experiments in field enclosures. I first examined the proximate influences of support size and support-matrix density on locomotor behavior by manipulating an artificial matrix of stems within a field

enclosure. Both structural features exerted significant effects, yet that of support-matrix density was more consistent. I then tested whether patterns observed in this experiment could be extrapolated to field comparisons of species (or intraspecific classes--juveniles, adult females, and adult males). Through standardized vegetation sampling, I quantified the structural configuration encountered by each anole class, and, through timed field observations, quantified patterns of microhabitat use and locomotor behavior. Again, support-matrix density explained most of the variation in locomotor behavior among anole classes, yet support diameter also exerted a significant, but weaker, effect. Finally, comparing different species in the same artificial matrix, I found them to differ in locomotor propensities independently of the proximate effects of microhabitat structure.

Using a morphometric approach, I tested predictions, derived from biomechanics and comparisons of locomotor behavior, concerning interspecific variation in morphology. Differences in limb proportions among species accorded well with these predictions, suggesting that selection for locomotor ability in relation to microhabitat structure is an important determinant of shape. Furthermore, functional relationships between body size and locomotion, and correlations between size and structural niche, suggested that microhabitat structure may exert important selective pressures, not only on shape, but also on size.

INTRODUCTION

Studies of locomotor behavior and morphology of animals in relation to habitat structure can enhance our understanding of morphological patterns in nature (e.g., Fleagle 1977a, 1977b; Moermond 1979a; Newton 1967). Of course, these studies must be tempered by an appreciation of the historical context and phylogenetic constraints on evolution. Only naively would one assume that organisms are at an evolutionary "equilibrium" (sensu Liem and Wake 1985) with current environmental demands. Nonetheless, by understanding the constraints of habitat on locomotion and morphology, one can construct predictive models of the evolutionary trajectories that morphological change is likely to follow. In comparing closely related species, for example, one can first assess interspecific differences in locomotor behavior that result from differences in habitat (or microhabitat) structure. One can then hypothesize, from biomechanics, the morphological consequences of these behavioral differences (e.g., Fleagle 1977a, 1977b). I followed this approach in examining the relationship between habitat structure and morphological patterns in a community of Anolis lizards (Iguanidae).

Anolis lizards have radiated extensively both in the West Indies and the mainland Neotropics. In the Greater Antilles, a series of ecological types, or "ecomorphs," each designated by its modal perch (grass-bush, trunk-ground, trunk, trunk-crown, twig, or crown), is repeated among communities (Collette 1961; Rand 1964, 1967; Rand and

Williams 1969; Schoener and Schoener 1971a, 1971b; Williams 1972; 1983). Ecologically analogous species resemble one another in morphology (size, shape, and coloration) irrespective of island or lineage (Rand and Williams 1969; Williams 1983). This remarkable example of convergence suggests that anoles are evolving in response to selective pressures that occur in regular, spatially repeated patterns, yet these selective pressures remain poorly understood.

From his study of seven Hispaniolan species, Moermond (1979a) proposed a model, hereafter referred to as the habitat-matrix model (described below), in which a given species of anole adapts behaviorally and morphologically to the three-dimensional structure of its environment. Using behavioral experiments, field observations, and morphometrics, I tested this model at Monteverde, a lower montane site in northwestern Costa Rica. The habitat-matrix model had not been tested previously for a complex Anolis community outside that for which it was formulated. Nor had it been applied to mainland anoles, which are poorly known in comparison to their West Indian counterparts (Williams 1983).

THE HABITAT-MATRIX MODEL

Locomotor Behavior

An arboreal lizard typically faces two challenges to its locomotor abilities. First, it must traverse supports of various sizes, strengths, flexibilities, and orientations. In doing so, it may employ several locomotor patterns--including running, walking, and crawling (e.g., Moermond 1979a, 1979b, 1981, 1986; Peterson 1984)--and special mechanisms for gripping supports (Peterson 1983, 1984; Peterson and Williams 1981; Russell 1979, 1981). Second, because habitat matrices are discontinuous, an arboreal lizard must cross gaps between supports. It may bridge a gap by extending long limbs and, afterward, transferring weight to the new support (e.g. Chamaeleo), or it may jump (e.g., Anolis) or glide (e.g., Draco) between supports (Evans 1982; Moermond 1979a; Peterson 1984). Because of the varying demands on locomotion, arboreal lizards commonly employ multiple locomotor patterns.

Moermond (1979a) hypothesized that the relative importance of various patterns of locomotion differs among anole species, depending on two structural-microhabitat features--the sizes of supports and the distances between them. These two attributes, he reasoned, should influence locomotion as follows. First, a broader or longer support allows more movement on the support itself; hence, an anole using larger supports should jump less frequently. Second, where distances

between supports are large, an anole should jump less frequently than where support-matrix density is higher. Of course, extremely high densities (i.e., nearly contiguous supports) might obviate jumping to cross gaps, but matrices used by anoles generally fall outside this range. Of movements contained on single supports, Moermond recognized two kinds--runs and crawls, defined by velocity. "Running" subsumes a continuum of speeds; technically, some "runs" would probably be better described as walking (sensu Hildebrand 1985), in which each foot is on the ground half or more of the time. "Crawling" comprises slower, more deliberate movements. Moermond expected crawls to be most frequent where supports are too far apart for jumping yet are too narrow for running. In his observational study on Hispaniola, microhabitat specialists differed predictably in the proportions of runs, jumps, and crawls they made. Categorizing species as "runners," "jumpers," and "crawlers," Moermond interpreted these behavioral differences as evidence of locomotor specialization. He then asked how locomotor specialty relates to morphology.

Functional Morphology

Moermond (1979a) reported several differences in bivariate shape among the behaviorally defined groups. First, the hind limbs of "jumpers" were disproportionately long relative to their fore limbs; fore and hind limbs were more similar in length in "runners" and "crawlers." Anoles primarily make standing jumps in which thrust is generated by extension of the hind limbs. Moermond therefore

reasoned (p. 158) that the hind limbs of "jumpers" should be elongated "to provide the necessary rapid thrust." The expected correlation between hind-limb length and jump distance (d) follows from the ballistic model:

$$d = \frac{v^2 \sin^2 \theta}{g}, \quad (1)$$

where g is the acceleration due to gravity, θ the angle of takeoff, and v the velocity at takeoff. One way to lengthen jump distance is to raise takeoff velocity by increasing the distance (or time) through which acceleration occurs; this can be achieved by lengthening the hind limbs (Emerson 1985).

Other selective forces may also favor long hind limbs. In theory, longer hind-limb elements (out-levers) result in greater out-velocities and greater stride length during running, thus enhancing speed (Hildebrand 1974). Among terrestrial lizards, cursorial species tend to have long hind limbs (Jackson 1973; Pianka 1973, 1986). Similarly, among the anoles studied by Moermond (1979a), fast-moving "jumpers" and "runners" had longer hind limbs relative to body length than did slow-moving "crawlers." "Jumpers" and "runners" were similar in this trait. Despite this similarity, jumping and running in arboreal habitats differ in that the latter, like crawling, is a decidedly quadrupedal mode of locomotion. This contrasts with running in terrestrial cursors, which tend toward bipedalism (Snyder 1952, 1954). Thus, long hind limbs relative to body length may evolve in anoles where either fast running or strong jumping is favored by

selection, but fore and hind limbs should be more similar in length in quadrupedal "runners" than in "jumpers."

Running speed may also be enhanced by changes in proportions within limbs. If a limb's center of gravity is nearer the girdle, the moment of inertia is lower, and angular velocity is therefore greater. Thus, proximal limb elements should be relatively short and heavy, whereas distal ones should be long and slender (Hildebrand 1974, 1985). The hind limbs of some cursorial lizards have distal elements that are long relative to proximal ones (Lundelius 1957). Likewise, in Moermond's (1979a) study, fast-moving "runners" and "jumpers" had longer tibiae relative to femora than did slow-moving "crawlers." This pattern, however, is less a general rule for lizards than for mammals (Hildebrand 1985).

Hind limbs that are disproportionately long relative to fore limbs may evolve in "jumpers" for a reason not directly related to jump distance. During a jump, an animal's center of mass must be in line with the propulsive force created by the hind limbs. Otherwise, the resulting torque will cause the body to rotate around an axis that passes (in a frontal plane) through the center of mass and lies perpendicular to the long axis of the body (Emerson 1985). If, for example, the center of mass is too near the anterior, the animal will rotate clockwise (viewed from the right) during a jump. This can be prevented by shifting the center of mass posteriad to be in line with the propulsive force by shortening the trunk, decreasing fore-limb size, or increasing hind-limb, or tail, size. These adjustments may contribute to a lower "intermembral index" (ratio of fore- to hind-limb length) in saltatorial species. Whatever its exact cause, the

tendency for arboreal animals that rely heavily on jumping to have low intermembral indices is well documented (Fleagle 1977b; Glassman 1983; Napier and Napier 1967; Napier and Walker 1967; Oxnard et al. 1981).

Interpreting a low intermembral index as an adaptation for shifting the center of gravity posteriad accords with another trend in Moermond's (1979a) data. "Jumpers" were relatively long-tailed compared to "runners" or "crawlers." Moermond attributed this pattern to the tail's function as a counterbalance during jumps. In terrestrial lizards, the tail may function as a counterbalance during running (Ballinger et al. 1979), but arboreal forms rarely run on flat horizontal surfaces. The tail also serves as a counterbalance for an anole perching on a narrow support (Ballinger 1973; personal observation), especially when the animal's orientation is perpendicular to the support--for example, when reversing direction, preparing for a jump, or landing after a jump.

As suggested by Moermond (1979a), "crawlers" may have short limbs for reasons not directly related to gait. Short limbs, he reasoned, are better suited for gripping narrow supports. An animal that is wider than the support it is traversing tends to topple sideways, as all points of contact with the support are essentially colinear. Unless the animal's center of gravity remains directly above the support, the resultant torque will cause the animal to rotate about the support (Cartmill 1985). For an animal with longer legs, this torque is stronger because the center of mass is farther from the support (unless the animal can progress effectively with its legs strongly flexed at the knees and elbows). Using prehensile extremities (tail or feet) to counter these rotational forces--among

lizards, a strategy best developed in chamaeleons (Peterson 1984)--is an alternative means of preventing toppling on narrow supports.

Another morphological feature that varies among Anolis species that differ in structural niche is the subdigital adhesive pad, which Peterson (1983) considered a "key innovation" in the adaptive radiation of anolines. Among populations and species of Anolis, the widths of the toe pads (and the number of toe-pad lamellae) may correlate with degree of arboreality (Collette 1961, Lister 1976b, Moermond 1979a), though body size, if also correlated with degree of arboreality, may be confounding (Collette 1961). Toe pads should be larger (taking into account body-size differences) in anoles that frequent broad, relatively smooth surfaces (e.g., tree trunks), where maintaining a grip depends on adhesion rather than grasping.

In summary, according to the habitat-matrix model, differences in locomotor behavior and morphology among species of Anolis evolve in response to support size and support-matrix density. The morphological patterns reported by Moermond (1979a) accord with biomechanics and form the basis for prediction in the present study.

STUDY SYSTEM AND METHODS

The System

From April 1983 through June 1985, I studied six species of Anolis in the vicinity of Monteverde, Puntarenas Province, Costa Rica. The study area was on the upper Pacific slope (1400-1600 m elev) in and near the Monteverde Cloud Forest Reserve, a 5000 ha tract of virgin forest that straddles the continental divide in the Cordillera de Tilarán.

I collected data in two habitat types--closed-canopy forest, chiefly Tropical Lower Montane Wet Forest (Hartshorn 1983), and anthropogenic gaps, shrubby pasture with scattered trees. I use "stratum," or "layer," in the following descriptions to imply recognizable but intergrading zones of vegetation, not discrete tiers. In the forest, a dense shrub layer (1-2 m tall), dominated by herbs in the Acanthaceae, Rubiaceae, and Piperaceae, graded into an open stratum of understory trees and treelets, mostly 3-10 m tall. Most canopy trees were 20-25 m tall. Epiphytes (e.g., bromeliads, orchids, ferns, and mosses) were common. In anthropogenic gaps (hereafter referred to as gaps), the shrub layer was relatively sparse, consisted mainly of saplings of second-growth trees, and graded abruptly into an open tree stratum. In closed-canopy forest, local heterogeneity in the vertical profile of vegetation structure was correlated with elevation, exposure to trade winds, and time since the latest treefall

disturbance (Lawton and Dryer 1980). This heterogeneity notwithstanding, variation in vegetation structure among strata greatly exceeded that within a stratum.

The six species of Anolis differed in their use of these habitats. Two gap specialists, Anolis altae and A. intermedius, were parapatric in distribution; largely separated by elevation, they overlapped in a narrow zone (< 0.5 km) at 1500 m. In contrast, A. woodi, A. tropidolepis, A. humilis, and A. insignis were sympatric throughout the elevational range of the study area, primarily in closed-canopy forest. The first three inhabited the shaded understory, and A. insignis the forest canopy. Fitch (1972, 1973a, 1973b, 1975) reported on the natural history of most of these species.

Approach for Testing the Model

My approach for testing the habitat-matrix model consisted of four steps. First, I examined the proximate influences of support size and support-matrix density on locomotor behavior by manipulating an artificial matrix of stems within a field enclosure. Second, I tested whether patterns observed in this experiment could be extrapolated to field comparisons of species (or intraspecific classes--juveniles, adult females, and adult males). Through standardized vegetation sampling, I quantified the structural configuration encountered by each anole class, and, through timed field observations, I quantified patterns of microhabitat use and locomotor behavior. Third, by comparing different species in the same artificial matrix, I tested whether they differed in locomotor

behavior independently of the proximate effects of microhabitat structure. Finally, using a morphometric approach, I tested predictions, derived from biomechanics and comparisons of locomotor behavior, concerning interspecific variation in morphology.

