

Concordant evolution of locomotor behaviour, display rate and morphology in *Anolis* lizards

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Abstract. Morphologically similar species of *Anolis* lizards use similar microhabitats on islands in the Greater Antilles. The habitat matrix model suggests that particular locomotor behaviours are favoured in different microhabitats, and that species evolve the morphology appropriate for a given locomotor mode. These predictions are confirmed for 13 species of Jamaican and Puerto Rican anoles. Species occupying similar microhabitats group together in a multi-dimensional 'behaviour space'. Phylogenetic analyses indicate that limb proportions and locomotor patterns (e.g. frequency of running or jumping) have evolved in tandem. Further, the rate of rapid movements (i.e. runs and jumps) and display rate have co-evolved. A suite of relatively extreme morphological and behavioural (both locomotor and social) changes accompanied the evolution of an active foraging mode in *A. valencienni*. Similar, but less extreme, behavioural changes have been associated with morphological evolution among the 12 species that are sit-and-wait foragers. Habitat structure is also important in determining locomotor behaviour, particularly jumping frequency and distance jumped.

Appendicular morphology and locomotor behaviour are correlated among flying (Findley & Wilson 1982; Norberg 1985), running (Hildebrand 1974, 1985; Coombs 1978) and swimming (Webb & Blake 1985) animals. The habitat matrix model (Moermond 1979a; Pounds 1988; see also Fleagle & Mittermeier 1980; Robinson & Holmes 1982) explains this relationship as a result of microhabitat differences. For example, in cluttered areas, bats with high manoeuvrability are more successful in foraging, whereas in open areas, rapid flight is more profitable (Aldridge & Rautenbach 1987; Crome & Richards 1988). Similarly, in a dense arboreal habitat, saltation may be most efficient, whereas for lizards on isolated branches and trunks, running and crawling are more effective modes of movement. The model predicts that species will evolve morphologies necessary for the locomotor mode appropriate for a given microhabitat.

Two corollaries to this hypothesis have received little attention. First, comparative analyses are implicitly investigations of adaptive evolution (Lauder 1981; Ridley 1983). If extant species have the morphology and locomotor patterns appropriate for their respective microhabitats, one would predict that morphology and behaviour have evolved in tandem. Second, both locomotor mode (Stamps 1977; Tollestrup 1983) and habitat (Jarman 1974; Packer 1986) are known to affect

social behaviour, which, consequently, may evolve synchronously with these variables. However, there are few examples of morphology, locomotor patterns and social behaviour evolving in a concerted manner, particularly within a closely related group.

The pattern of intra-island radiation and inter-island convergence of *Anolis* lizards in the West Indies provides an opportunity to examine these issues. Independent radiations on the Greater Antillean islands of Jamaica, Hispaniola, Puerto Rico and Cuba (Rand & Williams 1969; Williams 1972, 1983), have each produced a suite of morphologically distinct species, differing in leg, tail and body proportions, subdigital lamellae, colour and other characters. These species also differ in microhabitat and behaviour. The same set of ecomorphs (named for the microhabitats they use most frequently: 'twig', 'grass-bush', 'trunk-ground', 'trunk-crown' and 'crown-giant'), convergent in morphology, ecology and behaviour, has evolved on each of the islands (with several exceptions).

Williams' (1972) claim that morphologically similar anoles use similar patterns of locomotion has been substantiated by studies of Hispaniolan and Central American species (Moermond 1979a, b; Pounds 1988). These studies have also revealed the biomechanical basis for the relationship between morphology and locomotor behaviour. Biomechanical models predict that species that use

narrow supports should be slender, have short legs and walk slowly to prevent loss of balance and toppling (Cartmill 1985; Pounds 1988). On broader supports, longer hind limbs are better suited for running and jumping (Losos & Sinervo 1989). Relative to species that jump often, species that run frequently would also need long fore-limbs, because anoles always run quadrupedally (unlike some other lizards; Snyder 1962). These predictions were confirmed for the seven Hispaniolan and six Costa Rican species studied by Moermond and Pounds. Hind limb length and frequency of crawling are inversely related and species with long hind limbs relative to the length of their fore limbs tend to jump more frequently.

Here, with a larger and more morphologically and behaviourally diverse set of species, I first demonstrate that the different ecomorph categories, defined on the basis of morphology, do differ in behaviour. I then use phylogenetic character analysis to determine whether evolution in limb morphology has been associated with evolution in locomotor propensities and movement and display rates. For two species, I also assess the extent to which these variables differ between habitats.

