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THE ECOLOGICAL CONSEQUENCES OF HABITAT AND MICROHABITAT USE IN LIZARDS: A REVIEW

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ABSTRACT: We review the ecological consequences of habitat and microhabitat use in lizards. Different habitats have different biotic and abiotic properties and thus are likely to have different consequences for the lizards that occur in them. Individual performance and life histories are influenced by habitat use, particularly when habitats differ in thermal characteristics that may influence physiological processes or constrain activity. We know relatively little about how the effects of habitat use on individual performance translate into population dynamics. We do know that the ability of lizards to use particular habitats can influence the persistence of populations in the face of habitat changes. Community-level processes (e.g., competition) and community structure (e.g., diversity) can be influenced by habitat use in lizards, often by habitat use facilitating co-existence of two or more potentially competing species. We know relatively little about how other community processes, such as predation and parasitism, are influenced by habitat use.

INTRODUCTION

Why do animals occur where they do? Beyond the basic requirement that an individual must be able to survive, different locations or habitats may provide different conditions for an individual's existence. Thus, another question arises: What are the consequences of the choice of habitat or microhabitat on the biology and ecology of the organism being considered? From an ecological point of view, habitat selection can influence physiological processes (Huey 1991), population dynamics (Holt 1987; Pulliam and Danielson 1991), and community level processes (Morris 1988; Rosenzweig 1991).

Lizards are an excellent group of organisms with which to examine the ecological consequences of habitat and microhabitat use. First, there is a relatively long history of studying habitat and microhabitat use in lizards, at least qualitatively (reviewed by Heatwole 1977). Second, lizard ecology and physiology is well studied, at least for some species (see papers in Milstead 1967; Gans and Pough 1982a,b; Huey et al. 1983; Gans and Huey 1988; Vitt and Pianka 1994). Finally, recent studies have begun to examine the relationship between lizards and their environments in greater detail (see below) and provide a means to assess the role of habitat and microhabitat use in a lizard's ecology. There is also a practical reason for looking at the ecological conse-

quences of habitat and microhabitat use in lizards, and that is the on-going alterations of the environment by humans. We need to understand the role of habitat and microhabitat use in lizard ecology to be able to assess the potential impacts of such environmental changes and to suggest possible conservation measures.

Before we begin our review of habitat use in lizards, it is necessary for us to define what we mean by "habitat". Habitat can mean a number of things and its meaning can depend heavily on the scale one is considering (see Morris 1987a,b, 1992 for discussions of the interaction of scale and habitat use). For the majority of this review, habitat is used in a broader sense to include the general type of area in which an individual occurs (e.g., woodland or desert). However, in some instances, we use habitat and microhabitat synonymously to mean the actual substrate or perch on which an individual occurs. We feel our use of habitat in both these contexts is appropriate for our review because we believe that the general consequences of habitat (or microhabitat) use at any scale will be the same for a given species (i.e., certain requirements must be met for an individual or population to be successful).

CONSEQUENCES OF HABITAT AND MICROHABITAT USE

The consequences of living in a particular habitat can

be manifested at several levels, ranging from effects on the individual to effects on an entire community. Below we discuss the implications of using different habitats for (1) individuals, (2) populations, and (3) communities.

Individuals

Being ectotherms means that lizards are affected by the thermal and biophysical environments that they experience. Ectotherm physiology and ecology are intimately linked (Huey and Stevenson 1979) and so anything influencing physiology can affect performance or life histories (e.g., Congdon 1989; Dunham et al. 1989; Porter 1989). Different habitats often provide different biophysical environments (e.g., Bartlett and Gates 1967; Pearson 1977; Bakken 1989; Bashey and Dunham 1997). Indeed, lizards often choose habitats and microhabitats that facilitate thermoregulation or that allow them to maintain the appropriate body temperature (Table 1).

Table 1. Species of lizards that apparently use or shift habitats or microhabitats to maintain a certain body temperature or to facilitate thermoregulation, or for whom it has been shown that lizards in different habitats maintain different body temperatures.