In the following sections, I describe the data-collection procedures and statistical analyses for the four phases of the study. Using BMDP statistical software (Dixon 1983), I performed the multiway contingency table analyses (BMDP 4f) and the two-way and multiple discriminant analyses (BMDP 7m) on a VAX computer at the University of Florida. For other analyses, I used NWA STATPAK (Northwest Analytical, Inc.) on a KAYPRO 2000 personal computer. Unless stated otherwise, statistical tests used two-tailed probabilities.

Experiment I. Proximate Effects of Microhabitat Structure on Locomotor Behavior

This experiment examined the proximate influences of support-matrix density and support size on the locomotor behavior of Anolis altae. Preliminary field observations had indicated that this species was primarily a "runner" that also jumped regularly but crawled infrequently. I therefore focused on how structural features influence jump frequency.

I used fiberglass screen and bamboo to construct a hexagonal field enclosure (3m on each side and 1.3 m tall) with a blind on one side. An overhanging metal rim prevented lizards from escaping through the open top. Using 1-m-tall stems of second-growth trees and their saplings, I constructed artificial support matrices. I was thus

able to hold support diameter constant while varying support-matrix density, and vice versa.

I captured adult anoles by hand from their nocturnal sleeping perches. I noted the sex and snout-vent length of each lizard and placed them individually in 0.3-L plastic cannisters, where they stayed until used in trials the following day.

For each trial, I released an anole into the enclosure and, after a 20-min acclimation period, observed its locomotor behavior for 40 min. I recorded the type of each movement (jump vs not), and for each jump, noted whether it was between supports or from a support to the ground (or vice versa). I discarded the few trials in which the anole persistently tried to leave the enclosure instead of resuming normal behavior. The criterion for normal behavior was feeding activity, either prey capture or assumption of a head-down survey posture (sensu Stamps 1977) accompanied by scanning movements of the head. To enhance feeding rates and, consequently, frequency of movements, I augmented food in the enclosure by sweep-netting insects from surrounding vegetation. I performed trials in different structural configurations (see below) to assess proximate behavioral responses to support-matrix density and support diameter.

For each of these two factors, I used two levels; hence, the experimental design was 2×2 (i.e., four treatment combinations). Distance between adjacent supports was 25 cm for high support-matrix density and 40 cm for low. Mean diameter was $1.1 \text{ cm} \pm 0.3$ (SD) for small supports and $8.7 \text{ cm} \pm 1.6$ (SD) for large ones. For each sex in each treatment combination, I observed a minimum sample of 200 movements made by at least 10 individuals; in total I scored 1624

movements made by 89 individuals. As closely as possible, I matched anoles in the different treatments by body size; mean snout-vent length for a given sex did not differ significantly among treatments.

Following Moermond (1979a, 1979b), I treated each behavioral event as a datum and pooled data for individuals (of a sex) within each treatment. I then used log-linear models to analyze these data in a multiway contingency table (Brown 1983; Fienberg 1970).

I also analyzed behavioral data pooled by anole class during other phases of the study. Ideally, to avoid possible bias from serial dependency of observations (Machlis et al. 1985; Martín and Bateson 1986), one would calculate a proportion (e.g., number of jumps divided by total number of movements) for each individual, and then analyze these values. Unfortunately, during field observations, the number of events per individual averaged as low as three or four per individual for some anole classes, thus precluding calculation of these proportions. Moermond (1979a) found that for a given species-habitat combination, a composite sample consisting of a randomly drawn datum from each individual was statistically indistinguishable from the data set for each individual. Thus, serial dependency of observations should not seriously bias statistical analyses.

To check for bias, I re-analyzed data from Expt. I, in which the sample of events per individual was relatively large (≥ 10). Using a factorial analysis of variance of the proportion of jumps (arcsine-transformed) out of total movements for each anole, I obtained results equivalent to those from the multiway contingency table analysis of pooled data.

Field Test of Predictions Concerning Locomotor Behavior

Vegetation Sampling. I measured support-matrix density and dimensions of potential supports by sampling strata in each of the two habitats--closed-canopy forest and gaps. I sampled in the same areas in which I observed behavior (discussed below), and at the same times of year, but vegetation sampling and behavioral observations were independent. For closed-canopy forest, I sampled eight strata (0-34, 35-79, 80-124, 125-170, 171-270, 271-370, 371-470, and 471-600 cm above ground). During field observations (see below) all anoles foraged within the total height range comprising these eight strata. I omitted the canopy-dwelling Anolis insignis from the field study, as it was rarely observable; Pounds and Hayes (1987) studied the locomotor behavior of this species in a field enclosure. Because the two gap specialists, A. altae and A. intermedius, were active closer to the ground than was A. woodi in closed-canopy forest, I sampled only the first five strata in gaps. Quantifying support dimensions and support-matrix density by stratum (as described below) allowed me to assess the relationship of each of these variables to height above ground.

I used mean distance between neighboring potential supports as an index of support-matrix density. First, I selected a stratified random sample of points (five per stratum) along each in a series of 200-m transects (three in closed-canopy forest, two in gaps); in forest, transects corresponded to preexisting trails. To choose each point, I took three numbers from a random-numbers table to represent distance along the transect, horizontal distance from the transect,

and height within the stratum. For each point, I flagged the nearest potential support in each of six categories--leaves and five classes of stems (0.2-0.7, 0.8-1.4, 1.5-2.9, 3-9.9, and ≥ 10 cm diam)--following Andrews (1971). I then measured the distance from each of these flagged supports to its nearest neighbor (in the same stratum) in each of the same six categories. To aid measurements in the higher strata, I used a ladder and L-shaped and T-shaped measuring poles. These measurements provided a matrix of 36 distances (6 x 6) for each point initially chosen.

To analyze these data, I first calculated mean nearest-neighbor distances for each stratum. The effective support-matrix density encountered by an anole depends in part on the size distribution of supports it can use. If, for example, a larger anole is constrained to use a smaller subset of the available supports, it encounters (in effect) a lower support-matrix density than does a smaller anole in the same microhabitat. I therefore computed these mean nearest-neighbor distances three separate times, following different rules for including supports in the determination of nearest-neighbor distances. These rules (hereafter referred to as support-inclusion rules) were 1) only stems ≥ 1.5 cm diam included (leaves excluded); 2) only stems ≥ 0.8 cm diam included (leaves excluded); and 3) all stems (≥ 0.2 cm diam) and leaves included. For closed-canopy forest, for example, I calculated 24 estimates of mean nearest-neighbor distance for the three support-inclusion rules in the eight strata.

To examine the relationship between support-matrix density and height above ground for a given support-inclusion rule and habitat, I regressed mean nearest-neighbor distance for each stratum on mean

height of the stratum and performed a Spearman rank correlation analysis (Siegel 1956). I used Wilcoxon signed rank tests (Siegel 1956) to assess the significance of between-habitat differences in mean nearest-neighbor distances. As I describe later, I also used these mean nearest-neighbor distances, in conjunction with field data on the use of different strata and support categories by anoles, to estimate the average inter-support distance encountered (in effect) by a given anole class (adult males, adult females, or juveniles of a species).

To assess the size distribution of available potential supports, I again chose a stratified random sample of points along transects in each habitat. I selected, in the manner described earlier, 30 points from each of the eight strata in closed-canopy forest (10 points per stratum for each of the three transects) and from each of the lower four strata in gaps (15 points per stratum for each of the two transects). For each point, I measured the diameter and length of the closest stem.

I used nonparametric methods to analyze these data. First, using Spearman rank correlation analyses, I analyzed the relationships between support dimensions and height above ground. To compare size distributions of potential supports among strata within a habitat or between corresponding strata of different habitats, I constructed frequency histograms and applied chi-square analyses (Sokal and Rohlf 1981). As I describe later, I also used these data in conjunction with field data on behavior to test whether anoles used a nonrandom sample of the available stems.

Field Observations. As is typical for the genus (e.g., Scott et al. 1976), the anoles I observed were sit-and-wait foragers, spending most of their time in a head-down survey posture on a tree trunk or other perch. In most studies of the structural niche of Anolis, the investigator observes a sample of individuals, each at one point in time, to quantify the heights and diameters of their survey perches (e.g., Schoener and Schoener 1971a, 1971b). My goal, however, was to quantify, not only perch-height distribution, but also the total range of supports used in locomotion. These supports included the survey perches, but many others as well. Often, an anole perched for a long period, followed by a short bout of movements on a number of supports, many of which differed from the typical survey perch in size or height above ground. Quantifying the use of these supports required direct observation of movements.

I made timed observations of individual anoles during the wet seasons (middle of May to middle of November) of 1984 and 1985 to quantify locomotor behavior and the use of microhabitats and supports. Observing from a distance of 5-10 m and using intervening vegetation as a blind, I recorded the sex of the anole, estimated its size, and observed its behavior for an average of 40 min. As closely as possible, I equalized the sampling effort per individual, but unexpected events (e.g., sudden heavy rains) sometimes truncated observations. Tape-recording all events, I noted the type of each movement (run, jump, or crawl) and made detailed verbal notes describing supports, their locations, and landmarks on supports. At the end of each observation period, I attempted to capture the animal (success rate of about 75%) to measure, weigh, and mark it (by toe-

clipping). I then played back the recording in the field through headphones, measured the sizes of supports and distances of movements, and transcribed all data.

For each species except Anolis woodi, I made 60 timed observations (2400+ min) of adults (equally divided by sex). Individuals of A. woodi were difficult to find because they were less abundant and more arboreal than the other anoles. I therefore reduced by half the number of observations of this species, but doubled the length of each observation to maintain the same sampling effort, measured as total time. For all species, the number of observation periods approximates the number of individuals sampled. Because I was unable to capture and mark every anole observed, I may have sampled some individuals more than once; however, given the sizes of the areas in which I sampled behavior (the smallest was 6.5 ha), this repeated sampling was probably rare. In addition to observing adult anoles, I observed 30 hatchlings and small juveniles (snout-vent length ≤ 30 mm) of each of three species--A. tropidolepis, A. altae, and A. intermedius. In all, I made 360 timed observations, totaling over 15,600 min, during which I recorded data for 3424 sites occupied by anoles and 3070 events of locomotion.

When analyzing data on the diameters (or heights) of supports used by anoles, I treated diameter (or height), at each site occupied, as a datum and pooled data for each anole class. In doing so, I followed the rationale discussed earlier (Expt. I) for pooling behavioral events. To test for interactions among anole class, microhabitat (stratum), and support size, I used multiway contingency tables analyzed by log-linear models (Brown 1983; Fienberg 1970). As

mentioned earlier, I also tested whether the use of stems in the various size categories by a given anole class differed from that expected on the basis of availability. To estimate the proportion of total activity expected on stems in a particular diameter category, I multiplied the proportion of activity (out of total activity) in each stratum times the proportion of stems in the diameter category (out of the total stems sampled in that stratum) and summed over the strata. To compare observed and expected distributions, I used Kolmogorov-Smirnov goodness-of-fit tests (Sokal and Rohlf 1981). To analyze the data on locomotor behavior, I used simple and multiple regression (described below).

Estimation of the Average Effective Inter-support Distance Encountered by Each Anole Class. I used an index based on mean nearest-neighbor distances between potential supports, weighted for the proportional use of different strata and support categories. I derived the formula for this index as follows. Let z_{lj} be the mean nearest-neighbor distance between potential supports for the l th support-inclusion rule in the j th stratum (see Vegetation Sampling). Next, let q_{ijk} represent the proportion of the k th anole class's activity, out of total activity in the j th stratum, on supports in the i th category, where $i = 1, 2$, or 3 (1--stems ≥ 1.5 cm diam; 2--stems 0.8-1.4 cm diam; 3--leaves, and stems 0.2-0.7 cm diam). An estimate, z_{jk} , of the mean nearest-neighbor distance for the k th anole class in the j th stratum can be calculated as

$$z_{jk} = \sum_{i=1}^3 q_{ijk} z_{lj} \quad (2)$$

I estimated the overall mean nearest-neighbor distance encountered by the k th anole class as

$$D_k = \sum_{j=1}^n p_{jk} Z_{jk}, \quad (3)$$

where p_{jk} represents the proportion of the k th anole class's activity (out of total activity) in the j th stratum, and n is the number of strata inhabited. Substituting Eq.(2) in Eq.(3),

$$D_k = \sum_{j=1}^n p_{jk} \left(\sum_{i=1}^3 q_{ijk} z_{lj} \right). \quad (4)$$

Because a lizard may choose to travel in a particular direction rather than toward the nearest available support, D_k is a conservative estimate of the effective mean distance between potential supports. Yet measuring distances between supports along a randomly chosen line would inflate the estimate by assuming that an anole's direction of travel is independent of the positions of available supports.

As is the case for many derived variables, the variance structure of D_k is unknown. I used D_k , however, not for statistically comparing support matrices encountered by different anole classes, but as a descriptive statistic and as a predictor variable in regression analyses.

As an a posteriori check of whether D_k accurately estimates the average distance between supports, I compared values of D_k with d_k , the mean length of jumps made by members of the same anole class. In high-density matrices, where the jumps made by anoles should

approach a random sample of the available inter-support distances, D_k and d_k should be equivalent. In low-density matrices, in contrast, where the jumps made by anoles are a biased subsample of the shorter distances available, D_k should exceed d_k .

Statistical Tests of Predictions Concerning Locomotor Behavior.