MATERIALS AND METHODS

Field Studies

Field studies were conducted during June–August 1987 and 1988 in Jamaica and Puerto Rico on 13 *Anolis* species (Fig. 1; ecomorph designations in Fig. 2). Localities and raw data are presented in Losos (in press a). Behavioural focal samples were conducted following Moermond (1979a, b) and Pounds (1988). Lizards were located by walking transects through all appropriate habitats. Once spotted, lizards were watched quietly from a distance of 2–10 m. Only undisturbed lizards were chosen for observation. Each lizard was watched for 20 min or until it disappeared. All movements were noted as walks, runs or jumps. Walks (which correspond to Moermond's (1979a, b) crawls) were distinguished from runs by speed of movement. The longest jump was measured or estimated at the conclusion of each session. Jumps in which the lizard descended greater than 28 cm were excluded because they inflate the horizontal distance of the jump (28 cm was selected to standardize with the jumping performance measures described in Losos in press a,b). Jump distance data were included

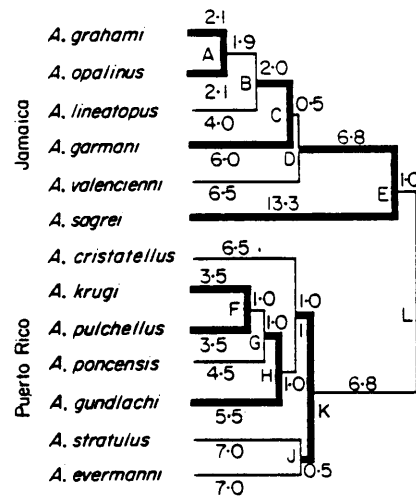


Figure 1. Phylogenetic relationships among Jamaican and Puerto Rican *Anolis* (from Losos, in press a). This cladogram is not meant to imply that the Jamaican and Puerto Rican anole radiations are sister taxa or monophyletic in the strict sense of including all descendant taxa. Numbers represent the relative length of each branch. The distances between major species groups (represented by *A. evermanni*, *A. cristatellus*, and *A. valencienni*) were calculated based on immunological studies (Losos, in press a). Within-group branch lengths were estimated based on immunological or electrophoretic studies, when available, or by partitioning distance equally among branches. Assignment of distances along branches was constrained to fit the phylogenetic tree. The 12 independent contrasts (identified by letters) are indicated by the line shading.

only from individuals that made more than two jumps. The amount of time spent displaying (bobbing and/or dew-lapping) was timed with a stopwatch and recorded as the proportion of total time observed. Only animals that made more than four moves were included in the analyses below; animals that moved less may have been disturbed by the observer. Additionally, movement and display rates are calculated using only animals observed for greater than 5 min; including animals that were active and then disappeared would inflate their overall activity rate because their periods of inactivity were not observed. Observations were not conducted during inclement weather or early in the morning or late in the afternoon, when lizards may not have been able to thermoregulate at preferred temperatures.

Anolis evermanni and *A. gundlachi* were commonly found in two distinctive habitats, on stream-side boulders and on trees. To test the influence of

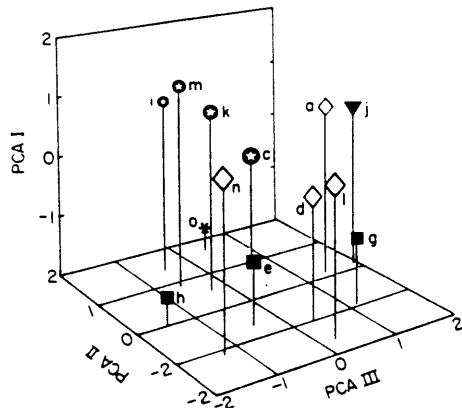


Figure 2. The distribution of species in a three-dimensional behaviour space, based on each species' score on the first three principal components axes (PCA). See text for definition of the axes. \diamond (trunk-ground species): *A. cristatellus*, a; *A. gundlachi*, d; *A. lineatopus*, l; *A. sagrei*, n; \bullet (trunk-crown): *A. evermanni*, c; *A. stratulus*, i; *A. grahamsi*, k; *A. opalinus*, m; \blacksquare (grass-bush): *A. krugi*, e; *A. poncensis*, g; *A. pulchellus*, h; $*$ (twig): *A. valencienni*, o; \blacktriangledown (crown-giant): *A. garmani*, j.

habitat on locomotor behaviour, individuals were observed in both habitats. More *A. gundlachi* were observed on trees than on rocks because observers often spotted lizards on the trees adjacent to the stream boulders, or because lizards initially spotted on boulders spent more time on trees, and were grouped in the tree habitat category.

Forelimb, hindlimb, and snout-vent length (SVL) were measured on more than 15 individuals of each species. Limb lengths were the distance of the distal toe on the right side of the body to the insertion of the limb in the body wall.

Statistical Analysis

The mean value of each variable of each species is used in subsequent analyses. Movement rate, maximum distance jumped and all morphological measurements were ln-transformed. Walk, run and jump frequency, as a proportion of all movements, and display rate, measured as a proportion of time observed, were arcsine-transformed. All statistical analyses were performed using Systat (1986), except the UPGMA clustering analysis, which was conducted using NTSYS (version 1.30, Rohlf 1987).