Species	Reference
<i>Amblyrhynchus cristatus</i>	Trillmich and Trillmich (1986)
<i>Anolis nebulosus</i>	Ramírez-Bautista and Benabib (2001)
<i>Cnemidophorus sexlineatus</i>	Paulissen (1988)
<i>Conolophus pallidus</i>	Christian et al. (1983 1984); Christian and Tracy (1985)
<i>Cophosaurus texanus</i>	Durtsche et al. (1997)
<i>Cordylus macropholis</i>	Bauwens et al. (1999)
<i>Lacerta monticola</i>	Martín et al. (1995)
<i>Podarcis hispanica</i>	Castilla and Bauwens (1991); Díaz et al. (1996)
<i>Podarcis melisellensis</i>	Grbac and Bauwens (2001)
<i>Podarcis muralis</i>	Grbac and Bauwens (2001)
<i>Pogona barbata</i>	Schäuble and Grigg (1998)
<i>Sceloporus jarrovi</i>	Middendorf and Simon (1988); Smith and Ballinger (1994b)
<i>Sceloporus occidentalis</i>	Davis and Verbeek (1972)
<i>Sceloporus virgatus</i>	Smith and Ballinger (1994a); Smith (1997)
<i>Tropidurus hispidus</i>	Vitt et al. (1996)
<i>Urosaurus ornatus</i>	Smith and Ballinger (1995)
<i>Varanus bengalensis</i>	Wikramanayake and Dryden (1993)
<i>Varanus salvator</i>	Wikramanayake and Dryden (1993)

Different habitats can influence thermoregulatory behavior. For example, *Anolis cristatellus* in Puerto Rico actively thermoregulate when in open habitats, but passively thermoregulate in closed habitats (Huey 1974; see also Gillis 1991 for an example from *Sceloporus undulatus*). Some habitats (e.g., those with low transmittance of solar radiation) virtually eliminate the possibility for active thermoregulation by lizards, as in the case of the Australian forest dragon (*Hypsilurus spinipes*) (Rummery et al. 1994), the crevice-dwelling lizard, *Xenosaurus newmanorum* (Lemos-Espinal et al. 1998), and the lacertid lizards *Podarcis melisellensis* and *P. muralis* in the autumn (but not other times of the year) (Grbac and Bauwens 2001). *Kentropyx calcarata* and *Mabuya nigropunctata* in lowland Amazonian tropical forest occur near opening or treefall clearings because they require sunlight to be able to maintain high body temperatures (Vitt et al. 1997).

Lizards inhabiting certain habitats providing a given biophysical environment can be expected to experience different internal environments than lizards in another habitat which could result in differences in physiologi-

cal performances (see Huey 1991), possibly resulting in differentiation of thermal preferences, physiology, and performance between individuals in different populations and habitat types (Garland and Adolph 1991; Miles 1994). Ultimately the habitat in which a lizard occurs can influence its energy budget (Bartlett and Gates 1967; Congdon et al. 1982) since digestive efficiency and capacity are often influenced by body temperature (Harlow et al. 1976; Harwood 1979; Troyer 1987; Zimmerman and Tracy 1989; van Marken Lichtenbelt 1993), suggesting that lizards in different habitats may experience different digestive efficiencies. The metabolic rate of lizards in habitats with different thermal regimes can be different (e.g., Beaupre et al. 1993; Beyer and Spotila 1994). Often metabolic rates increase with temperature (e.g., Christian et al. 1998; Mouton et al. 2000). Feeding rate and energy expenditure can also differ between habitats (Karasov and Anderson 1984), as can other aspects of foraging behavior (e.g., capture rate; Bullock et al. 1993). In addition, temperature can affect other aspects of feeding behavior, such as foraging activity and handling time (Moermond 1979a,b; Avery et al. 1982; Karasov and Anderson 1984; DeQuiroz et al. 1987; Grant and Dunham 1988; Avery and Mynott 1990), as well as capture success (Díaz 1994).

Lizard sprint speed and behavior are often significantly affected by body temperature (Rand 1964b; Hertz et al. 1982, 1983; Mautz et al. 1992; Torr and Shine 1993). Lowered sprint speeds conceivably influence susceptibility to predation (see Christian and Tracy 1981). Habitat use, by its effects on body temperature, can generate habitat specific sprint speeds for lizards (e.g., Waldschmidt and Tracy 1983), resulting in habitat specific predator escape ability; as well as habitat specific escape behavior. For example, during periods of the year when vegetation is sparse (e.g., early spring), *Psammodromus algirus* flee from the approach of a possible predator earlier than when vegetation is more dense (e.g., summer) (Martín and López 1995a). Within a season, escape behavior by *P. algirus* is also dependent on the amount of vegetation present: in more open microhabitats flight distances are greater than in more vegetated microhabitats (Martín and López 1995a,b; see also Martín and Lopez 2000). Snell et al. (1988) got similar results in a study on *Tropidurus albemarlensis* in the Galápagos Islands. In three species of *Anolis* from Cuba, the habitat used affected escape strategies: anoles on trees with big trunks ran around to the other side of the trunk whereas anoles on trees with small trunks jumped to another tree or perch (Regalado 1998). However, escape tactics are not always affected by habitat structure (e.g., *Sceloporus virgatus*; Smith 1996a). In addition, lizard morphology can interact with habitat use to affect sprint speed and clinging ability (Losos and Sinervo 1989; Losos et al. 1993b). For example, Irschick and Losos (1999) found that eight species of *Anolis* tend to use habitats whose structure (e.g., distribution of perch diameters) allows maximal performance (e.g., sprint speed).