To test the predictions concerning jump frequency in relation to structural-microhabitat variables, I employed multiple linear regression (Sokal and Rohlf 1981). The dependent variable was jump frequency (proportion of jumps out of total moves) for a given anole class. I treated each intraspecific class as an independent point ($n = 13$) in this analysis because intraspecific classes occupied different structural niches and differed in morphology, especially size. I chose six independent variables to represent the structural-microhabitat parameters. Some of these variables expressed support diameter or inter-support distance relative to anole snout-vent length, whereas others were absolute measures. I included the former because size may influence jumping ability (Emerson 1985; Gabriel 1984) and possibly surface-area effects of supports. These independent variables were 1) D_k , average distance between neighboring supports (Eq. 4); 2) $D_{REL,k}$, $D_k / \text{mean SVL}$; 3) PLD_k , proportion of total activity in low-density strata (i.e., where $Z_{jk} > d_k$); 4) Dm_k , mean support diameter; 5) $Dm_{REL,k}$, mean support diameter / mean SVL; 6) PSS , proportion of total activity of small supports (leaves, or stems < 3.0 cm diam). Independent variables entered the analysis in a step-up fashion according to their F values. Because proportions generally follow a binomial, rather than normal,

distribution, I used arcsine-transformed proportions (Sokal and Rohlf 1981) for this and other parametric analyses.

The habitat-matrix model also predicts that crawling will be most frequent where supports are too far apart for jumping yet are too narrow for running. I tested this prediction by regressing the frequency of crawling (proportion of crawls out of total moves), for a given anole class, on the proportion of activity on small supports (leaves, or stems <3.0 cm diam) in low-density strata ($Z_{jk} > d_k$). Using a Fisher's exact test (Sokal and Rohlf 1981), I also compared crawling frequency (proportion of crawls out of the combined sample of runs and crawls) on stems in two diameter categories ($< \text{vs } \geq$ median) for adults of each species.

Experiment II. Interspecific Differences in Locomotor Propensities

This experiment addressed the question of whether species differed in locomotor behavior independently of the proximate influences of microhabitat structure. More specifically, I tested whether species differed in propensity for jumping by observing each in the same artificial matrix. Employing the field enclosure and procedure described for Expt. I, I repeated one treatment (high support-matrix density with small-diameter supports) twice, substituting, in turn, adults of A. intermedius and A. tropidolepis in place of those of A. alatae. I used this treatment because it provided the option of jumping (or not) at any point within the matrix. I chose these species because they were similar in size and differed in jump frequency in the field. Using data on 1295 movements made by 66

anoles, I tested for differences among species in a multiway contingency table analysis with log-linear models (Brown 1983; Fienberg 1970).

Morphometrics

Measurements. I obtained morphological data from live anoles. For A. insignis I supplemented these data with those from preserved material from Costa Rica. All measurements were distances, except for mass, which I recorded to the nearest 0.01 g on an Ohaus balance. I measured tail length (Tl) (vent to tail tip) to the nearest 0.5 mm with a clear plastic ruler; I excluded individuals with broken or regenerated tails. Using the reticle of a Wild dissecting stereomicroscope, I measured toe-pad width (TP) (fourth digit of right hind foot) to the nearest 0.04 mm. I then restrained the animal with elastic bands and measured the following lengths to the nearest 0.1 mm with a dial caliper, aided where necessary by the dissecting microscope: 1) snout-vent (SVL); 2) femur (F)--with the femora perpendicular to the long axis of the body and the tibiae parallel to this axis, the distance between the knees, divided by 2; 3) tibia (T)--with lizard in same position as above, but with the right hind foot perpendicular to the tibia, the distance from the right knee to a point just medial to the base of the right fifth toe; 4) hind foot (HF)-- with the fourth and fifth toes perpendicular to the long axis of the right foot, the distance from the point just medial to the base of the fifth toe to the distal end of the fourth metatarsal; 5) fourth toe (FT)--with the fourth toe of the right foot positioned as above,

the distance from the base of the first phalanx to the proximal border of the claw; 6) humerus (H)--with the humeri perpendicular to the body's long axis, and the ulnae parallel to this axis, the distance between the elbows, divided by two; and 7) ulna (U)--with the right ulna positioned as above, the distance from the elbow to the flexed wrist. Although I designated several of the above measurements by the name of a major bone, the measurements differed from actual bone lengths.

Analyses. For multivariate analyses of the distance measurements, I used discriminant functions (Blackith and Reyment 1971). With two-way discriminant analyses, I compared anoles that relied heavily on jumping to those that jumped infrequently. I used multiple discriminant analyses to assess morphological differences among the six species (adult males and females analyzed separately). The latter analyses allowed me to assess the importance of size and various aspects of shape in the phenetic structure of the community and to examine the positions of "runners," "jumpers," and "crawlers" in a multivariate morphospace.

I also calculated several log shape variables (James 1982; Kiltie in press; Mosimann and James 1979). These variables, which were similar to the bivariate ratios used by Moermond (1979a), were 1) $\ln [T/(T+F)]$; 2) $\ln [(U+H)/(T+F)]$; 3) $\ln [(HF+T+F)/SVL]$; and 4) $\ln (T1/SVL)$. Taking $\ln SVL$ as a size variable, I examined correlations between the shape variables and size to test whether differences in shape among species were a consequence of interspecific allometry.

Although Moermond (1979a) focused on limb proportions (and relative tail length) in his analysis of shape, anoles also differ in

mass-length relationships (e.g., Corn 1981; Fitch 1975; Schoener 1969a; Williams 1983). Some species are more slender than others, and this might affect locomotor behavior and the use of supports and structural microhabitats. To examine interspecific differences in mass-length relationships, I employed linear regression. Using average mass and body length (SVL) for adult males of a sample of 12 Costa Rican species (Fitch 1975, plus my data for A. altae), I plotted log mean mass vs log mean SVL. I used this relationship to calculate an expected mean mass for each of the six species at Monteverde, given mean SVL of each. I then expressed observed mean mass as percent of expected, and used these values as an index of mass-length relationships. To test for a relationship between this index and jump frequency, I used Kendall's Tau (Siegel 1956).

RESULTS

Experiment I. Proximate Effects of Microhabitat Structure on Locomotor Behavior

Support-matrix density and support diameter interacted significantly in their effects on jump frequency (Fig. 1). I therefore tested the effect of support-matrix density at each level of support diameter, and the effect of support diameter at each level of support-matrix density, while controlling for the effect of sex in each analysis.

To test the effect of support-matrix density at a given support diameter, I performed a three-way contingency table analysis (sex x support-matrix density x type of movement) (Table 1). At each support diameter, a log-linear model including all two-factor interactions fit the data well (G^2 test of goodness of fit). From this model, I removed, in turn, each two-factor interaction of interest and judged that interaction to differ from zero if the reduced model fit the data poorly, or if the difference between the initial and reduced models was significant (i.e., a significant reduction of goodness of fit). Irrespective of support diameter, the only significant two-factor interaction was that of support-matrix density (low vs high) x type of movement (jump vs not). Whereas sex had no significant effect on type of movement, the increased tendency to jump at higher support-matrix density (Fig. 1) was significant at both levels of support diameter.

Figure 1. Jump frequency, characterized as the proportion of jumps out of total movements, in relation to support diameter and support-matrix density in Expt. I. Shaded symbols indicate adult males, and open ones adult females, of *Anolis altae*. Mean diameter was $1.1 \text{ cm} \pm 0.3 \text{ (SD)}$ for small supports and $8.7 \text{ cm} \pm 1.6 \text{ (SD)}$ for large ones. Distance between adjacent supports was 25 cm for high support-matrix density and 40 cm for low. See Tables 1 & 2 for statistical analyses of these data.

Table 1. Multiway contingency table analyses, using log-linear models, to test effects of support-matrix density and sex on frequency of jumping by Anolis altae at two levels of support diameter (Expt. I).

Interactions included ^a in model		df	Likelihood ratio ² chi-square (G)	p
Large-diam Supports:	DxS, DxT, TxS	1	< 0.01	> .90
	DxS, DxT	2	0.10	> .90
	Diff. due to deleting TxS	1	0.10	> .75
	TxS, DxS	2	8.98	< .02
	Diff. due to deleting DxT	1	8.98	< .003
Small-diam supports:	DxS, DxT, TxS	1	0.29	> .50
	DxS, DxT	2	0.34	> .80
	Diff. due to deleting TxS	1	0.05	> .80
	TxS, DxS	2	31.61	< .0001
	Diff. due to deleting DxT	1	31.33	< .0001

^a

D = support-matrix density (high vs low); T = type of locomotion (jump vs not); S = sex. The data upon which these analyses are based, and definitions of the levels of support-matrix density and support diameter, are given in Fig. 1. See text for an explanation of the statistical models and their interpretation.

Analogously, I tested the effect of support diameter at a given level of support-matrix density with a three-way contingency table analysis (sex x support diameter x type of movement) (Table 2). Regardless of support-matrix density, a model containing all two-factor interactions fit the data well; I therefore applied the method of partitioning described above. The only significant two-factor interaction at high support-matrix density was that of support diameter (small vs large) x type of movement (jump vs not), while none was significant at low support-matrix density. Thus, whereas sex had no significant effect, increasing support diameter negatively affected jump frequency at high, but not at low, support-matrix density (Fig. 1).

To explore this interaction further, I examined the effect of support diameter on the proportion of jumps (out of total jumps) between supports (vs support to ground, or vice versa) at each level of support-matrix density. I again used a three-way contingency table analysis (sex x support diameter x type of movement) (Table 3). Following the same partitioning method as before, I found no significant effect of sex. In contrast, the effect of support diameter was significant at low, but not at high, support-matrix density. An anole's probability of jumping between supports increased significantly with an increase in support diameter in low-density matrices.

Table 2. Multiway contingency table analyses, using log-linear models, to test effects of support diameter and sex on frequency of jumping by Anolis altae at two levels of support-matrix density (Expt. I).

	Interactions included ^a in model	df	Likelihood ratio ² chi-square (G)		p
High density:	dxS, dxT, TxS	1	0.06		> .80
	dxS, dxT	2	0.06		> .90
	Diff. due to deleting TxS	1	<0.01		> .90
	dxS, TxS	2	6.63		< .04
	Diff. due to deleting dxT	1	6.57		< .02
Low density:	dxS, dxT, TxS	1	0.05		> .80
	dxS, dxT	2	0.38		> .80
	Diff. due to deleting TxS	1	0.33		> .55
	dxS, TxS	2	0.05		> .90
	Diff. due to deleting dxT	1	<0.01		> .90

^a

d = support diameter (large vs small); T = type of locomotion (jump vs not); S = sex. The data upon which these analyses are based, and definitions of the levels of support-matrix density and support diameter, are given in Fig. 1. See text for an explanation of the statistical models and their interpretation.

Table 3. Multiway contingency table analysis, using log-linear models, to test effects of support diameter and sex on frequency of jumping between supports (vs support to ground, or vice versa) by *Anolis altae* at two levels of support-matrix density (Expt. I).

Interactions included ^a in model		df	Likelihood ratio ² chi-square (G)	p
High density:	dxS, dxT, TxS	1	0.60	> .40
	dxS, dxT	2	0.60	> .70
	Diff. due to deleting TxS	1	<0.01	> .90
	dxS, TxS	2	0.79	> .65
	Diff. due to deleting dxT	1	0.19	> .65
Low density:	dxS, dxT, TxS	1	<0.01	> .90
	dxS, DxT	2	0.84	> .65
	Diff. due to deleting TxS	1	0.84	> .35
	dxS, TxS	2	18.07	< .001
	Diff. due to deleting dxT	1	18.07	< .0001

^a

d = support diameter (large vs small); T = type of movement (jump between supports vs jump from support to ground, or vice versa); S = sex. Definitions of the levels of support diameter and support-matrix density are the same as in Fig. 1. See text for an explanation of the statistical models and their interpretation.

Field Test of Predictions Concerning Locomotor Behavior

Vegetation Structure. Support-matrix density varied with height above ground, support-inclusion rule, and habitat. Irrespective of support-inclusion rule or habitat, mean distance between neighboring supports in a stratum was positively correlated with height above ground (Table 4). In closed-canopy forest, the relationship between mean nearest-neighbor distance and height was significantly nonlinear; a power function ($b < 1$) provided the best fit (Fig. 2). Mean nearest-neighbor distance was higher in gaps than in the corresponding strata of closed-canopy forest, regardless of support-inclusion rule (Wilcoxon signed-rank test, $T = 0$, $p < .05$).

In both habitats, length and diameter of randomly chosen stems were positively correlated with one another and with height above ground (Table 5). In gaps, however, the shift toward greater representation of larger supports with increasing height was more abrupt (Fig. 3). I compared corresponding strata of the two habitats in the proportion of stems < 2.0 cm diam. In the first two strata, the habitats did not differ significantly (stratum 1, chi-square = 3.49, 1 df, $p > .05$; stratum 2, chi-square = 1.42, 1 df, $p > .10$). (Here and elsewhere, chi-square analyses employ the Yates correction where $df=1$.) In contrast, the habitats differed significantly in the third stratum (chi-square = 12.13, 1 df; $p < .001$) and in the fourth stratum (chi-square = 13.41, 1 df; $p < .001$). In closed-canopy forest, the average diameter of supports continued to increase up through the eighth stratum (Fig. 3); yet even in this uppermost

Table 4. Spearman rank correlation coefficients for the relationship between mean nearest-neighbor distance between potential supports, in a given stratum, and height above ground (by support-inclusion rule and habitat).

Habitat	Inclusion rule ^a	(n) No. strata	r s
Closed-canopy Forest	1	8	.95***
	2	8	.88**
	3	8	.99***
Gaps	1	5	.90*
	2	5	.90*
	3	5	.90*

^a

Support-inclusion rules: 1) only stems ≥ 1.5 cm diam included (leaves excluded); 2) only stems ≥ 0.8 cm diam included (leaves excluded); 3) all stems (≥ 0.2 cm diam) and leaves included.