For interspecific comparisons, Moermond (1979a, b) and Pounds (1988) used each behav-

ioural event (e.g. each movement) as a separate datum. However, multiple points from one individual are not statistically independent; further, pooling data results in inflated sample size (Machlis et al. 1985). Consequently, for each individual, I calculated the proportion of moves that were jumps, runs and walks and used the means of these values for interspecific comparisons. I also restrict my analysis to adult males to avoid confounding interspecific, intersexual and ontogenetic differences.

Phylogenetic Analysis

The comparative approach asks whether variation in two characters of interest is associated among species. Because species are linked by a network of shared ancestry, however, species may be similar in a character or characters solely because they share a recent ancestor. Because character states among species are consequently not independent, statistical analyses based on among-species comparisons are invalid (Felsenstein 1985, 1988). To circumvent this difficulty, two methods, the ancestor reconstruction and contrast approaches, have been advanced recently. These methods explicitly test the hypothesis implicit in the comparative approach, i.e. that two characters have evolved synchronously. These approaches are discussed more fully by Felsenstein (1985, 1988), Huey (1987) and Losos (in press a).

To assess the degree to which two variables have evolved synchronously, one can estimate the values of the variables for all hypothetical ancestral taxa (the nodes on the phylogeny labelled with letters in Fig. 1) following the methods of Huey & Bennett (1987; also see Losos in press a). Then, by comparing the value for a variable in an ancestor and a descendant, one can determine how much the variable evolved and in which direction. When the amount of change is calculated for all ancestor-descendant pairs of taxa for two variables, one can determine to what extent evolutionary change in one is associated with evolutionary change in the other using least-squares regression (Huey & Bennett 1987). The ancestor-reconstruction algorithm has the effect of partitioning change in such a manner as to minimize the total amount of evolution squared along the branches of the phylogeny. I have not used an alternative approach that minimizes the absolute amount of evolution along the branches (Farris 1970; Larson 1984;

Sessions & Larson 1987) because this approach can, and in this case did, produce an overwhelming number of equally parsimonious possibilities (Swofford & Maddison 1987).

Felsenstein (1985) developed an alternative method. Every hypothetical ancestor in a phylogenetic tree has two immediate descendants. The degree to which these descendants differ in a given trait reflects the amount of evolution since their differentiation and is independent of evolutionary change occurring elsewhere on the tree. For a tree with N extant species, there are $N-1$ independent contrasts. One can ask whether the calculated differences in these contrasts for one variable are related to differences in a second variable, i.e. is differentiation in these variables associated? If one assumes that random changes accumulate in time in a manner similar to Brownian motion (i.e. small and independent change between generations), then each contrast can be scaled by a function of the time elapsed since the two descendants differentiated to guarantee equal variance among contrasts. The hypothesis that the two characters have evolved concordantly can then be tested by correlating the values for the contrasts for the variables (analogous to a regression through the origin; see Felsenstein 1985, 1988 for further details).

To calculate contrasts, one needs not only data on extant species and an understanding of their phylogenetic relationships, but also information on the length of the branches in the phylogenetic tree. Given the phylogenetic relationships in Fig. 1, branch lengths were assigned based on immunological (primarily Shochat & Dessauer 1981; also Wyles & Gorman 1980) and electrophoretic (Gorman et al. 1980a, b, 1983) studies, with the much-debated assumption that the distance values generated are proportional to time since divergence. In cases in which no information was available, length was partitioned equally among the branches (see Losos, in press a).

I test the hypotheses that various locomotor parameters are correlated with limb proportions and display rate among *Anolis*. Limb length scales strongly and positively with body size among extant species; ancestor reconstruction analyses indicate that evolution in body size and limb length have been strongly linked (Losos, in press b). To remove the effect of size, I calculated the residuals of change in hindlimb length regressed on change in snout-vent length using both ancestor-

Table I. Principal components analysis

Factors	Axis		
	I	II	III
% Walk*	-0.855	0.446	0.083
% Run*	0.947	-0.149	0.060
% Jump*	-0.125	-0.881	-0.318
Movement rate	0.342	0.803	-0.378
Display rate	0.785	0.153	-0.386
Maximum jump	0.512	0.068	0.794
Variation (%)	44.0	28.1	17.2

*% Walk, run and jump is the percentage of all movements that are of a given type.

reconstruction and contrast analyses. Forelimb and hindlimb length scale against body size with different slopes (Losos, in press b). In the forelimb: hindlimb ratio-jump frequency analysis, I used the residual of evolution in forelimb length regressed on change in hindleg length, again using both phylogenetic methods.

RESULTS

Existence of Ecomorphs

Principal components analysis results are presented in Table I. Only the first three axes are presented because the remaining three account for little variation (10.7%) and are biologically uninformative. The first axis indicates a strong inverse relationship between frequency of running and walking. Species that run often also display at high rates and, to a lesser extent, make long jumps. The second axis indicates that species that move at high rates tend to jump infrequently. The third axis loads strongly only for maximum jump distance.