Life histories in lizards are often influenced by the proximate environment (see Ballinger 1983; Dunham et al. 1989). Habitat use can affect lizard life histories by determining the proximate environment (biotic or abiotic) experienced by the lizard. For example, the habitats and microhabitats used by lizards may differ in the amount of food available for consumption (e.g., Alberts 1993; Hews 1993; Durtsche 1995; Vitt and de Carvalho

1995; Vitt et al. 1996; Smith 1998). In combination with the potential thermal differences between habitats outlined above, use of different habitats and microhabitats could easily affect the growth, reproduction, and survivorship of lizards (i.e., their life histories).

Several studies have demonstrated an effect of habitat use on the life history traits of lizards (see Table 2). Often the effects of habitat are due to differences in food availability or activity periods that can be affected by the habitat an individual is in. Along an elevational gradient populations of *Sceloporus merriami* experience different biophysical environments which determine activity regimes (Grant and Dunham 1988; Grant 1990). *Podarcis torquatus*, which occur in forest habitats in Chile, have longer activity periods than *P. volcanensis*, which occur in more open habitats (Labra and

Rosenmann 1992). The activity regime of a population can interact with the amount of food available to create life history differences between populations (Grant and Dunham 1990; Niewiarowski and Roosenburg 1993).

The habitat that a parent lizard uses, particularly a pregnant female (if viviparous) or an ovipositing female (if oviparous), can have consequences for the performance of their offspring (see Overall 1994 for a detailed discussion). Many of these consequences arise from the thermal or hydric environments experienced by the pregnant female or the incubating eggs. In many species, cooler incubation sites lead to slower embryonic developmental rates than warmer incubation sites (e.g., Qualls and Andrews 1999; Shine 1999). Incubation conditions can also affect hatchling performance such as growth rate, sprint speed, and endurance (e.g., Qualls and Andrews 1999; Shine 1999). *Sceloporus undulatus* eggs incubated at different temperatures differed in tail length (shorter at cooler temperatures), SVL (shorter at cooler temperatures), growth rate of hatchlings in the laboratory (faster at cooler temperatures), 42 d and overwinter survival (higher at cooler temperatures) (Andrews et al. 2000). Hatchlings from *Cyclura nubila* eggs incubated at warmer temperatures were no different in size at hatching than eggs incubated at lower temperatures, but did grow faster during their first year (Alberts et al. 1997). In four species of *Sceloporus* (*S. aeneus*, *S. scalaris*, *S. undulatus*, *S. virgatus*), eggs incubated at a range of temperatures did not differ in mortality (except for a high elevation population of *S. virgatus* which showed higher mortality at low temperatures) but did show a delay in hatching at low incubation temperatures (Andrews et al. 1997). In addition to the effects on aspects of offspring performance (e.g., growth and survivorship), the physical characteristics of the habitat in which a female lizard lays her eggs can determine the sex of her offspring in some species (e.g., *Agama agama*, Charnier 1966; *Chlamydosaurus kingii*, Harlow and Shine 1999; *Ctenophorus decresii* and *C. ornatus*, Harlow 2000; *Eublepharis macularis*, Viets et al. 1993).

Pregnant females often use their habitats in such a way as to maintain a body temperature that is different from those maintained by males or non-pregnant females (e.g., Garrick 1974; Beuchat 1986; Smith and Ballinger 1994a,b; Mathies and Andrews 1997; Rock et al. 2000). Such thermoregulation may influence embryonic development and neonate performance (e.g., Beuchat and Ellner 1987; Beuchat 1988; Shine and Harlow 1993; Mathies and Andrews 1997). Swain and Jones (2000) experimentally evaluated the effects of manipulating the opportunity for pregnant female *Niveoscincus metallicus* to thermoregulate (i.e., bask) on aspects of their reproduction and offspring performance. They found that females that could not bask as often gave birth less often, had a longer gestation period, and had smaller neonates that grew slower after birth as females that could bask without restrictions.