* $p < .05$, ** $p < .005$, *** $p < .0001$.

Figure 2. Nearest-neighbor distances between potential supports in closed-canopy forest in relation to height above ground and support-inclusion rule. Values are means ($\pm$ SE) for each combination of stratum and support-inclusion rule. Support-inclusion rules were as follows: 1) (squares) only stems ≥ 1.5 cm diam included (leaves excluded); 2) (open circles) only stems ≥ 0.8 cm diam included (leaves excluded); 3) (shaded circles) all stems (≥ 0.2 cm diam) and leaves included.

Table 5. Spearman rank correlation coefficients for the relationships among diameter, length, and height of potential supports (by habitat).

Habitat	Variables ^a	n	r s
Closed-canopy Forest	d, l	240	.78*
	d, h	240	.58*
	l, h	240	.81*
Gaps	d, l	120	.92*
	d, h	120	.70*
	l, h	120	.80*

^a

d = diameter; l = length; h = height.

* $p < .0001$

Figure 3. Size distributions, by stratum, of randomly sampled stems in closed-canopy forest and gaps (shrubby pasture with scattered trees).

stratum, the diameters of randomly sampled supports averaged smaller than in the fourth stratum of gaps (Mann-Whitney $U = 658$, $p < .003$).

Patterns of Microhabitat and Support Use. Species differed in their use of habitats and strata. Anolis humilis, A. tropidolepis, and A. woodi, the three species occurring sympatrically in the understory of closed-canopy forest, were vertically stratified (Fig. 4). They therefore occupied microhabitats differing in support-matrix density and the size distribution of available supports. By comparison, A. aliae and A. intermedius, the two parapatrically distributed gap specialists, were more similar to one another in microhabitat use, and were intermediate between A. tropidolepis and A. woodi in perch-height distribution (Fig. 4). In comparison to the mature-forest species, A. aliae and A. intermedius occupied microhabitats of lower support-matrix density and greater relative availability of larger supports.

The heights and diameters of supports used by anoles varied not only among species but also among intraspecific classes (Tables 6 and 7). Males were active higher above ground than were females (chi-square, $p < .01$), and, except for A. humilis, used supports of significantly greater diameter (chi-square, $p < .025$). Juveniles used supports that were lower (chi-square, $p < .05$) and smaller in diameter (chi-square, $p < .001$) than those used by adult females. In each habitat, the proportional use of larger stems ($\text{diam} \geq 3.0$ cm) by different classes of anoles was positively correlated with height above ground and, therefore, with the availability of these larger stems (closed-canopy forest, $r_s = 0.893$, $p < .005$; gaps, $r_s = .94$, $p < .003$). Also, use of the largest supports ($\text{diam} \geq 10$ cm) was greater

Figure 4. Perch-height distributions of anoles in closed-canopy forest and gaps (shrubby pasture with scattered trees). Proportions of observation time are for adults (sexes combined) of each species. The gap specialists, *Anolis alatae* and *A. intermedius*, were parapatric at Monteverde. Largely separated by elevation, they overlapped only in a narrow zone (< 0.5 km wide) at 1500 m elev. The other three species were sympatric throughout the elevational range of the study area in the shaded understory of closed-canopy forest. A sixth species, *A. insignis*, not shown here, was largely restricted to the forest canopy.

Table 6. Height distributions of sites occupied by anoles in the field.

Anole class ^a	b n	Height above ground (cm)				
		0-35	35-79	80-124	125-170	>170
<u>A. humilis</u>	(f)	192	1.000	0	0	0
	(m)	343	0.904	0.097	0	0
<u>A. tropidolepis</u>	(j)	244	0.750	0.193	0.057	0
	(f)	130	0.654	0.292	0.054	0
	(m)	249	0.260	0.527	0.164	0.024
<u>A. woodi</u>	(f)	95	0.168	0.084	0.032	0.105
	(m)	132	0.038	0.023	0.038	0.024
<u>A. altae</u>	(j)	399	0.807	0.183	0.008	0.003
	(f)	228	0.315	0.399	0.167	0.084
	(m)	328	0.128	0.314	0.293	0.128
<u>A. intermedius</u>	(j)	413	0.557	0.383	0.058	0.002
	(f)	243	0.300	0.379	0.218	0.045
	(m)	428	0.136	0.215	0.220	0.164

^a

j = juveniles; f = adult females; m = adult males.

^b

n = total no. of sites occupied by anoles during field observations. Other values are the proportions of n in each stratum.

Table 7. Proportional use of support categories (and ground) by anoles in the field.

Anole class ^a		b n	Stem, categorized by diam (cm)					
			Ground	Leaf	0.2-0.7	0.8-1.4	1.5-2.9	3.0-9.9 ≥10.0
<u>A. humilis</u>	(f)	192	.469	.052	.052	.078	.057	.146 .146
	(m)	343	.429	.064	.032	.038	.061	.184 .192
<u>A. tropidolepis</u>	(j)	244	.246	.131	.176	.152	.143	.074 .078
	(f)	130	.254	.023	.092	.169	.101	.130 .231
	(m)	249	.096	.016	.052	.080	.181	.226 .349
<u>A. woodi</u>	(f)	95	.084	.032	.032	.042	.274	.410 .126
	(m)	132	.015	.098	.084	.077	.083	.319 .324
<u>A. altae</u>	(j)	399	.035	.133	.378	.065	.035	.023 .331
	(f)	228	.038	.136	.136	.145	.061	.118 .360
	(m)	328	.030	.055	.061	.123	.049	.216 .466
<u>A. intermedius</u>	(j)	413	.051	.063	.257	.065	.138	.094 .332
	(f)	243	.091	.045	.087	.041	.124	.246 .366
	(m)	428	.021	.063	.051	.014	.005	.341 .505

^a

J = juveniles; f = adult females; m = adult males.

^b

n = the total no. of sites occupied by anoles during field observations. Other values are the proportions of n in each support category (or on ground).

in gaps, where these stems were relatively more abundant, than in closed-canopy forest (chi-square, $p < .05$).

Although these results indicate a relationship between patterns of support use and availability, each anole class used larger stems than expected on the basis of availability alone (Table 8). I therefore performed a separate three-way contingency table analysis for each of three species--A. tropidolepis, A. altae, and A. intermedius--to explore interactions among anole class, support size, and height (Table 9). I used two levels of height (< 80 cm vs ≥ 80 cm) and support size (leaf, or stem < 1.5 cm diam vs stem ≥ 1.5 cm diam). For A. tropidolepis, a log-linear model containing all two-factor interactions fit the data well. Partitioning (as described earlier) revealed that all two-factor interactions were significant. For example, the use of supports in the two support-size categories depended on both the intraspecific class and the height above ground. For both A. altae and A. intermedius, a model containing all two-factor interactions fit the data poorly, indicating a significant three-factor interaction in each case.

Analyses of two-way contingency tables revealed the nature of these three-factor interactions. For A. altae, intraspecific class and support size interacted significantly irrespective of stratum (chi-square, $p < .005$); however, the interaction between height and support size was significant for adult males and females (chi-square, $p < .05$), but not for juveniles (chi-square, $p > .05$). For A. intermedius, height and support size interacted significantly regardless of intraspecific class (chi-square, $p < .05$), whereas intraspecific class interacted significantly with support size below

Table 8. Goodness-of-fit tests comparing the proportional use of stems in the various diameter categories to that expected on the basis of availability.

a		b	Kolmogorov-Smirnov D
Anole class		n	
<u>A. humilis</u>	(f)	92	.593**
	(m)	174	.663**
<u>A. tropidolepis</u>	(j)	152	.344**
	(f)	94	.453**
	(m)	221	.620**
<u>A. woodi</u>	(f)	84	.311**
	(m)	117	.164*
<u>A. altae</u>	(j)	332	.360**
	(f)	188	.401**
	(m)	300	.386**
<u>A. intermedius</u>	(j)	366	.473**
	(f)	210	.506**
	(m)	392	.324**

a

j = juveniles; f = adult females; m = adult males.

b

n = the total no. of sites that anoles occupied on stems during field observations.

* $p < .005$, ** $p < .001$.

Table 9. Multiway contingency table analyses, using log-linear models, of interactions among intraspecific class, support diameter, and support height in the field for each of three species of Anolis in the field.

Interactions included ^a in model		df	Likelihood ratio ² chi-square (G)	p
<u>Anolis</u>				
<u>tropidolepis</u> :	Cxd, Hxd, HxC	2	3.20	> .20
	Cxd, Hxd	4	16.23	< .003
	Diff. due to deleting HxC	2	13.02	< .002
	Cxd, HxC	3	16.12	< .002
	Diff. due to deleting Hxd	1	12.91	< .0005
	Hxd, HxC	4	79.21	< .0001
	Diff. due to deleting Cxd	2	76.00	< .0001
<u>Anolis</u>				
<u>altae</u> :	Cxd, Hxd, HxC	2	6.27	< .05
<u>Anolis</u>				
<u>intermedius</u> :	Cxd, Hxd, HxC	2	8.53	< .02

^a

C = intraspecific class (adult males, adult females, or juveniles); d = diameter (leaf, or stem < 1.5 cm diam vs stem $\geq$ 1.5 cm diam), H = height (< 80 cm vs. $\geq$ 80 cm).

80 cm (chi-square, $p < .001$) but not above this height (chi-square, $p > .05$).

Jump Distance. Mean jump distance (d_k) for a given anole class was positively correlated with D_k , the average distance between neighboring supports ($r = .621$, $n = 13$, $p < .03$; Fig. 5). For A. humilis and A. tropidolepis, which inhabited high-density matrices in the shrub layer of closed-canopy forest, d_k approximated D_k ; the points for these species fell on or near the iso-distance line ($d_k = D_k$). In contrast, males and females of A. woodi, which were active in lower-density matrices higher in the forest understory, fell well below the iso-distance line. The same was true for A. intermedius and A. altae in gaps, but the differences between D_k and d_k were more pronounced.

Mean jump distance (d_k) was also correlated with mean snout-vent length (SVL) ($r = .951$, $n = 13$, $p < .0001$). This correlation remained when I considered only adults and analyzed the sexes separately (males, $r = .98$, $n = 5$, $p < .003$; females, $r = .99$, $n = 5$, $p < .002$). In a partial correlation analysis of d_k , D_k , and mean SVL, d_k was positively correlated with both mean SVL and D_k (partial correlations, one-tailed tests, $n = 13$: mean SVL, $r = .94$, $p < .0005$; D_k , $r = .52$, $p < .05$).

Habitat Structure and Patterns of Locomotion. Proportional use of different patterns of locomotion (jumping, running, and crawling) varied among species and intraspecific classes (Fig. 6). Regression analyses revealed significant relationships between locomotor behavior and habitat structure.

Figure 5. Mean jump distance ($\pm$ SE), d_k , in relation to D_k (effective mean distance between neighboring supports) for anole classes in closed-canopy forest and gaps (shrubby pasture with scattered trees). The dashed line is the iso-distance line ($d_k = D_k$). Shaded symbols are for adult males, open ones for adult females, and half-shaded ones for juveniles. Species included are *A. humilis* (∇), *A. tropidolepis* ($\circ$), *A. woodi* ($\triangle$), *A. altae* ($\diamond$), and *A. intermedius* ($\square$).

Figure 6. Proportions of different types of movements by anoles in the field, by species and intraspecific class--adult females (f), adult males (m), and juveniles (j).

The frequency of crawling was positively correlated with the proportion of activity on small supports (leaves, or stems < 3.0 cm diam) in low-density strata ($Z_{jk} > d_k$) ($r = .56$, $p < .025$, one-tailed test), yet the regression explained only 31% of the variation in crawling frequency. When I compared the frequency of crawling (proportion of combined sample of runs and crawls) on stems $< vs \geq$ the median diameter, for each species of which the adults crawled appreciably, I found a significant difference only for A. woodi. For this species, the proportion of crawls was 0.42 on the smaller supports and 0.05 on the larger supports (Fisher Exact Test, $p < .001$). I also tested this for A. intermedius (Fisher Exact Test, $p = .462$) and for A. altae (Fisher Exact Test, $p = .193$).

In the stepwise multiple regression with jump frequency as the dependent variable and structural-microhabitat attributes as the independent variables, the best model explained 92% of the variation in jump frequency (Table 10). The independent variable D_{REL_k} (mean nearest-neighbor distance between supports, divided by mean snout-vent length) alone accounted for 88% of the variation in jump frequency (Fig. 7). Of the remaining variables, only the effect of D_m (mean support diameter) was significant when partialled on the other independent variables in the model (partial correlations, one-tailed tests, $n = 13$: D_m , $r = -.50$, $p < .05$; D_{REL_k} , $r = -.92$, $p < .0005$; PLD_k , $r = -.46$, $p > .05$). In the absence of D_{REL_k} , D_m was the best predictor of jump frequency, explaining 65.5% of the variation in the dependent variable; D_k did not enter the analysis because of its high correlation with $D_k REL$ ($r = .82$, $n = 13$, $p < .0005$).

Table 10. Stepwise multiple regression analysis of structural-microhabitat variables influencing frequency of jumping in the field.

Step no.	Independent variables	2 R	F
	^a in model		
1	D REL _k	.88	80.63*
2	D REL, Dm _k	.90	46.77*
3	D REL, Dm, PLD _k	.92	36.31*

Note: The dependent variable was frequency of jumping (arcsine-transformed proportion of jumps out of total movements) for a given anole class.

^a

D_kREL = mean nearest-neighbor distance between potential supports, expressed in mean body lengths, for the kth anole class; Dm = mean support diameter; PLD = proportion of activity in low-density matrices. See text for other independent variables analyzed, and partial correlation coefficients for step no. 3.