The deployment of species in a three-dimensional behaviour space is not random; ecomorphologically similar species tend to group together (Fig. 2). Multivariate analysis of variance (MANOVA), using principal component scores as variables and ecomorph category as the grouping variable, indicates that the position of ecomorphs differs significantly (Wilk's $\lambda = 0.019$, $F_{12,16} = 4.67$, $P < 0.01$). Analyses of variance treating the principal component axes individually show that ecomorphs differ on principal component axis I ($F_{4,8} = 9.70$,

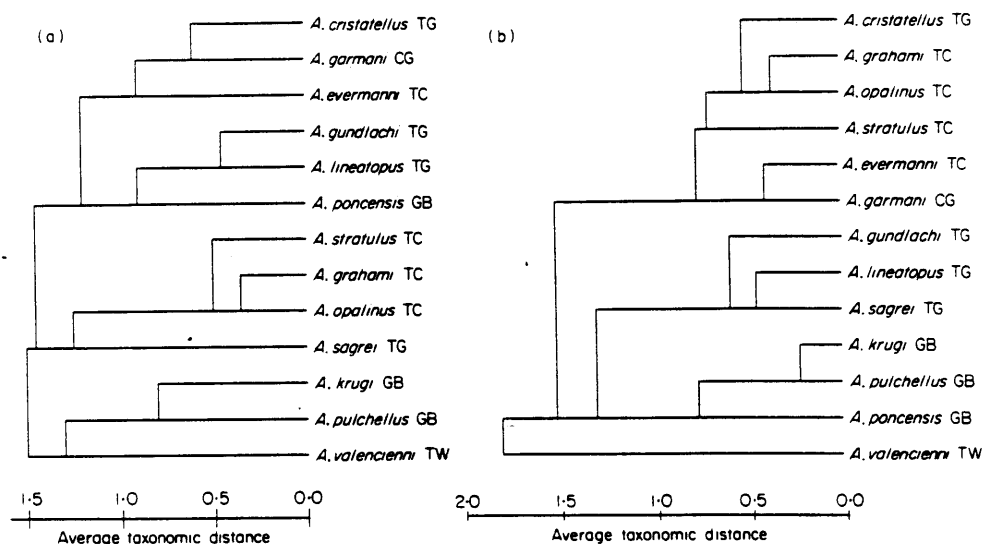


Figure 3. UPGMA clustering of species based upon their scores on the principal components axes. (a) Uses scores on the first three axes; (b) uses only the first two axes. The scale indicates average taxonomic distance between clusters (Rohlf 1987).

$P < 0.05$) and II ($F_{4,8} = 8.46$, $P < 0.01$), but not III ($F_{4,8} = 1.32$, NS; probability values corrected for multiple tests). Unfortunately, no method yet exists to incorporate phylogenetic information into such an analysis. However, with the exception of the grass-bush anoles, each category has evolved at least twice among the species studied (Fig. 1). Thus, the similarities within each ecomorph do not result primarily from shared ancestry.

Although ecomorph centroids differ in position, in several cases, nearest neighbours are not members of the same ecomorph category (Fig. 3a). Figure 2 and ANOVA (above) indicate that ecomorphs do not segregate along principal component axis III, which accounts for relatively little variation and reflects only maximum distance jumped (Table I). When the clustering analysis is performed using only principal component I and II scores, species group by ecomorph category (Fig. 3b), except that *A. cristatellus* (trunk-ground) and *A. garmani* (crown-giant) cluster with the trunk-crown ecomorphs.

Morphology-Behaviour

As predicted, hind limb length (relative to body size) and walking frequency (as a proportion of all moves) are inversely related (contrast: $r = -0.753$, $P < 0.005$; ancestor reconstruction: $r^2 = 0.533$,

$P < 0.001$; Fig. 4). Similarly, species with relatively short forelimbs (relative to the length of their hindlimbs) jump more frequently than species with long forelimbs (contrast: $r = -0.713$, $P < 0.01$; ancestor reconstruction: $r^2 = 0.509$, $P < 0.001$; Fig. 5). Maximum distance jumped increases with body size. However, jump frequency is associated with neither absolute (contrast: $r = 0.087$, NS; ancestor reconstruction: $r^2 = 0.023$, NS) nor residual distance jumped (contrast: $r = 0.036$, NS; ancestor reconstruction: $r^2 = 0.000$, NS).

No relationship exists between display and movement rate (contrast: $r = 0.438$, NS; ancestor reconstruction: $r^2 = 0.000$, NS). The principal components analysis indicates that species that run frequently tend to walk infrequently, and vice-versa. Display rate is related to the rate of non-walk movements (i.e. runs and jumps; contrast: $r = 0.677$, $P < 0.025$; ancestor-reconstruction: $r^2 = 0.309$, $P < 0.01$; Fig. 6).