One of the things that becomes clear as one considers the studies above is that we have a fairly good understanding of how variations in the thermal environment affect individual lizard performance. It is also clear that we do not have a full understanding of how other aspects of a habitat or microhabitat (e.g., predation risk, food availability, water relations) affect individual performance, nor do we understand how these different aspects of a habitat or microhabitat interact to determine

Table 2. Species for which habitat use has been shown to affect various aspects of a lizard's life history.

Survivorship	Comments	Source
<i>Lacerta vivipara</i>	Winter survival of juveniles lower in resource poor habitats than resource rich habitats	Boudjemadi et al. (1999)
<i>Psammidromus algirus</i>	Juvenile survivorship decreased with increase in vegetative cover due to higher densities of predators	Civantos and Forsman (2000); see also Civantos et al. (1999), Civantos (2000)
	Survival higher in parts of shrub patches that allow easiest access to basking sites	Díaz (1992)
<i>Sceloporus virgatus</i>	Lizards in a wooded habitat tended to survive better than lizards in an open habitat	Smith (1998)
<i>Uta stansburiana</i>	Dominant lizards have „higher quality“ home ranges with better microhabitats, which increase survivorship compared to subordinate lizards	Fox et al. (1981)
Reproduction		
<i>Anolis bimaculatus</i>	Females forced to perch lower than normal produced fewer eggs	Rummel and Roughgarden (1985)
<i>Anolis gingivus</i>	Female anoles forced to perch higher than normal produced fewer eggs	Rummel and Roughgarden (1985)
<i>Cnemidophorus gularis</i>	Higher proportion of females reproductive in mesquite upland habitat than juniper habitat	Gannon and Willis (1990)
<i>Sceloporus virgatus</i>	Females in a wooded habitat matured earlier than females in an open habitat	Smith (1998)
Growth		
<i>Anolis bimaculatus</i>	Anoles forced to perch lower than normal grew slower	Rummel and Roughgarden (1985)
<i>Anolis gingivus</i>	Anoles forced to perch higher than normal grew slower	Rummel and Roughgarden (1985)
<i>Cnemidophorus hyperythrus</i>	Lizards in different habitat grew at different rates	Karasov and Anderson (1984)
<i>Lacerta vivipara</i>	Yearlings grew faster in wetter habitats than in drier habitats	Lorenzon et al. (1999)
<i>Sceloporus virgatus</i>	Lizards in a wooded habitat grew faster than lizards in an open habitat	Smith (1998)

individual performance, let alone the consequences for lizard populations (see Populations). There is a definite need for additional studies to assess the relative importance of various habitat characteristics for individual performance in lizards.

Populations

While it is clear from the studies above that the physical and biotic characteristics of a habitat have ecological consequences for the performance of individual lizards, the impacts on lizard populations are often assumed to follow from the impacts on individual lizards. Unfortunately, there are few studies that have attempted to directly assess the link between the correspondence between habitat quality from the individual lizard's perspective and the performance of lizard populations in the same habitat. One exception is a study by Díaz (1997). He studied two populations of *Psammodromus algirus*, one at high elevation and one at low elevation. From a performance perspective (e.g., sprint speed, ability to thermoregulate), the low elevation site would be considered a higher quality habitat than the high elevation site. Interestingly, the abundance of lizards was significantly higher at the high elevation site, suggesting that simply measuring various aspects of individual performance in a habitat may not be sufficient to understand the consequences of habitat use on population performance and abundance. We need more studies like this to determine whether the consequences for individuals also necessarily have consequences for populations, or whether we can overestimate the importance of a single aspect of habitat use, such as thermal quality, while not considering other consequences such as predation risk, prey availability, as suggested by Díaz (1997).

There are several studies that assess the impact of habitat and microhabitat changes on lizard populations; however, the specific mechanisms causing the population changes are often poorly understood. The habitat used and preferred by lizards has definite consequences for the success of populations of lizards in the face of habitat changes. For example, lizards that use open habitats tend to be positively affected at a population level by livestock grazing whereas lizards that need vegetative cover tend to be negatively affected at a population level by livestock grazing (Table 3). Similarly, some lizard species (e.g., *Urosaurus ornatus*) are able to exploit residential areas along an urbanization gradient, whereas other lizards are only able to exploit the natural habitats (e.g., *Cnemidophorus* spp.) along the urbanization gradient (Germaine and Wakeling 2001).