* $p < .001$.

Figure 7. Jump frequency (proportion of jumps out of total movements) in relation to D_kREL (effective mean distance between neighboring supports, expressed in mean body lengths). The least-squares regression line is $y = -2.1x + 54.4$; $r^2 = 0.88$. Error bars are 95% confidence intervals based on point estimators of the proportions, which are arcsine-transformed. Shaded symbols are for adult males, open ones for adult females, and half-shaded ones for juveniles. Species included are A. humilis (∇), A. tropidolepis ($\circ$), A. woodi ($\triangle$), A. altse ($\diamond$), and A. intermedius ($\square$).

The strong negative correlation between jump frequency and D REL remained when I considered only adult males ($r = -.99$, $n = 5$, $p < .001$, one-tailed test) or only adult females ($r = -.96$, $n = 5$, $p < .005$, one-tailed test). In partial correlation analyses (performed separately for each sex) of jump frequency, D REL, and Dm, jump frequency was again significantly correlated with D REL (partial correlations, one-tailed tests, $n = 5$: females, $r = -.95$, $p < .01$; males, $r = -.99$, $p < .05$), but not with Dm (partial correlations, one-tailed tests, $n = 5$: females, $r = -.34$, $p > .25$; males, $r = -.19$, $p > .25$).

Although a linear model of the relationship between jump frequency and D REL fit the data well (Fig. 7), I also tested other possibilities. For example, an exponential model ($y = 60.31 e^{-.064x}$) fit the data at least as well ($r^2 = .914$). Because a nonlinear relationship could result from a difference between gap specialists and forest-understory anoles in the relationship of jump frequency to D REL, I plotted the linear regression line for gap anoles and extrapolated it to the range of support-matrix densities inhabited by mature-forest species. The latter species fell above this line (Fig. 8). To compare locomotor behavior of these two groups of anoles in this higher range of support-matrix densities, I conducted Expt. II.

Experiment II. Interspecific Differences in Locomotor Propensities

When observed in the same artificial matrix, Anolis intermedius, A. altae, and A. tropidolepis differed in jump frequency in the same rank order as in the field (Table 11). In a three-way contingency

Figure 8. Relationship of jump frequency to $D_k \text{ REL}$ (effective mean distance between supports, expressed in body lengths) for anoles in closed-canopy forest and gaps (shrubby pasture with scattered trees). The dashed regression line ($y = -1.5x + 45.9$) is for gap anoles.

Table 11. Proportions of jumps (out of total movements) for adults of three species in the same artificial support matrix (Expt. II).

Species	Sex	^a n	Proportion of jumps (out of n)
<u>A. intermedius</u>	males	266	.248
	females	211	.265
<u>A. altae</u>	males	210	.367
	females	206	.359
<u>A. tropidolepis</u>	males	202	.505
	females	200	.470

^a
n is the total number of movements by individuals in each anole class.

table analysis (species x sex x type of locomotion), a log-linear model containing all two-factor interactions fit the data well (Table 12). Following the method of partitioning described earlier for similar analyses, I observed a significant effect of species identity, but not of sex, on jump frequency.

Morphometrics

Two-way Discriminant Analyses. I first asked what morphological traits best discriminate between species that jumped frequently ($\geq 40\%$ of total moves)--Anolis humilis, A. tropidolepis, and A. woodi--and those that jumped infrequently ($< 30\%$ of total moves)--A. altae, A. intermedius, and A. insignis. Anolis insignis is primarily a crawler with little propensity for jumping (Pounds and Hayes 1987). Because I studied locomotor behavior of juveniles for only three of the species, I based the above categorization on locomotor behavior of adults only. The difference in jump frequency between A. woodi and A. altae was greater than that for any other adjacent pair along the jump-frequency spectrum.

I used morphometric data from a random sample of 10 individuals (five males, five females) of each of the six species. Dividing these 60 data vectors into two groups of 30 "jumpers" and 30 "nonjumpers," I performed a stepwise discriminant analysis (Table 13). I chose snout-vent length (SVL) as a size variable and forced it into the analysis first. The program then chose additional variables (from the remaining eight) that best discriminated in relation to SVL.

Table 12. Multiway contingency-table analysis, using log-linear models, to test effects of species identity and sex on frequency of jumping (Expt. II).

Interactions included in model ^a	Likelihood-ratio ²		
	df	chi-square (G)	p
IxS, TxI, TxS	2	0.63	> .70
IxS, TxI	3	0.70	> .85
Diff. due to Deleting TxS	1	0.07	> .75
IxS, TxS	4	51.72	< .0001
Diff. due to Deleting TxI	2	51.09	< .0001

^a

I = species identity (Anolis tropidolepis, A. altae, or A. intermedius); T = type of locomotion (jump vs not); S = sex. See text for an explanation of the statistical models and their interpretation. This analysis is based on data in Table 11.

Table 13. Stepwise two-way discriminant analysis (and multivariate analyses of variance) comparing the morphologies of "jumpers" and "nonjumpers."

Step no.	Variables in model ^a	Wilks' Lambda	df	F ^b	p
1	SVL	.984	1, 58	3.18	> .10
2	SVL, HF	.361	2, 57	50.49	< .001
3	SVL, HF, TP	.328	3, 56	38.22	< .001
4	SVL, HF, TP, Tl	.317	4, 55	29.61	< .001

^a

SVL = snout-vent length; HF = right hind-foot length; TP = toe-pad width (right hind fourth toe); Tl = tail length; see text for other variables analyzed. Snout-vent length was forced into the analysis at step one; other variables entered according to their F values.

^b

Approximate F statistic for MANOVA is a transformation of Wilks' Lambda; for step 1, F is the one-way ANOVA between group means.

SVL alone discriminated poorly (Table 13), correctly categorizing only 51.7% of the anoles as "jumpers" or "nonjumpers." (Percentages of anoles correctly categorized are based on the jackknifed classification matrix.) Hind-foot length (HF) entered second, and in combination with SVL, discriminated well, correctly categorizing 98.3% of the anoles. Of the remaining variables, only toe-pad width (TP) and tail length (Tl), entered the analysis (partial F criterion). The discriminant function based on these four variables correctly categorized 100% of the sample of 60. To verify this analysis, I classified an additional 298 specimens (adults and juveniles) of the same six species; 99% were correctly categorized. The discriminant function was

$$y = 0.12(\text{SVL}) + 0.03(\text{Tl}) + 1.53 (\text{TP}) - 1.65 (\text{HF}). \quad (5)$$

The sign and magnitude of each coefficient reflect the influence of the corresponding original variate (Blackith and Reyment 1971, Sanathanan 1975). Whereas body length (SVL) and tail length (Tl) discriminated little, hind feet (HF) were longer, and toe pads (TP) narrower, in "jumpers" than in "nonjumpers."

As in stepwise regression, colinearity among the original variates in a stepwise discriminant analysis may result in some of these variates being excluded (Sanathanan 1975). I therefore removed HF and repeated step two. Femur length (F), in relation to SVL, became the best discriminator (Wilks' Lambda = 0.362; $F_{2,57} = 50.25$; $p < .001$), correctly categorizing 96.1% of the total sample of 358 anoles. Removing FL, I again repeated step two. Tibia length (T), in relation to SVL, became the best discriminator (Wilks' Lambda = 0.365;

$F_{2,57} = 49.5$; $p < .001$), correctly categorizing 98.0% of the total sample. The hind-limb elements of "jumpers" were longer, relative to body length, than those of "nonjumpers," and discriminated better than fore-limb elements.

For a more direct test of the prediction of longer hind limbs relative to fore limbs in "jumpers" compared to "nonjumpers," I performed a stepwise discriminant analysis in which I forced fore-limb length (U+H) into the analysis first, followed by hind-limb length (T+F). Fore-limb length alone discriminated poorly between "jumpers" and "nonjumpers" (Wilks' Lambda = 0.982, $F_{1,58} = 1.17$, $p > .5$), correctly categorizing only 52.0% of the individuals. In contrast, hind-limb length in relation to fore-limb length discriminated well (Wilks' Lambda = 0.364, $F_{2,57} = 49.74$, $p < .001$), correctly categorizing 98.3% of the total sample (Fig. 9). I obtained similar results in analyses considering only distal, or only proximal, limb elements. Clearly, "jumpers" had longer hind limbs relative to fore limbs than did "nonjumpers."

Multiple Discriminant Analyses. The first two canonical variables accounted for over 90% of the interspecific variation in adult morphology (Fig. 10). The first was largely a size axis; the mean score for a species was highly correlated with mean body length, although SVL was not included as an original variate (females, $r = -.89$, $n = 6$, $p < .02$; males, $r = -.92$, $n = 6$, $p < .006$). (See Table 14 for a summary of SVL data for the six species.) The second canonical variable was primarily a shape axis that loaded most heavily on limb-element lengths; canonical coefficients for all fore-limb elements were positive, whereas those for hind-limb elements were

Figure 9. Frequency distribution of discriminant function scores for "jumpers"--individuals of Anolis humilis, A. tropidolepis, and A. woodi--and "nonjumpers"--individuals of A. aliae, A. intermedius, and A. insignis--along an axis representing hind-limb, relative to fore-limb, length. See text for original variates used. This discriminant function correctly categorized 98.3% of individuals as "jumpers" or "nonjumpers" (jackknifed classification matrix).

Figure 10. Multiple discriminant analysis of morphological variation among adults of the six species of *Anolis*. Open symbols represent scores for individual anoles, and shaded ones are centroids for each species, on the first two canonical axes, which account for over 90% of the total variation. The first is largely a size variable; mean score (for each species) showed a perfect rank correlation with mean body length. The second canonical axis is primarily a shape variable that loads most heavily on limb-element lengths; a species's mean score was negatively correlated with hind-limb length relative to body length, and positively correlated with the intermembral index (ratio of fore- to hind-limb length). "Jumpers" have negative scores on the second axis, whereas "runners" and "crawlers" have positive scores. "Crawlers" (*Anolis insignis*) have the highest scores; "runners" are intermediate between "crawlers" and "jumpers." See text for original variates used. This plot is based on the analysis for adult males; the corresponding plot for females is virtually identical.

Table 14. Summary of data on adult snout-vent lengths (SVL).

^a Species/Sex		Mean SVL (mm)	SE	n
<u>A. humilis</u>	(f)	36.2	0.3	30
	(m)	32.2	0.2	41
<u>A. tropidolepis</u>	(f)	49.6	0.5	40
	(m)	49.4	0.5	43
<u>A. woodi</u>	(f)	80.8	0.9	28
	(m)	83.7	1.1	38
<u>A. insignis</u>	(f)	127.3	8.3	4
	(m)	133.8	8.1	6
<u>A. intermedius</u>	(f)	43.6	0.4	46
	(m)	42.6	0.4	42
<u>A. altae</u>	(f)	45.6	0.4	47
	(m)	44.4	0.4	42

^a

f = females; m = males.

negative. Accordingly, a species' mean score on this axis was negatively correlated with the mean ratio of hind-limb length ($HF+T+F$) to SVL (females, $r = -.88$, $n = 6$, $p < .02$; males, $r = -.89$, $n = 6$, $p < .02$), and was positively correlated with the mean intermembral index, $(U+H)/(T+F)$ (females, $r = .91$, $n = 6$, $p < .008$; males, $r = .88$, $n = 6$, $p < .02$). "Jumpers" (*A. woodi*, *A. tropidolepis*, and *A. humilis*) had negative scores on the second canonical axis, whereas "runners" (*A. intermedius* and *A. altae*) and "crawlers" (*A. insignis*) had positive scores. "Crawlers" had the highest scores; "runners" were intermediate between "crawlers" and "jumpers" (Fig. 10).

Log Shape Variables. The log shape variables also reflected these differences in body proportions (Table 15). Values of $\ln [(HF+T+F)/SVL]$ were smaller, and those of $\ln [(U+H)/(T+F)]$ larger, for "runners" and "crawlers" than for "jumpers." Also, $\ln [(HF+T+F)/SVL]$ was lower for "crawlers" than for "runners" and "jumpers" (comparing *Anolis insignis* to *A. intermedius*: males, $t = 4.0$, $p < .0002$; females, $t = 3.9$, $p < .0003$). In contrast, $\ln [T/(T+F)]$ did not differ between *A. intermedius* and *A. insignis*. Finally, in accordance with the above discriminant analyses, $\ln (T1/SVL)$ and jump frequency were not correlated (Kendall's Tau, one-tailed tests: females, $\text{Tau} = -.20$, $p > .2$; males, $\text{Tau} = .03$, $p > .4$).

To test whether interspecific differences in limb proportions were an allometric consequence of size differences, I examined correlations between log shape variables and log SVL. I found no significant correlations for either $\ln [(HF+T+F)/SVL]$ (one-tailed tests, $n = 6$: females, $r = -.18$, $p > .25$; males, $r = -.34$, $p > .25$) or for $\ln [(U+H)/(T+F)]$ (one-tailed tests, $n = 6$: females, $r = .26$, p

Table 15. Data summary for log shape variables.