Microhabitat Effects on Behaviour

Differences in locomotor propensities exist between *A. evermanni* and *A. gundlachi* independent of habitat (two-way ANOVA, species effect, $F_{1,65} = 6.92$, $P < 0.015$). Habitat affects locomotor behaviour of both species. Both *A. evermanni* and *A. gundlachi* jump proportionally more on

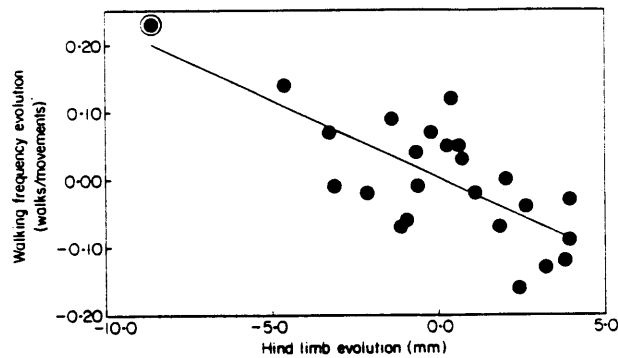


Figure 4. The relationship between the evolution of relative hind limb length and of walking frequency (as a proportion of all moves). Each point corresponds to the amount of evolutionary change in one ancestor–descendant pair. The X -axis is the residual of the change in limb length relative to the corresponding change in snout–vent length (see text). The circled point here and in subsequent figures represents the evolution of *A. valencienni* from its immediate ancestor (node D in Fig. 1). The regression equation is: $Y = 0.002 - 0.023X$. The probability estimates in the ancestor–reconstruction analyses use the number of species (13), rather than the number of ancestor–descendant pairs, to avoid inflating the sample size (Losos, in press a).

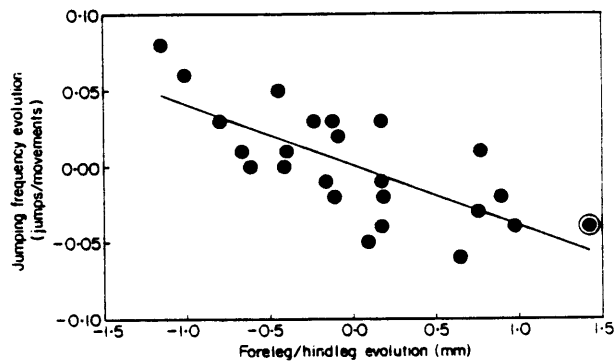


Figure 5. The relationship between the evolution of forelimb:hindlimb length and jumping frequency. The X -axis is the residual of the change in forelimb length regressed against change in hindlimb length for each ancestor–descendant pair. The regression equation is: $Y = 0.001 - 0.040X$.

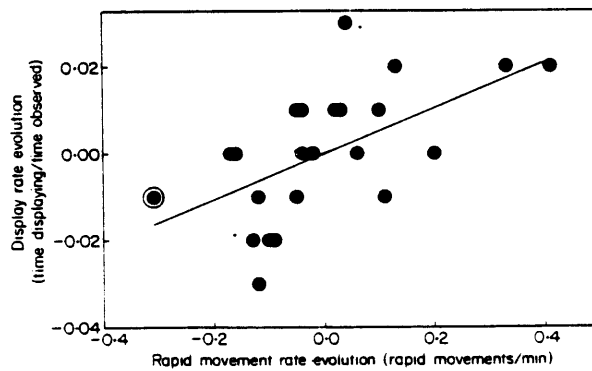


Figure 6. The relationship between evolutionary change in rapid movement (runs and jumps) rate and display rate. Each point corresponds to the amount of evolutionary change in movement and display rate for an ancestor–descendant pair. The regression equation is: $Y = 0.00 + 0.053X$.

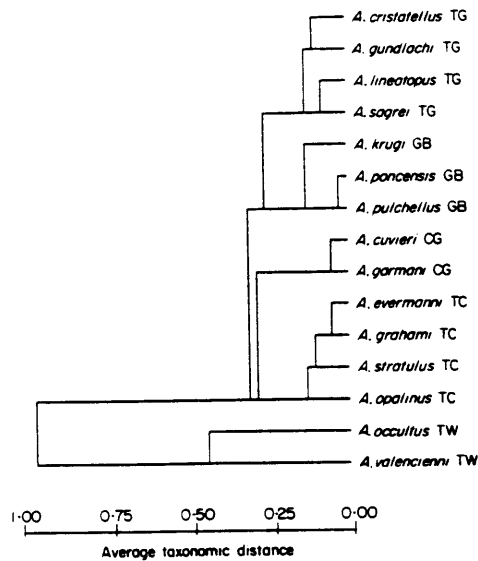


Figure 7. UPGMA Clustering of species based upon morphology (based on data in Losos, in press a). No behavioural data are available for *A. occultus* and *A. cuvieri*. The scale is average taxonomic distance between clusters (Rohlf 1987).