In some cases, habitat use may increase the possibility of a decline in a lizard population. For example, the common chameleon (*Chamaeleo chamaeleon*) in Spain often uses habitats that are closely associated with human activity, thus making them more susceptible to possible declines due to over collection, road related mortality, and agricultural practices (Hódar et al. 2000). Clearcutting has a strong negative effect in arboreal lizards and decreased total lizard biomass in a north Florida flatwood (Enge and Marion 1986). In Argentina, a change in habitat structure due to road building changes a lizard assemblage due to loss of particular habitats (e.g., *Spartina ciliata* patches) used by some species but not others (Vega et al. 2000). Those that use that habitat decreased while those that did not use the habitat did not show changes in abundance

Table 3. Species of lizards which have been shown to be negatively or positively affected by livestock grazing, or for whom no effect was detected after grazing or between grazed and ungrazed plots.

Positively Affected	Source
<i>Crotaphytus collaris</i>	Sexton et al. (1992)
<i>Holbrookia maculata</i>	Ballinger and Jones (1985), Ballinger and Watts (1995)
<i>Uta stansburiana</i>	Romero-Schmidt and Ortega-Rubio (1999)
Sit-and-wait species	Jones (1981: Table 2)
Negatively Affected	
<i>Cnemidophorus tigris</i>	Brooks (1999)
<i>Diplodactylus granariensis</i>	Smith et al. (1996)
<i>Diplodactylus pulcher</i>	Smith et al. (1996)
<i>Sceloporus magister</i>	Brooks (1999)
<i>Sceloporus scalaris</i>	Bock et al. (1990), Ballinger and Congdon (1996)
<i>Urosaurus nigricaudus</i>	Romero-Schmidt and Ortega-Rubio (1999)
Actively foraging species	Jones (1981: Table 2)
No Effect Detected	
<i>Phrynosoma cornutum</i>	Fair and Henke (1997)

(Vega et al. 2000). Rock collectors removing rocks from the environment of the velvet gecko, *Oedura lesueurii*, reduces the amount of habitat available for it to use (Schlesinger and Shine 1994), thus possibly leading to a decline in velvet gecko abundance (Shine et al. 1998). The rocks appear to be important for thermoregulation by these geckos (Downes and Shine 1998; Webb and Shine 2000), which may affect gecko growth and survivorship (Webb and Shine 2000).

In other cases, habitat use may facilitate population persistence in the face of human alterations of habitat. For example, *Egernia major* uses basking to maintain its body temperature and this is commonly found in more open or edge habitats and thus they may actually benefit from some human activities such as logging (Klingenböck et al. 2000). In French Guiana, one species of lizard, *Kentropyx calcarata*, becomes the most abundant and the dominant species on habitat islands created by flooding due to the creation of a hydroelectric dam reservoir, in part because of its generalist habitat use (Cosson et al. 1999). Timber practices in the Amazon, by altering the thermal and solar insolation properties of the habitat alter the make up of the lizard assemblage by increasing the number of heliothermic species in a particular area (Vitt et al. 1998a; Sartorius et al. 1999). Fire and other disturbances, such as clear-cutting timber, by maintaining a variety of successional stages of vegetation often associated with varying amounts of habitat structure and complexity allowing open habitat species and closed habitat species to persist, can be important influences on lizard distributions and abundances in many systems (e.g., mallee woodlands and heathlands of Australia, Friend 1993; sand-pine scrub of Florida, Mushinsky 1985; Greenberg et al. 1994).

Communities

Differential habitat use by two or more lizard species, whether the result of current ecological interactions or past ecological interactions that have led to evolutionary change (e.g., "ghost of competition past"), may per-

mit coexistence of potential competitors thus affecting community structure and composition. Several authors have suggested that their observations of habitat segregation between lizard species indicate current or past competition. In several cases, experimental evidence is absent, and the conclusions are based upon supposition (Table 4). Clearly, the strongest evidence for the role of habitat use in allowing coexistence of potential competitors comes from experimental studies. Such studies do exist and the results of these experiments have found evidence for habitat use mediated coexistence or competition enforced habitat segregation in lizards (Table 5). On the other hand, many authors have used observational evidence and supposition to argue that habitat segregation is not reducing competition, but rather is serving another function (e.g., each species is filling its specific needs independently of the presence or absence of other species) (Table 4). Experimental evidence also sometimes supports the lack of competition's importance in habitat segregation (Table 5).