Mean $\pm$ SE for each variable ^b						
Species/Sexa		Limb proportions			Rel. tail length	
		$\ln(T/T+F)$	$\ln[(U+H)/(T+F)]$	$\ln[(HF+T+F)/SVL]$	$\ln(Tl/SVL)$	n
<u>A. insignis</u>	(f)	-.778 $\pm$.011	-.238 $\pm$.007	-.574 $\pm$.003	.640 $\pm$.047	5
("crawlers")	(m)	-.771 $\pm$.007	-.253 $\pm$.011	-.548 $\pm$.005	.670 $\pm$.022	8
<u>A. intermedius</u>	(f)	-.778 $\pm$.002	-.241 $\pm$.003	-.512 $\pm$.004	.365 $\pm$.009	43
("runners")	(m)	-.776 $\pm$.002	-.232 $\pm$.002	-.507 $\pm$.003	.363 $\pm$.008	48
<u>A. altae</u>	(f)	-.761 $\pm$.002	-.294 $\pm$.003	-.494 $\pm$.006	.564 $\pm$.018	40
("runners")	(m)	-.758 $\pm$.002	-.288 $\pm$.002	-.484 $\pm$.004	.579 $\pm$.009	50
<u>A. humilis</u>	(f)	-.754 $\pm$.003	-.344 $\pm$.003	-.380 $\pm$.005	.282 $\pm$.017	18
("jumpers")	(m)	-.739 $\pm$.002	-.379 $\pm$.003	-.334 $\pm$.006	.393 $\pm$.014	26
<u>A. tropidolepis</u>	(f)	-.764 $\pm$.002	-.376 $\pm$.003	-.286 $\pm$.005	.531 $\pm$.012	37
("jumpers")	(m)	-.755 $\pm$.002	-.381 $\pm$.003	-.271 $\pm$.004	.592 $\pm$.015	42
<u>A. woodi</u>	(f)	-.751 $\pm$.003	-.378 $\pm$.005	-.296 $\pm$.004	.811 $\pm$.012	11
("jumpers")	(m)	-.739 $\pm$.002	-.378 $\pm$.004	-.292 $\pm$.005	.763 $\pm$.015	30

^a

f = females, m = males.

^b

T = tibia length, F = femur length, H = humerus length, U = ulna length, SVL = snout-vent length, HF = hind-foot length, Tl = tail length.

> .25; males, $r = .32$, $p > .25$). Figure 11 illustrates the relationship between $\ln [(HF+T+F)/SVL]$ and $\ln SVL$ for males.

Mass-length Relationships. The relationship between log mean mass and log mean SVL of adult males of the 12 Costa Rican species was linear ($r = .97$); the least-squares regression was $\log \text{ mean mass} = 3.22 \times \log \text{ mean SVL} - 5.1$. At Monteverde, average mass for a species, expressed as percent of that expected given mean SVL, was not correlated with frequency of jumping (Kendall's Tau = $-.048$, $n = 5$, $p > .35$). Some "jumpers" were relatively slender (A. woodi, mean mass = 82.3% expected), whereas others were stout (A. humilis, mean mass = 109.1% expected; A. tropidolepis, mean mass = 125.6% expected). Figure 12 plots log mass as a function of log SVL for males of A. tropidolepis and A. woodi.

Figure 11. Mean ln (hind-limb length / body length) vs mean body length for adult males ($r = -.34$; $p > .5$). The species included are *A. humilis* (▽), *A. tropidolepis* (○), *A. woodi* (△), *A. altae* (◇), *A. intermedius* (□), and *A. insignis* (◊).

Figure 12. Log mass vs log body length for males of Anolis tropidolepis (open circles) and A. woodi (shaded circles). The least-squares regressions are $y = 3.0x - 4.6$ (A. tropidolepis) and $y = 2.8x - 4.4$ (A. woodi). The slope for A. woodi is significantly lower than that for A. tropidolepis.

DISCUSSION

Microhabitat Structure and Locomotor Behavior: Proximate Influences

Microhabitat structure influences the locomotor behavior of animals in both an evolutionary and a proximate sense. In the evolutionary sense, a species (or population) evolves a locomotor repertoire suited to the structure of its environment, and may become highly specialized in this regard (e.g., Oxnard 1984). In the proximate sense, an animal may employ different patterns of locomotion as it moves through different habitats (or microhabitats) or on different types of supports (e.g., Dykyj 1980; Fleagle 1977a; Gittins 1983; Mittermeier 1978; Napier 1966; Robinson 1986; Robinson and Holmes 1984). Studying these proximate responses can help us identify the structural features of importance from an animal's viewpoint, and may provide clues to understanding evolutionary responses, which often parallel proximate ones.

According to the habitat-matrix model, both support-matrix density and support size should exert a proximate influence on the locomotor behavior of anoles. At Monteverde, these two factors were negatively correlated in the field; hence, Expt I. was necessary for evaluating their independent effects and possible interaction between them. In this experiment, both factors influenced jump frequency, but their effects were more complex than envisioned by Moermond (1979a). As predicted, jump frequency increased with support-matrix density,

irrespective of support diameter. The effect of support diameter was less consistent; the tendency to jump decreased with support size in high-density, but not in low-density, matrices. This interaction was probably due to larger supports being easier targets than smaller ones, in low-density matrices. In these matrices, an anole's probability of making a given long jump between supports increased with the diameter of the target support. This target-size effect, which is to be expected if a loss of accuracy is associated with longer jumps, compensated for a lower tendency to jump from larger supports, compared to smaller ones, in low-density matrices. These results suggest that the sizes of available supports may constrain the frequency of jumping in relatively low-density matrices.

Microhabitat Structure and Locomotor Behavior in the Field

Microhabitat Use and Structural Configurations Encountered by Anoles. The pattern of microhabitat specialization at Monteverde was comparable to that of some West Indian Anolis communities (e.g., Moermond 1979a; Rand 1964, 1967; Rand and Williams 1969; Schoener and Schoener 1971a, 1971b); sympatric forest species were vertically stratified. Likewise, the differences in structural niche among intraspecific classes were similar to those reported for other Anolis (e.g., Andrews 1971; Jenssen 1970; Moermond 1979a; Scott et al. 1976; Sexton et al. 1972; Schoener 1967, 1968; Stamps 1978). As in Moermond's (1979a) study, anoles occupying different microhabitats encountered different support-matrix densities and different size distributions of available supports.

Intrinsic constraints, as well as the size distribution of available supports, influenced patterns of support use. These intrinsic effects underscore the importance of using an index such as D_k , which adjusts for patterns of support use, in estimating the average distance between neighboring supports for a given anole class. But was D_k a suitable index? Data on jump distances indicate that it was. Whereas distances jumped by anoles in low-density matrices averaged lower than D_k , jump distances in high-density matrices, where distances jumped should approach a random sample of the available inter-support distances, averaged close to D_k .

Locomotor Behavior. At Monteverde, only Anolis insignis used crawling as its principal mode of locomotion. Because field data for this species are scant, little is known of its foraging behavior under natural conditions. Its locomotor behavior is like that of some West Indian forms that are described as searching predators (Williams 1983). Crawling was used to a lesser extent by the other anoles at Monteverde.

The positive correlation between the frequency of crawling by a given anole class and the proportion of activity (out of total activity) that occurred on small supports in low-density matrices accords with the prediction that crawling should be most frequent where supports are too narrow for running yet are too far apart for jumping. Nevertheless, this analysis left almost 70% of the variation in crawling frequency unexplained. Moreover, only for Anolis woodi was the tendency to crawl greater on stems below the median diameter than on supports at or above the median. Anolis altae and A. intermedius commonly crawled on supports that were large enough to

permit running. Although moving on small supports in low-density matrices favored crawling, anoles apparently crawled for other reasons as well.

Crawling may be the pattern of locomotion least likely to draw the attention of a predator (Schmidt and Inger 1957), and may therefore be advantageous when speed is unimportant--for example, when shuttling between sun and shade for thermoregulation. Fitch (1975) noted that individuals of A. woodi sometimes crept to the other side of a tree trunk after detecting, at a distance, a person's presence. I observed similar behavior for A. intermedius and A. altae, the two gap specialists at Monteverde. This behavior is a slow-motion version of the more familiar "squirreling", rapidly retreating to the other side of a tree trunk when closely threatened by a predator (Williams 1983). Schoener and Schoener (1982) found that survivorship of A. sagrei in open areas in the Bahamas was lower than in forest, suggesting stronger predation pressure in open habitats. For gap specialists, vulnerability to visually oriented predators such as birds (e.g., Adolph and Roughgarden 1983; Wunderle 1981) may be a one impetus for crawling.

The positive correlation of jump frequency with support-matrix density, and the negative correlation between jump frequency and support diameter, accord with predictions of the habitat-matrix model. Yet the latter correlation was weaker, paralleling the results of Expt. I, which showed support diameter to be less consistent than support-matrix density in its effect on jump frequency. The field study not only confirmed the importance of support-matrix density but also demonstrated an important body-size effect. When expressed

relative to body length, the average distance between neighboring supports accounted for 34.4% more of the variation in jump frequency among anole classes.

Interspecific Differences in Locomotor Behavior:
Proximate Responses Or Evolved Propensities?

Because microhabitat structure influences the locomotor behavior of Anolis lizards in a proximate sense, differences in locomotor behavior among species that occupy different microhabitats may be attributable to these proximate influences. This is especially likely where differences in microhabitat distribution are a consequence of ongoing species interaction (e.g., interspecific competition) rather than of species-typical microhabitat affinities (e.g., Jenssen 1973, Jenssen et al. 1984; Roughgarden et al. 1983; Salzburg 1984).

Alternatively, patterns of locomotor behavior may reflect evolved propensities that underlie structural-microhabitat preferences. Several studies have demonstrated species-specific microhabitat affinities (Heatwole 1977; Klester et al. 1975; Pounds, 1987a; Talbot 1977). Yet the existence of microhabitat affinities alone does not imply evolved locomotor propensities, as the evolution of these affinities may precede locomotor adaptation. Moermond (1979a, 1979b, 1986) interpreted interspecific variation in locomotor behavior in the field as evidence of locomotor propensities, but his behavioral data are inconclusive, as he made no distinction between proximate and evolved responses.

Because my goal was to test morphological predictions derived from an understanding of behavior, establishing the existence of

locomotor propensities without resorting to morphological evidence was crucial. Only by doing so can one avoid the fallacy of assigning species to behavioral categories partly on the basis of morphology, and then comparing morphologies among these categories (Oxnard 1984). If one assumes that behavioral differences observed in the field reflect evolved propensities where they do not, wrong predictions will be erected. In testing for these propensities, the important question is this: When placed in an identical environment, do species differ in locomotor behavior?

The interspecific differences in locomotor behavior in Expt. II strongly suggest differences in evolved propensities, yet this experiment did not control for possible effects of experience. Doing so would require hatching different species from eggs and raising them in the same structural matrix. Although experience may have played a role, field observations of hatchlings indicate that interspecific differences in locomotor propensity were not due to experience alone. Hatchlings of A. tropidolepis sometimes inhabited the shadier portions of gaps (especially on overcast days) where they co-occurred, in the lowest stratum, with hatchlings of A. altae or A. intermedius, depending on elevation. In these areas, hatchlings of A. tropidolepis jumped more frequently than did hatchlings of the other species. Thus, the differences in locomotor propensity observed in Expt. II provided a reasonable basis for proceeding with tests of morphological predictions.

Microhabitat Structure and Morphology:
Patterns and Predictions

As predicted by the habitat-matrix model, differences in shape among species in Monteverde were strongly associated with differences in locomotor behavior and structural niche. Two aspects of morphological variation among "runners," "jumpers," and "crawlers" accord with predictions from biomechanics and parallel Moermond's (1979a) results. First, "crawlers" had shorter hind limbs relative to body length than did "runners" or "jumpers." Second, "jumpers" had longer hind limbs relative to fore limbs than did "runners" or "crawlers." These patterns suggest a degree of convergence--similar adaptive solutions to equivalent ecological problems (Karr and James 1975, Niemi 1985)--between these mainland anoles and the West Indian species studied by Moermond (1979a).

Nevertheless, the morphological patterns in these two areas differed somewhat. At Monteverde, the hind limbs of "runners," although longer (relative to body length) than those of "crawlers," were shorter than those of "jumpers." This contrasts with Moermond's (1979a) study in which "runners" and "jumpers" were comparable in relative hind-limb length. Also, tibiae of "crawlers" were not shorter (relative to femora) than those of faster-moving anoles. These results suggest that selection for fast running has been less important at Monteverde than at Moermond's lowland sites on Hispaniola. That A. intermedius and A. alatae run more slowly than many other anoles is obvious (Fitch 1973; personal observation), and even though individuals of both species often run to elude predators (Pounds, 1987b), they rely more on crypsis than on speed during

these escape sequences. Typically escaping up tree trunks, these lizards intersperse short runs with abrupt stops, and are thus difficult to follow visually.

A reduced emphasis on speed might relate to the cool climate of Monteverde, compared to the lowland tropics. Although individuals of A. intermedius bask to raise their body temperatures above the ambient temperature, these lizards experience reduced sprint speeds, compared to several lowland species, for the lower quartile of field body temperatures (van Berkum 1986). At low body temperatures, individuals of A. intermedius are slower than their lowland relatives in both relative sprint speed (observed speed divided by the maximum at a thermal optimum for running) and absolute speed. The evolution of thermal sensitivity apparently has not completely compensated for the differences in field body temperatures experienced by these anoles. This is probably also true for A. altae, which occurs at even higher elevations.

Another difference between Moermond's (1979a) results and mine regards tail length relative to body length. Whereas Moermond found tail length to be greater in "jumpers," I found no relationship between tail length and jumping tendency. Several explanations are possible. First, an anole's tail functions as a counterbalance, not only in jumping, but also in perching on narrow supports, especially when the lizard's orientation is perpendicular to the support (Ballinger 1973; personal observation). Second, alignment of the center of mass with the propulsive force of jumping may be achieved without increasing tail size--for example, by reducing the fore limbs or enlarging the hind limbs. Finally, because some anoles have more

slender tails than others, length may not be the best indicator of effectiveness as a counterbalance.