stream boulders (two-way ANOVA, habitat effect: $F_{1,65} = 4.33$, $P < 0.05$; Table II). Habitat affects the species differently in other aspects of locomotor behaviour (Table II). *Anolis evermanni* jumps and walks at the same rate on boulders and trees, but increases its rate of running 238% on trees. By contrast, *A. gundlachi* increases its rate of walking 36% on trees, but decreases its rate of running (33.3%) and jumping (52%). Consequently, on trees, *A. evermanni* moves 46% more often, whereas *A. gundlachi* moves 28% less often. There was no habitat effect on maximum distance jumped (two-way ANOVA, habitat effect: $F_{1,33} = 0.71$, NS) or display rate ($F_{1,62} = 0.02$, NS).

DISCUSSION

Co-evolution of Morphology and Behaviour

Implicit in the concept of ecomorphs (Rand & Williams 1969; Williams 1972, 1983) is the hypothesis that morphology and locomotor behaviour have evolved synchronously. I have confirmed this prediction and demonstrated that other aspects of behaviour co-evolved as well. Moermond (1979a, b) and Pounds (1988) demonstrated

relationships between limb length and walking frequency and between hindlimb:forelimb ratio and jumping frequency. In a less-detailed study, Estrada & Silva Rodriguez (1984) classified 23 *Anolis* species as runners, jumpers or crawlers, using unpublished observations and reports in the literature. Based on limb and tail measurements, they concluded that members of each locomotor group cluster morphologically. Using a more morphologically diverse sample of anoles than these studies, my analysis indicates that these relationships represent evolutionarily established patterns. The consensus among these studies appears particularly robust given the numerous differences in methodology.

Reality of Ecomorphs

When jumping distance is excluded, species cluster according to ecomorph category based on behavioural data (Fig. 3b). Thus, variation in microhabitat does not affect locomotor or display behaviour enough to cause members of different ecomorphs to group together (see below). Among ecomorph categories, the patterns of clustering based on behaviour and morphology are almost identical (cf. Fig. 7). Morphologically, trunk-ground and grass-bush anoles are similar in having relatively long limbs and tails, whereas trunk-crown and crown-giant anoles tend to have shorter legs and tails. These two groups are more morphologically similar to each other than they are to the short-legged and tailed twig anoles. I have shown (Losos, in press a) that position in a three-dimensional morphospace predicts a species' position in a similar space defined using nine behavioural and ecological variables. The analysis confirms that morphology and behaviour are related independent of the relationship between morphology and ecological variables.

The two behavioural exceptions to species clustering according to ecomorph are the trunk-crown *A. evermanni*, which groups with the crown-giant *A. garmani*, and the trunk-ground *A. cristatellus*, which clusters with the trunk-crown anoles. Trunk-crown and crown-giant anoles are similar in morphology, except for body size (as their name implies, crown-giants are considerably larger than all other ecomorphs), and microhabitat (Williams 1972, 1983; Losos, in press a), so the former association is not surprising. The position of *A. cristatellus*, a normal trunk-ground anole in

Table II. Locomotor and display behaviour of *A. evermanni* and *A. gundlachi* on boulders and trees ($\bar{X} \pm SE$)

	<i>A. evermanni</i>		<i>A. gundlachi</i>	
	Boulders (<i>N</i> = 14)	Trees (<i>N</i> = 14)	Boulders (<i>N</i> = 10)	Trees (<i>N</i> = 31)
% Walks	0.63 ± 0.077	0.50 ± 0.079	0.20 ± 0.074	0.39 ± 0.053
% Runs	0.18 ± 0.069	0.40 ± 0.088	0.52 ± 0.073	0.39 ± 0.053
% Jumps	0.19 ± 0.034	0.10 ± 0.026	0.28 ± 0.042	0.22 ± 0.033
Movement rate*	0.85 ± 0.11	1.24 ± 0.20	0.93 ± 0.14	0.67 ± 0.10
Walk rate	0.56 ± 0.09	0.66 ± 0.12	0.14 ± 0.05	0.19 ± 0.03
Run rate	0.13 ± 0.06	0.44 ± 0.11	0.54 ± 0.12	0.36 ± 0.10
Jump rate	0.15 ± 0.03	0.13 ± 0.03	0.25 ± 0.04	0.12 ± 0.02
Jump distance	35.0 ± 3.3	37.4 ± 8.8	43.0 ± 5.6	34.5 ± 4.7
Display rate*	0.038 ± 0.011	0.049 ± 0.015	0.039 ± 0.018	0.053 ± 0.012

*Locomotor rates measured as movements of a given type per min; display rate measured as proportion of time spent displaying.

morphology and ecology, is more puzzling. In jump frequency and activity rate, *A. cristatellus* is more like the trunk-crown anoles. Further research is necessary to determine whether I studied an atypical population of *A. cristatellus*, and, if not, what factors are responsible for this discrepancy.