Predator-prey interactions can also be influenced by habitat use. Lizards may use habitats based upon the presence of predator refuges, and thus alter their predation risk by using particular habitats. Densities of adult *Sceloporus jarrovi* are dependent on the number of rocks present as well as the number of rock cracks which presumably provide predator refuges (Ruby 1986). Trees with holes in them and surrounded by brush are preferred by *Eumeces laticeps* because the holes, in addition to serving a role in nesting, may act as predator refuges (Cooper 1993; Cooper and Vitt 1994). In Chile, two species of *Liolaemus* (*L. platei* and *L. nigromaculatus*) partition rock and ground habitats, with *L. platei* on the ground and *L. nigromaculatus* on rocks (Fuentes and Cancino 1979). Both morphology and behavior suggest partitioning is based on predation. *Liolaemus platei* has both anti-predator behavior and morphology whereas *L. nigromaculatus* does not. In this situation, it actually appears that predation and competition interact to influence the observed habitat use in these two lizards: predation limits *L. nigromaculatus* to the rocks while competition from *L. nigromaculatus* excludes *L. platei* from the rocks. *Anolis stratulus* (Reagan 1992) and *Anolis cristatellus* (Chandler and Tolson 1990) use smaller perches presumably because their predators (two larger species of *Anolis*, and *Epicrates monensis*, respectively) are unable to use the smaller perches. Other anoles have been shown to alter their perch heights in response to the introduction of rats (Campbell 1989 cited in Chandler and Tolson 1990). The use of lower and narrower perches by juvenile *Anolis lineatopus* and *A. gundlachi* may alter the ability of juveniles to detect predators, and thereby alter predation risk compared to other perches (Irschick et al. 2000). *Ctenosaura hemolopha* preferentially select perches on cacti with holes that presumably serve as predator refugia (Blázquez and Rodríguez-Estrella 1997). Pygmy blue tongue lizards, *Tiliqua adelaidensis*, select deep, narrow burrows that increase their ability to protect against predators (Milne and Bull 2000). Bauwens et al. (1999) suggest that the exclusive use of *Euphorbia caput-medusae* plants may in part reflect the possible decrease in predation risk these plants provide due to the number of potential shelters found in these plants. Martín and López (1998) argued that a seasonal shift in habitat use by *Psammotromus algirus* occurs to allow the lizards to exploit those habitats that provide

the most protection from predators: In the spring, lizards avoid shrubs that have lost their leaves and use shrubs that retain their leaves, however, in the summer the lizards prefer to use the shrubs that had lost their leaves in the spring but now have leaves relative to the shrub that keeps its leaves throughout the year. Velvet geckos (*Oedura lesueurii*) use experimental rock refuges in such a way as to avoid scent cues of predatory snakes (Downes and Shine 1998).

While the logic of the conclusions made in many of these studies appears to be valid, few studies have actually estimated predation risk or differences in predation risk in different habitats. Tail break frequency can often serve as a rough estimate of predation risk, and so by looking for differences in tail break frequency between lizards using different habitats may give us information on whether the habitat used by a lizard affects predation risk. Among *Liolaemus* lizards, species that tended to use perches that reduced their visibility to predators had lower tail break frequencies than species using perches that increased their visibility to predators (Jaksic and Fuentes 1980). Elevational differences in tail break frequency between high and low elevation populations of *Sceloporus jarrovi* may arise through differences in the amount of vegetative cover and complexity (e.g., more tail loss in more open habitats) (Brown and Ruby 1977). Parker (1994) also found that *Sceloporus undulatus* in more open habitats had higher tail break frequencies than those in more closed habitats. However, Smith (1996b) found that tail break frequencies did not differ between a wooded habitat and an open habitat in a population of *Sceloporus virgatus*.

One might also expect habitat use to affect parasite-host interactions. The evidence for an impact of habitat use on ectoparasite loads is variable. In some cases, such as *Sceloporus occidentalis* (Tälleklint-Eisen and Eisen 1999), mite loads vary between different habitats. However, in other cases (e.g., *Sceloporus virgatus*, Smith 1996c), mite loads do not vary between different habitats. Endoparasites (e.g., malaria) have also been shown to differ among sites, often because of the thermal or humidity properties of the habitat that may affect both the parasite and their vectors (e.g., Ayala and Spain 1976; Rand et al. 1983; Schall 1992; Schall and Marghoob 1995; Staats and Schall 1996; Schall et al. 2000); however, detailed studies on the effects of habitat on the distribution and effect of endoparasites are unfortunately lacking. Little else is known about the impact of habitat on parasite loads in lizards.