Although Moermond's (1979a) results and mine differ in some details, the patterns of morphological variation among species at Monteverde accord well with predictions from biomechanics and documented differences in locomotor behavior and structural niche. Of course, selective pressures other than those related to locomotion may act on morphology. An animal's shape, as well as its coloration, for example, affects its ability to be cryptic. Nonetheless, the results suggest that selection for differences in locomotor behavior in relation to microhabitat structure is an important determinant of limb morphology in these animals.

The observed patterns do not necessarily imply adaptation to the particular vegetational matrices now occupied. In fact, whereas most of Monteverde's anoles are montane species (occurring mainly above 1200 m elev) restricted to the central cordilleras of Costa Rica and Panama, A. humilis is mainly a lowland, Central American form that invades Monteverde only marginally. Nonetheless, the patterns do indicate adaptation to abstracted features of the various microhabitat types.

That attributes of microhabitats exert important selective pressures on anoles is well known. For example, Anolis carolinensis shifts its microhabitat from island to island in the eastern Caribbean in response to congeneric competitors; its coloration changes concomitantly, apparently to match backgrounds (Schoener 1975). Likewise, differences in body size (and toe-lamellae numbers) among populations of A. sagrei in the West Indies correlate with shifts in

perch height (Lister 1976b). The habitat-matrix model may provide further insights into the evolutionary consequences of shifts, such as these, in the structural niche. As the structural configurations encountered by populations vary over the landscape or through time, so should locomotor behavior and attendant morphological adaptations.

Body Size and the Habitat-matrix Model

The consequences of body size permeate virtually every aspect of an animal's biology (Calder 1984; McMahon and Bonner 1983; Peters 1983; Schmidt-Nielsen 1984). Body size is therefore subject to a diversity of selective pressures, though one or a few may seem to prevail in a particular case. For Anolis lizards, body size correlates with prey size (e.g., Roughgarden 1974; Schoener and Gorman 1968), and most studies of body size in anoles focus on its relationship to the trophic niche (e.g., Roughgarden et al. 1983; Schoener 1969a, 1969b, 1970; Williams 1972). Body size, however, also correlates with the structural niche. In the Greater Antilles, for example, members of an ecomorphic category occupy similar structural microhabitats and resemble one another in size (Williams 1983). This convergence suggests that structural features of microhabitats exert important selective pressures on size.

My goal here is to consider, more fully than has been done before, how anole body size might be functionally related to locomotor behavior and microhabitat structure. Others have attempted this for arboreal primates (e.g., Fleagle and Mittermeier 1980). My intention is not to enter the debate over the body-size--prey-size hypothesis

(Levinton 1982, Schoener et al. 1986) or to argue, as Levinton (1982) has, that size differences are simply a consequence of structural habitat differences. Instead, I hope that by elucidating the functional relationship between microhabitat structure and body size, we may gain a more accurate null expectation for size patterns, upon which the effects of species interaction--for example, character displacement along a prey-size axis--may be superimposed.

On the Lesser Antillean islands inhabited by two species of Anolis, the larger species tend to perch higher than their smaller, sympatric congeners (Roughgarden et al. 1983; Williams 1969). In an important experiment, Rummel and Roughgarden (1985) forced A. bimaculatus to perch lower than normal, reducing its perch-height separation with the smaller A. wattsi. Competition between these species is normally asymmetric; A. bimaculatus affects A. wattsi more than A. wattsi affects A. bimaculatus. In this experiment, the competitive effect on A. wattsi was unchanged, but perch-height lowering had negative effects on growth rates, egg production, and food intake of A. bimaculatus. These effects suggest that the perch niche normally occupied by the smaller A. wattsi is somehow unsuitable for the larger A. bimaculatus. Rummel and Roughgarden hypothesized that by perching higher, a larger anole can scan a greater area in search of relatively rare, large insects; spotting these larger prey would carry less advantage for a smaller anole, which normally feeds on smaller prey, and perching higher would increase the time required to reach prey on or near the ground.

Congeneric competition, or release from such competition, may cause shifts in perch height (e.g., Jenssen 1973; Jenssen et al. 1984;

Lister 1976a, 1976b; Roughgarden et al. 1983; Schoener 1975). Among populations of A. sagrei, which is widespread in the West Indies, upward shifts in perch height are correlated with changes in body size (Lister 1976a, 1976b). Selection on size could follow these shifts, or, alternatively, size changes might cause shifts in perch height.

Whatever the case, the correlation between body size and perch height suggests a functional relationship between the two. The habitat-matrix model suggests other ways in which body size and microhabitat structure might be functionally related.

Whereas a positive correlation between anole body size and the sizes of survey perches used in territorial surveillance and sit-and-wait foraging is well documented (reviewed by Scott et al. 1976), size constraints on the use of supports during locomotion have received relatively little attention. Moermond (e.g., 1979a, 1986) recognized that the minimum-diameter support that an anole can use in locomotion increases with the lizard's body size. This is true for several reasons, some of which are obvious. First, a cylindrical beam's resistance to bending, and its critical length for resisting bending, increases with its diameter (assuming a constant modulus of elasticity) (McMahon 1975). Thus, a support that is too slender may bend excessively under the impact of an animal jumping onto it, or may not support the weight of an animal moving along its length. Also, when an animal jumps from a support that is too small to resist adequately the bending forces exerted against it, energy is diverted from the jump, decreasing its distance. Because anoles are small, they can use supports in a relatively broad size range. Nevertheless, these lizards commonly try to use supports that are too small to

support their weight, especially when fleeing a predator or conspecific aggressor (personal observation).

Besides the problems resulting from bending of supports, a relatively large lizard crawling along a narrow support tends to topple sideways for reasons discussed earlier (e.g., Anolis insignis; Pounds and Hayes 1987) (see HABITAT-MATRIX MODEL). In addition to the possible solutions to this problem that were discussed before, another is to reduce body width so that points of contact with the support can be spread more widely, relative to body width, over the support's surface (Cartmill 1985). This reduction in body width may be achieved by becoming more slender or laterally compressed, as is the case for many arboreal lizards (Schmidt and Inger 1957), or by decreasing overall body size.

Through its influence on support-use patterns, body size helps determine the effective support-matrix density encountered by an anole; size may also influence aspects of locomotor performance, including running speed and jump distance (Emerson 1985; Gabriel 1984; Garland 1985). Because the relationship between body size and jumping ability is crucial to the habitat-matrix model, a brief look at underlying theory is warranted.

Hill (1950) reasoned that jump distance should be independent of size. Hill's model, derived from the ballistic equation (1), can be expressed as follows. Let $E = kn$, where n is the mass of muscles used in jumping and k the kinetic energy per unit mass of these muscles.

Combining this relationship and the equation for kinetic energy, $E = \frac{1}{2} m v^2$, with Eq. (1), jump distance (d) can be expressed as follows:

$$d = \frac{2 k n \sin^2 \theta}{m g} . \quad (6)$$

Maximal jump distance is achieved where k is maximal and $\theta = 45^\circ$. According to this model, animals capable of producing the same kinetic energy per unit of muscle should jump the same distance irrespective of size (i.e., mass) if body shape and n/m remain constant. Although some authors (e.g., Alexander 1968; Schmidt-Nielsen 1984) have concluded, as Hill did, that jump distance should be independent of body size, empirical studies show that absolute jump distance may increase with body size (e.g., Emerson 1978, 1985).

Hill's model does not take into account the problem that small animals face in generating power (Emerson 1985; Gabriel 1984). Assuming constant shape, the distance (c) traversed by the animal's center of mass (and hence time) between the beginning of muscular contraction and when the hind feet leave the ground is shorter for a smaller animal. Smaller animals must therefore accelerate faster and generate greater mass-specific energy per unit time to jump the same distances that larger animals do. Power (P) is E/t , where t is time. Substituting $E = \frac{1}{2} m v^2$, P becomes $\frac{1}{2} m v^2 t^{-1}$. Assuming constant acceleration and a standing jump (i.e., initial velocity of zero),

$$c = \frac{1}{2} v t , \quad (7)$$

or

$$t = \frac{2c}{v} \quad (8)$$

If q is the power generated per unit of jumping muscle, then $P = qn$.

Thus, $qn = 1/2 mv t^{-1}$. Substituting from Eq. (8),

$$qn = \frac{mv^3}{4c} \quad (9)$$

or

$$v = \left(\frac{4qn c}{m} \right)^{1/3} \quad (10)$$

Substituting in the ballistic equation, Eq. (1),

$$d = \left(\frac{4qn c}{m} \right)^{2/3} \sin^2 \theta g^{-1} \quad (11)$$

Assuming n/m is constant, animals of different sizes should be able to jump distances proportional to $c^{2/3}$, but jump distance should be independent of mass (assuming c is constant). If this model is correct, Hill's (1950) model is also correct, but incomplete. As I will discuss later, anoles may increase in length (and therefore c ,

assuming constant limb proportions), within certain limits, without increasing in mass (or vice versa).

Two lines of evidence in the present study support the prediction, from the above power-generation model, that absolute jump distance should increase with body size. First, the average distance between neighboring supports, the best predictor of jump frequency, accounted for one-third more of the variation in jump frequency when I expressed this independent variable relative to body length rather than as an absolute distance. The second line of evidence is the strong positive correlation between mean jump distance (for a given anole class) and mean body length, a correlation that remained significant when partialled on average distance between neighboring supports, or when I included only one anole class (i.e., adult males or adult females) per species in the analysis. These results accord with a recent demonstration that jumping ability in Anolis carolinensis is positively correlated with snout-vent length (Losos, personal communication).

Moermond (1979a) was therefore correct in assuming that larger anoles can out-jump smaller ones. Noting that juveniles invariably occupied higher-density matrices than did adults, he reasoned that larger anoles are more efficient in using low-density matrices, and that larger species can therefore be more generalized--that is, "span a greater range of perch matrices" (p. 161). My observations of anoles in the understory of closed-canopy forest at Monteverde support these ideas for species that rely heavily on jumping. Anolis humilis, A. tropidolepis, and A. woodi, which were similar in limb proportions but markedly different in size, differed concordantly in structural-

niche breadth (Simpson's index, treating strata as resource states). Mean body length followed the same rank order as did the diversity of support matrices used, and the same rank order as the average distance between neighboring supports. Apparently, no particular body size is best-suited for jumping per se, but one size may be better suited than another in a particular support matrix. If so, the three-dimensional structure of an anole's environment may exert important selective pressures, not only on shape, but also on size.

Are Differences in Proportions Among Species an Allometric Consequence of Body Size?

Emerson (1985) criticized studies that compare the relative limb lengths of saltatorial species to those of their nonjumping relatives without considering the possible effects of interspecific allometry. Several lines of evidence in the present study indicate that interspecific differences in shape were not simply a consequence of size differences. First, in the stepwise two-way discriminant analysis, body length alone did not discriminate between "jumpers" and "nonjumpers," whereas limb proportions did. Second, in the multiple discriminant analyses most of the variation in limb proportions was resolved on the second canonical axis, which was not correlated with body length. Finally, log shape variables (Mosimann and James 1979, James 1982, Kiltie in press) computed for each species were not correlated with log body length.

Mass-length Relationships

Arboreal lizards in general tend to be relatively slender (Pianka 1973, 1986). Anolis is the classic example, yet species differ in this regard. Some anoles are relatively stout, compared to their more gracile relatives (e.g., Schoener 1969a, Fitch 1973, Corn 1981, Williams 1983). The idea that these mass-length relationships are adaptive is not new. Schoener (1969a) suggested that an increase in length without an increase in mass might be advantageous for twig-inhabiting anoles. Also, a gracile form is characteristic of grass-bush anoles, which often use slender, flexible supports (Williams 1983). On narrow supports, a gracile form might enhance crypticity, but might also be advantageous during locomotion. Nevertheless, interspecific differences in mass-length relationships have not been considered with respect to the habitat-matrix model.

Mass may influence the size range of supports usable by an anole of a given body length, and this in turn may influence the effective support-matrix density. Do mass-length relationships affect jumping performance? Emerson (1985, p. 60) reasoned that mass, not body length, is the appropriate size variable when comparing body proportions of jumping vs nonjumping species, as mass is more important "in terms of energy of the jump." She therefore expressed limb lengths relative to the cube root of mass. But in both Hill's (1950) model and the power-generation model discussed earlier, jump distance is independent of mass as long as n/m (the proportion of mass consisting of muscles used in jumping), the physiological properties of these muscles, and c (acceleration distance) remain constant. Furthermore, I found no

correlation between jumping tendency and mass-length relationship, suggesting that a slender form is not an adaptation for jumping per se.

Following the power-generation model, Eq. (14), I propose the following hypothesis (shown graphically in Fig. 13) to help explain the evolution of the more slender form exhibited by some anoles. As an anole that relies heavily on jumping evolves a greater body length (assuming constant limb proportions), acceleration distance (c) increases proportionally. Therefore, assuming n/m is constant, absolute jump distance (d) increases according to a negatively allometric relationship ($d = \text{constant} \times c^{2/3}$). Because mass increases concomitantly, however, the animal's choice among the available supports narrows, and the effective support-matrix density therefore decreases. Increasing body size may allow the lizard to operate in successively lower-density matrices until it reaches a critical size (SVL_c), at which the effective average distance between available supports begins to exceed the distance the animal is capable of jumping. The important point is that a species, by evolving a more slender form, may increase further in linear dimensions and occupy even lower-density matrices before reaching this critical point.