Habitat Effects on Jumping

Most of the variance in Fig. 2 not explained by ecomorph category is on principal component III, which loads mainly for jumping distance in nature. This variance illustrates the importance of habitat structure in determining jumping behaviour. Pounds (1988) demonstrated, both in the field and in experimental enclosures, that anoles jump farther in habitats in which the nearest available perch is more distant. The grass-bush anoles, which, among the ecomorph categories, exhibited the greatest interspecific diversity in habitat use, illustrate this point. At the Luquillo Mountains study site, *A. pulchellus* was found almost exclusively on grass blades and thin stems, where it jumped primarily to the ground or to other nearby perches, and consequently made short jumps. *Anolis krugi* occurred on bushes and branches at the edge of a wood plot, where the nearest perch was more distant and longer jumps were required. In southwest Puerto Rico, *A. poncensis* was found on small diameter trees, which were generally situated in the open. Nearest available perches tended to be quite distant, which forced the lizards to take even longer jumps (Losos, in press a). Similarly,

A. sagrei occupied limestone outcroppings at my study site at Discovery Bay, Jamaica and was seen on tree trunks much less frequently than other trunk-ground anoles. Because it often jumped from one rock peak to a nearby rock peak, it jumped shorter distances than other trunk-ground anoles.

At other localities, both *A. sagrei* and *A. pulchellus* occupy microhabitats more similar to other members of their ecomorph category. Both biotic and abiotic factors may be responsible for such habitat shifts and, thus, indirectly affect locomotor behaviour. Interspecific interactions affect *Anolis* microhabitat use (Jenssen 1973; Schoener 1975; Jenssen et al. 1984; Pacala & Roughgarden 1985; Rummel & Roughgarden 1985). For example, *Anolis sagrei* occurs in more trunk-ground type habitats elsewhere in Jamaica, including localities in which *A. lineatopus* is absent or restricted to cool microhabitats (Williams 1969; Schoener & Schoener 1971a). In contrast, the use of grass stems by *A. pulchellus* in the Luquillo Mountains might be a result of thermal abiotic contingencies. To thermoregulate efficiently, *A. pulchellus* may have been forced into open grassy areas to maintain its temperature at appropriate levels. At the xeric *A. poncensis* study site, *A. pulchellus* avoided the sun and was found almost exclusively in the shade, where, like other grass-bush anoles, it used bushes and small trees rather than grass stems. However, interspecific interactions may be involved in this case as well. *Anolis krugi*, which occupied the bushes in more shaded areas at the Luquillo Mountains site, was not present at the desert site.

Habitat Effects on Behaviour

Because members of the same ecomorph category occupy similar microhabitats (Rand 1964, 1967; Rand & Williams 1969; Schoener & Schoener 1971a, b; Williams 1972, 1983; Losos, in press a), the habitat matrix model predicts that they should be similar in behaviour. Pounds (1988) demonstrated experimentally that behaviour varies intraspecifically in a predictable manner as a consequence of microhabitat structure. My observations on *A. evermanni* and *A. gundlachi* on trunks and boulders also demonstrate that species differ in behavioural patterns in different environments. Stream-side boulders represent a discontinuous habitat matrix; to get from one boulder to another, a lizard could either jump from one boulder to the other or it could run down one boulder, across to the second, and up it. By contrast, tree trunks represent continuous surfaces which do not require jumping. As predicted, both species jump more frequently in the discontinuous habitat, a relationship also exhibited by monkeys (Fleagle & Mittermeier 1980). No simple explanation is available for why the species differ in the effect of habitat on run and walk frequency and activity rate. Differences in which part of the trunk they use are probably relevant.

This interspecific comparison also illustrates how factors other than the structural environment affect habitat use. *Anolis evermanni* is relatively heliophilic, whereas *A. gundlachi* is restricted to the cool forest interior at high elevations (Rand 1964; Schoener & Schoener 1971b; personal observation). In the forest *A. gundlachi* was commonly seen on boulders and *A. evermanni* rarely so. Along an open, sunny stream, the situation was reversed, although *A. gundlachi* was common on trees in the shade bordering the stream. *Anolis gundlachi* was rarely seen in the sun, presumably because body temperatures commonly experienced by heliophilic anoles are fatal to it (Huey & Webster 1976). By contrast, although *A. evermanni* was more abundant in the canopy and sunny gaps within the forest, it was also observed in shady and cool parts of the forest, even on trees bordering the boulder-stream in the forest. Its relative rarity on these boulders may be the result of interspecific interactions. In several cases in which *A. evermanni* and *A. gundlachi* were observed in close proximity, *A. evermanni* displayed often, moved seemingly to avoid the other (e.g. by squirrelling around the tree), and reacted strongly when *A. gundlachi*

approached nearby or ran past. *Anolis gundlachi*, which is considerably larger, 7.1 versus 5.6 g (Losos, in press a), never showed any response to *A. evermanni*. The exposed boulder field was in a continuously flowing stream, whereas the forest boulder stream only flowed after heavy rains. Consequently, other factors (e.g. the availability of certain moisture-loving prey) might be responsible for these patterns as well.