CONCLUSIONS

It is quite apparent from the studies reviewed above that habitat (and microhabitat) use has the potential to be of great importance for individual lizards, populations of lizards, and communities of lizards. At the individual level, the thermal properties of an environment have a major influence on performance, and in many cases, may be the most important factor in determining the consequences of using a particular habitat. Unfortunately we know fairly little about how other characteristics of habitat (e.g., structure, predation risk, food availability, etc.) influence individual performance. We definitely need more studies investigating the consequences of these other habitat characteristics on individual performance. At the population level, the studies reviewed above suggest that how lizards use their environment can influence their persistence in the face

Table 4. Studies reporting the results of observational studies on the use of habitats by communities of lizards. Some studies conclude that competition is important (either currently or in the past), while other studies conclude that something other than competition is driving the observed habitat use in the community.

Studies concluding competition important	
Barbault and Maury (1981); Barbault (1991)	Two or more species may coexist because species-specific preferences allow for coexistence
Dunham (1983)	Overlap in microhabitat use between <i>Sceloporus merriami</i> and <i>Urosaurus ornatus</i> decreased when food abundance is lower and increased when food abundance is higher.
Fuentes and Cancino (1979)	Interaction between habitat use and predation allow <i>Liolaemus platei</i> and <i>L. nigromaculatus</i> to coexist.
Howard and Hailey (1999)	Four species of sympatric lizards living on rocks in Zimbabwe segregate spatially. Indirect evidence (e.g., a habitat shift by another species <i>Mabuya striata</i> in the absence of <i>M. quinquetaeniata</i>) possibly implies niche segregation on the basis of habitat use allows coexistence.
Huey et al. (1974)	Two species of fossorial lizards (<i>Typhlosaurus</i>) from the Kalahari desert use different microhabitats perhaps as the result of interference competition, but may also result from species specific adaptations to different habitats that allow coexistence.
Jenssen (1973)	When <i>Anolis opalinus</i> is sympatric with <i>A. lineatopus</i> it perches higher than where it is not sympatric with <i>A. lineatopus</i> .
Lister (1976)	In the absence of potential competitors, anoles in the West Indies expand their structural niche (i.e, they use a broader range of perches).
Marcellini and Mackey (1970)	The arboreality of <i>Sceloporus occidentalis</i> and the terrestriality of <i>S. graciosus</i> where they are sympatric reduces competition.
Medel et al. (1988)	<i>Liolaemus tenuis</i> shifts to higher perches in the presence of <i>L. pictus</i> , presumably as the result of observed aggressive interactions between members of these two species.
Moermond (1979a)	The presence or absence of suitable habitat or suitable perch structures in a given area can determine the presence or absence of <i>Anolis</i> species in a community.
Ortiz and Jenssen (1982); Jenssen et al. (1984)	<i>Anolis cooki</i> shift their habitat use in the presence of <i>A. cristatellus</i> , and intraspecific competition might explain male perches in both species.
Patterson (1992)	Microhabitat use and food use differs between species of New Zealand skinks (genus <i>Leiopisma</i>) and may allow coexistence by reducing overlap. Differences in microhabitat use appear to be enforced by aggressive interactions, suggesting competition may be driving the segregation.
Rand (1964a)	Habitat segregation observed in the anoles of Puerto Rico may be explained by competition.
Rose (1976)	Competition is one of many possible explanations for the habitat segregation of <i>Sceloporus occidentalis</i> and <i>S. graciosus</i> .
Schoener (1970)	Sympatric <i>Anolis</i> species in the Bahamas often have cycling perch use such that no two species use the same perch at the same time of day.
Schoener (1975)	Habitat shifts observed in West Indian <i>Anolis</i> and some species of <i>Leiocephalus</i> are driven by competition.
Schoener (1977)	Partitioning of resources based on habitat segregation can reduce competition and allow coexistence of two or more lizard species.
Schoener and Adler (1991)	When habitat is taken into account, signs of species interactions based on distributional patterns in the Bahamas become increasingly negative, suggesting habitat may influence the importance of species interactions in affecting species distributions.
Vitt (1995)	Lizards of the caatinga of NE Brazil apparently segregate on the basis of microhabitat use.
Vitt and Avila-Pires (1998)	Differential habitat use appears to facilitate the coexistence of two sympatric <i>Neusticurus</i> species.
Vitt et al. (1998b)	Suggest that the fact that <i>Neusticurus ecleopus</i> only occurs along the edges of streams and swamps in Amazonian rain forest precludes it from interacting with other lizard species that might be competitors.
Vitt et al. (1999 2000)	Differences in habitat use are, in part, responsible for niche segregation in Amazonian teiid lizards, as well as a larger group of Amazonian lizards, and may be the result of past species interactions, such as competition.
Studies concluding something else important	
Ballinger et al. (1990)	Did not think that competition influenced the niches of the lizards occurring on Arapaho Prairie in western Nebraska.
Barbault and Maury (1981)	Segregation between species in the Chihuahuan Desert need not be the result of competition, in spite of the fact that species appear to be in very distinct habitats.
Davis and Verbeek (1972)	Competition for rock perches is „unlikely“ between <i>Sceloporus occidentalis</i> and <i>Uta stansburiana</i> .
Martín-Vallejo et al. (1995)	Suggested that the difference in microdistribution of <i>Podarcis muralis</i> and <i>P. hispanica</i> may be due to physiological/historical constraints, or competition.
Ortega et al. (1982); Bar- bault et al. (1985)	Habitat specialization of lizards in the Sierra Madre probably not due to competition, but instead is the result of the effects of several other factors.
Rand and Humphrey (1968)	Did not believe competition was the primary force driving habitat use in lizards in Panama.
Stamps (1983)	Ontogenetic habitat shift of <i>Anolis aeneus</i> not influenced by interspecific aggression.
Vitt et al. (1981)	Perch use differences among <i>Urosaurus graciosus</i> , <i>U. ornatus</i> , and <i>Sceloporus magister</i> are not necessarily due to competition but instead may be related to responses to the physical environment.