The above hypothesis is consistent with the patterns for understory anoles in closed-canopy forest at Monteverde. Individuals of Anolis humilis and A. tropidolepis, small lizards that inhabited dense matrices near the ground, were relatively heavy for their body lengths. In contrast, individuals of A. woodi, larger anoles that inhabited a greater range of support-matrix densities, including relatively low-density matrices above the shrub layer, were relatively

Figure 13. Hypothetical relationships of jump distance and effective inter-support distance to body size. In this model, an anole's jumping ability has a negatively allometric increase with snout-vent length, but at the same time, the animal's choice among available supports narrows (the effective support-matrix density decreases) and average effective inter-support distance increases. At a critical body size, SVL_c , average distance between available supports begins to exceed the distance the animal is capable of jumping. A more slender anole may increase further in linear dimensions and occupy a lower-density matrix before reaching this critical point. Other shapes are possible for the hypothetical curves; empirical work is needed to determine which shapes are most realistic.

light for their body lengths. The above model applies only to species that rely heavily on jumping; a slender form may evolve for other reasons as well.

Functioning of the adhesive subdigital pad could also constrain the evolution of mass-length relationships. Andrews and Rand (1974) reasoned that toe lamellae may be limited in the weight they can bear and that this constraint may have influenced the evolution of clutch size and relative clutch mass. This logic might be extended to the evolution of mass-length relationships in general; anoles that rely heavily on toe lamellae in climbing might be expected to retain a gracile form, but more data are needed to evaluate this. In the present study, A. altae and A. intermedius, two climbing species with well-developed subdigital pads, were each close to the mass expected for anoles of their body length.

The above discussion suggests another constraint on the evolution of relative clutch mass in anoles. An increase in clutch mass would decrease n/m (the proportion of total mass consisting of muscles used in jumping), and would therefore reduce a gravid female's jumping ability and, consequently, her proficiency in moving about in a three-dimensional matrix.

What Measure of Locomotor Performance Do Anoles Maximize?

Because arboreal animals typically employ multiple patterns of locomotion (e.g., Fleagle 1977a; Fleagle and Mittermeier 1980; Mittermeier 1978; Moermond 1979a, 1979b, 1986), questions concerning locomotor performance are complex. Locomotor performance of these

animals may be viewed hierarchically. At one level, we may ask how fast a lizard can run, how far it can jump, or what kinds of supports it can use effectively. At a higher level, we may consider the overall performance of a sequence of movements that comprises multiple locomotor patterns. We may ask, for example, how fast (or how efficiently) a lizard can move through its three-dimensional habitat.

Of the possible higher-level measures of locomotor performance, which is most important to anoles? The answer to this question probably varies through time and among species. Although Moermond (1971a, 1971b, 1986) emphasized energetic efficiency during foraging, its relative importance is unclear. An anole traveling unhurriedly through its habitat--for example, changing foraging sites or shuttling between sun and shade for thermoregulation--should maximize the economy (distance/energy) of its locomotion. In contrast, a lizard fleeing a predator or conspecific aggressor, might maximize its speed or maneuverability. Or, if the lizard is fleeing from a predator that is persistent but not fast, endurance may come into play. These distinctions are important, as different combinations of locomotor patterns may maximize different measures of performance in a given structural configuration.

During predator-escape sequences, for example, Anolis lizards may shift to locomotor behavior that differs from that typical of normal activities. A tendency to flee into a particular microhabitat may enhance this shift. At Monteverde, interspecific differences in locomotor behavior during simulated predatory attacks were concordant with differences during foraging; anoles that jumped frequently when fleeing also jumped frequently when foraging. Yet the magnitude of

differences in jump frequency between "runners" and "jumpers" was greater during predator-escape sequences (Pounds 1987b).

Adaptation Versus "Phylogenetic Inertia"

Morphological similarity of ecologically analogous species suggests convergence, yet, in the absence of genealogical information, similarity due to shared ancestry (i.e., "phylogenetic inertia") cannot be ruled out (Gould and Lewontin 1978). The anoles of Costa Rica comprise two major lineages, which Guyer and Savage (1987) consider separate genera--Dactyloa, the mainland "giants" of the latifrons series (Williams 1976), and Norops, the beta anoles (sensu Etheridge 1960). All of Monteverde's anoles, except for A. insignis, belong to the latter lineage. Within this lineage, two of the currently recognized series (auratus and petersi) are represented in Monteverde. The auratus series includes A. intermedius, A. humilis, A. tropidolepis, and A. altae, and the petersi series includes A. woodi. Unfortunately, this infrageneric classification is only tentative. If it is correct, the auratus series includes some species that resemble A. insignis in body proportions and others that resemble A. woodi; this incongruity between phylogeny and ecomorphology suggests convergent evolution.

Locomotor or Microhabitat Specialization?

Because understanding locomotor adaptations is important in the study of arboreal animals, many workers, especially primatologists, have categorized species according to locomotor specialty (reviewed in

Oxnard 1984). The resultant "locomotor classifications," which are often criticized as simplistic (e.g., Oxnard 1984; Ripley 1967), may or may not be useful, depending on one's purpose and on the animals in question. Nevertheless, categorizing movements by locomotor pattern provides a means of quantifying locomotor behavior and making comparisons among species (e.g., Fleagle 1977a; Fleagle and Mittermeier 1980; Mittermeier 1978; Moermond 1979a, 1979b, 1981, 1986).

Moermond (1979a) categorized species of Anolis into three locomotor specialties--"runners," "jumpers," and "crawlers"--according to principal mode of locomotion. At Monteverde, some species are locomotor specialists, whereas others are not. Anolis insignis, for example, is a specialized "crawler" (Pounds and Hayes 1987) and A. intermedius and A. altae are primarily "runners." The remaining species, although referred to as "jumpers" are not locomotor specialists in the sense used by Moermond. For A. woodi, jumps made up only 40% of total movements. Likewise, adult males of A. tropidolepis and both sexes of A. humilis scarcely jumped more than they ran.

The latter three species are specialized for relatively high-density matrices and are adapted for jumping, but they are not specialized in jumping per se. Anolis altae and A. intermedius, in contrast, are more generalized in their use of support matrices. In naturally occurring treefall gaps, which were probably the primary habitat of these species when the area's vegetation was in a primeval state, support-matrix density in the lowermost strata is higher than in the corresponding strata of mature forest, but decreases sharply

with height. Thus, under primeval conditions, these two species probably inhabited a greater range of support-matrix densities than the other Monteverde species.

In summary, anoles adapt behaviorally and morphologically to the structural configurations of their preferred microhabitats, and may specialize for a particular locomotor pattern. Nevertheless, microhabitat specialization and locomotor adaptation do not automatically imply locomotor specialization.

Habitat Structure and Community Structure

A central question in ecology concerns the phenotypic component of community structure: What determines the combination of phenotypes present at a given locality? Most empirical studies that address this question focus on pattern and process at the community level. These studies either analyze phenotypic patterns and infer underlying community-level processes such as interspecific competition (e.g., Abbot et al. 1977; Bowers and Brown 1982; Grant and Schluter 1984; Hutchinson 1957, 1959; Lack 1947; Ricklefs et al. 1981; Ricklefs and Travis 1980; Schoener 1984), or they examine these processes experimentally (e.g., competition experiments reviewed by Connell 1983, Schoener 1983). Less commonly, drawing on ideas central to behavioral, physiological, and functional-morphological ecology, studies focus on the "mechanisms" by which an animal's phenotype constrains its use of habitats or resources (e.g., Moermond 1979a, 1986, Price 1986; Price and Waser 1985; Schluter and Grant 1984). By

elucidating these mechanisms, one may identify the types of species likely to inhabit a given locality.

Mechanistic approaches, by stressing the fundamental niche, force a detailed understanding of how each species responds to the structural and physicochemical features of habitats, and to the dispersion of resources within these habitats. Recent emphasis on these species-typical responses (e.g., Collins et al. 1982; Holmes et al. 1986; James et al. 1984) is an outgrowth of the "individualistic concept" of species associations first articulated by phytosociologists (e.g. Gleason 1926) and later substantiated through gradient analyses of species distributions and abundances (e.g., Bray and Curtis 1957; Whittaker 1956, 1967).

Mechanistic approaches in community ecology are controversial (Schoener 1986). Some ecologists reject them as reductionistic, arguing that reductionism cannot work in ecology. In fact, the question of reducibility of community-ecological phenomena is central to current debate over the importance of species interactions in shaping community structure (e.g., Strong et al. 1984). Besides the antireductionist perspective, two other viewpoints have emerged. Advocates of an extreme reductionism (e.g., Simberloff 1983) argue that the individualistic responses of organisms, along with chance and history, are sufficient to explain community composition. In contrast, advocates of mechanistic reductionism (e.g., Schoener 1986) hold that understanding these individualistic responses is necessary, but often not sufficient, for interpreting community patterns. In the latter view, reductionism generates a mechanistically based picture, upon which the effects of species interactions may be superimposed.

Proponents of both views agree that understanding the mechanisms that underlie species-typical responses to environmental heterogeneity is essential, yet these mechanisms remain at best dimly understood for most species.

Ecologists have long been interested in how habitat structure influences community structure (e.g., James 1971; James and Wamer 1982; MacArthur 1958; Robinson and Holmes 1982), particularly in relation to species diversity (e.g., August 1983; Dueser and Brown 1980; Karr and Roth 1971; MacArthur 1964; Recher 1969). Yet essential information on how species respond to habitat structure is usually lacking. Specialization by structural microhabitat is a prominent feature of many animal communities (Napier 1966; Schoener 1974). If the morphologies of animals influence their abilities to exploit various structural configurations, the presence or absence of various morphological types of species at a given locality may depend on the array of available microhabitats (e.g., Moermond 1979a; 1986; Price 1986).

Moermond proposed that the availability of structural matrices at a given West Indian locality helps explain the presence or absence of the various Anolis ecomorphs, and that the local spatial distribution of these matrices influences the within-habitat distribution of each species. The patterns at Monteverde support this view. The functional relationship between anole phenotype and habitat structure explains much of the community's phenetic structure, including patterns of shape and possibly size.

The four species inhabiting closed-canopy forest in Monteverde appear evenly spaced along a size axis (Table 14). Also, the minimum

size ratio (mean adult body length of a species : mean adult body length of next smallest species) is large (1.53 for males and 1.37 for females) relative to that expected by chance. Using a computer simulation, I found these ratios to be greater than 100% of those of four-species assemblages ($n = 100$) drawn at random from a pool of 20 Costa Rican species, and larger than 97% of those from a pool of 12 species that inhabit the highlands (> 1200 m elev) of Central America. The mean body lengths of these species also follow a perfect rank order with mean height above ground, suggesting that the body-size and structural-niche axes are nonindependent. The spectrum of vegetational matrices may have contributed to a nonrandom pattern of interspecific variation in size, as well as shape. The importance of species interaction in the evolution of these patterns is unknown.

Several studies have demonstrated interspecific competition in West Indian Anolis communities (e.g., Pacala and Roughgarden 1985; Roughgarden et al. 1983), but the population densities of anoles on the islands are much higher than on the mainland, where lizards are inconspicuous elements of more species-rich biological communities (Andrews 1971; Rand and Humphrey 1968; Williams 1983). Complementarity between bird and lizard densities within the islands (Lister 1976a; Schoener and Schoener 1978; Wright 1981) and in Panama (Wright 1979) suggests that competition with, or predation by, birds depresses anole densities on the mainland (Moermond 1983). Recently, Guyer (personal communication) found that anole populations in lowland Costa Rica may be food-limited, yet several studies suggest that competition is less intense among anoles on the mainland than on the islands (Andrews 1971, 1976, 1979). Furthermore, because lizards are a relatively

small part of continental faunas, the effects of competition among mainland anoles, where it occurs, are likely to be diluted by the effects of interactions with more distantly related organisms.

Predation might also influence the structure of mainland Anolis communities, as limiting-similarity barriers may exist among species that share predators, irrespective of competition for food (e.g., Holt 1977, 1984). Consider a relatively abundant species of anole that specializes on a particular microhabitat, where it is heavily preyed upon by birds. A second, less abundant species, if similar in appearance to the more abundant anole, may be included in the search image used by the birds. If the birds habitually search where lizards are most abundant, members of the rarer Anolis species could improve their chances of avoiding predation by shifting to a different microhabitat. Besides this possible apostatic selection on microhabitat use, predation might select for escape-behavior diversity (Schall and Pianka 1980). Attendant morphological (and behavioral) adaptations could influence microhabitat use during foraging and general activities through effects on locomotor performance in relation to structural configuration.

Whatever its evolutionary impetus, segregation of coexisting species by microhabitat is characteristic of Anolis lizards, and structural features of microhabitats exert important selective pressures on locomotor behavior and functional morphology. Therefore, understanding microhabitat specialization is likely an important key to understanding much of the adaptive radiation of anoles.

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BIOGRAPHICAL SKETCH

Joseph Alan Pounds was born on March 7, 1953, in Glenwood, Arkansas. He attended public schools in Hot Springs and Little Rock, Arkansas, graduating from McClellan High School in Little Rock in 1971. He attended the University of Arkansas at Little Rock, majoring in biology and minoring in anthropology, and graduated with the degree of Bachelor of Science in 1976. In 1980, he completed the Master of Science degree at the University of Southwestern Louisiana in Lafayette, Louisiana, also with a biology major. His thesis was entitled "Riverine Barriers to Gene Flow and the Differentiation of Fence Lizard Populations." He began his work in the zoology graduate program at the University of Florida in 1980. From 1983 through 1985, he did the field work for his dissertation in and near Monteverde, Costa Rica. He married Willow Zuchowski from Northampton, Massachusetts, in 1983. He plans to continue his work in tropical biology in Central America.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Martha L. Crump, Chairperson
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Archie Carr
Graduate Research Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Peter Feinsinger
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Frank G. Nordlie
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

A handwritten signature in dark ink, reading "Frank Slansky", written over a horizontal line.

Frank Slansky
Associate Professor of Entomology and
Nematology

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

May, 1987

Dean, Graduate School