Ecomorphs, Foraging Mode and Social Behaviour

Anoles are generally considered to be sit-and-wait foragers (Andrews 1971; Moermond 1979b), but *A. valencienni* is an exception (Hicks & Trivers 1983). This species is an active forager, constantly moving at a slow pace and carefully inspecting the substrate for cryptic prey (Hicks & Trivers 1983, personal observation). I have shown that the movement rate of *A. valencienni* is not exceptional; three of the trunk-crown anoles move more frequently (Losos, in press a). However, the amount of time *A. valencienni* spends moving is exceptional. While other anoles move in short, rapid bursts, interspersed with relatively long periods of inactivity (Moermond 1979b, personal observation), *A. valencienni*, an active forager, moves slowly, sometimes covering considerable distances along trunks and branches (e.g. more than 5 m) without stopping (Hicks & Trivers 1983; Losos, personal observation).

Walking frequency is associated with foraging mode; *A. valencienni* walks considerably more frequently (as a proportion of all moves) than other sit-and-wait species. The low display rate of *A. valencienni* is also probably a consequence of its active foraging. Because it is continuously moving and scanning a smaller area than sit-and-wait foragers, *A. valencienni* may be more vulnerable to predation (Hicks & Trivers 1983); its low display rate, as well as its cryptic coloration (Rand 1967; Hicks & Trivers 1983), may function to minimize detection by predators. *Anolis valencienni* is also much less territorial than other anoles, presumably because its wide foraging makes territorial defence infeasible (Hicks & Trivers 1983). Intra-sexual displaying is common among male anoles as a means of proclaiming territorial occupancy, which may also explain the low display rate of *A. valencienni*.

Based on Hicks & Trivers (1983) and my detailed observations of foraging, and on its low display rate, the high activity rate of *A. valencienni* is probably a result of its active foraging mode. Whether

differences in activity rate among other anoles represent differences in foraging strategies, social behaviour, predator avoidance or other factors is unclear. Moermond (1979b) attributed differences in rate of movement among ecomorphs to differences in microhabitat. He contended that anoles on trunks can scan an area for prey more quickly and consequently move more often than anoles in cluttered habitats (e.g. grasses or bushes), which, in turn, scan and move more quickly than anoles in even more cluttered habitats near the ground. My data only partially support this finding. Trunk-crown anoles move more frequently than other anoles, but the crown-giant *A. garmani*, which also spends a considerable portion of the time on trunks (Schoener & Schoener 1971a; Losos, unpublished data), moves considerably less. Further, grass-bush anoles move less frequently than trunk-ground anoles.

An alternative hypothesis is that activity rate is related to social behaviour. Although no relationship exists between activity and display rates, the principal components analysis indicates that species can have high activity rates either because they walk (*A. valencienni*) or run (other anoles) frequently. If movement rate is divided into rapid and slow movement rate, display rate correlates with rate of rapid (running + jumping) movements. Whether social behaviour dictates activity rate is not clear. Males of some species may patrol their territories in search of males and females more frequently than other species. These species would be expected to have high display rates as well. Alternatively, activity rate may dictate display rate. Because males often display every time they switch positions simply to proclaim their presence (Stamps 1977; Jenssen 1978), species that move from one foraging location to another more often would be expected to display more frequently as well. My observations favour the former explanation. For example, trunk-crown anoles such as *A. grahami* often rapidly moved a long distance, displayed, paused relatively briefly, then moved and repeated the cycle again. These movements, which occasionally went on continuously for 10 min or more, seemed more related to social interactions than to foraging.

Within communities of lizards, morphological and locomotor differences are often associated with substantial differences in foraging and social behaviour. Sit-and-wait predators tend to be specialized for rapid bursts of speed, maintain

territories and move infrequently, whereas wide foragers move often at a relatively slow pace and are less territorial (Stamps 1977). This dichotomy recurs in *Anolis*; contrast *A. valencienni* with the other species studied here. This study indicates, however, that the same patterns occur within a foraging mode. Figures 4–6 indicate that although the evolution of active foraging in *A. valencienni* has been associated with the evolution of extreme morphology and behaviour, the same relationships hold among the remaining species (all statistically significant results, using either the contrast or ancestor-reconstruction analyses, remain significant (one contrast analysis becomes marginally non-significant) when *A. valencienni* is removed). Consequently, among sit-and-wait foraging *Anolis*, morphology, locomotor patterns, activity rate and social behaviour have evolved in concert. Whether differences in microhabitat are causally responsible for this suite of correlated variables, as proposed by the habitat matrix model, requires further investigation.

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