Table 5. Studies reporting the results of experimental studies on the use of habitats by communities of lizards. Some studies conclude that competition is important (either currently or in the past), while other studies conclude that something other than competition is driving the observed habitat use in the community.

Studies concluding competition important	
Losos et al. (1993a)	In a natural experiment, <i>Anolis conspersus</i> has shifted perch height in habitats where <i>A. sagrei</i> has colonized.
Pacala and Roughgarden (1982, 1985)	Removal experiments showed that the presence of <i>Anolis wattsii</i> increased the perch height of <i>A. gingivus</i> .
Petren and Case (1998)	Competition between the geckos <i>Hemidactylus frenatus</i> and <i>Lepidodactylus lugubris</i> was reduced when the complexity of their habitat was increased. The change occurred because of changes in how each species foraged and behaved. The changes were substantial enough to allow coexistence of these two species.
Vanhooydonck et al. (2000)	In laboratory experiments, <i>Podarcis sicula</i> appears to be aggressively dominated by <i>P. tiliguerta</i> , causing it to be more secretive, suggesting <i>P. sicula</i> may be competitively inferior to <i>P. tiliguerta</i> . However, in the field these two species use different microhabitats (Van Damme et al. 1990), possibly facilitating coexistence.
Studies concluding something else important	
Leal et al. (1998)	Removal of <i>Anolis gundlachi</i> (typically occurs within 2 m of the ground) from plots in a Puerto Rican rainforest caused no change in habitat use by sympatric <i>A. evermanni</i> (typically occurs at 2 m or higher), but <i>A. evermanni</i> did increase in numbers, indicating that competition or intraguild predation is probably occurring between these species despite apparent habitat segregation.
Rummel and Roughgarden (1985)	Experimental results led them to conclude that competition was not important in determining perch use in <i>Anolis bimaculatus</i> and <i>A. wattsii</i> .
Tinkle (1982)	Removal of two sympatric species (<i>Sceloporus clarki</i> and <i>Urosaurus ornatus</i>), had no effect on habitat use or perch height of a third species (<i>Sceloporus undulatus</i>), and leading Tinkle to conclude that competition was not important.

of changes in the structure of their habitat, but we actually have little information on the actual mechanisms behind the relationship between habitat use and population dynamics. We need more such studies, and more studies looking for the links between consequences at the individual and population level. In many cases, the mechanistic explanations are assumed, but not investigated. The results may not be what we expect (see discussion of Díaz 1997 in the Population section). Finally, at the community level, it is clear that habitat use can often either be a consequence of competition (past or present) or be a mechanism of coexistence. Unfortunately, many studies draw conclusions on the role of habitat use mediating community structure without experimental evidence, and just as with populations, conclusions are drawn based on observations that are consistent with certain hypotheses (but actually are consistent with alternative hypotheses as well). Basically, it is time to start moving from studies describing habitat use and its consequences (such studies form the basis of further investigations, and as such should not be abandoned entirely, rather they should be used to focus future research), to studies investigating the specific mechanisms by which habitat use causes the effects on lizards that we see in nature.

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