Colonization and saturation of habitats by lizards

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We studied the colonization of habitats by four species of iguanid lizard (Urosaurus ornatus, Sceloporus graciosus, S. undulatus, and Uta stansburiana) to determine differences among the species in colonization, differences among habitat types in colonization, and the time trajectory of colonization. We surveyed lizards on eight study plots in three habitats after a density reduction experiment. We discovered no difference among lizard species in their recovery relative to numbers removed. However, there were significant differences in recovery among habitats, suggesting an important role of habitat type in the resilience of the lizards to the perturbation. Colonization by lizards was rapid and most study plots were colonized within 2 to 3 mo of the manipulation. One year after the experiment, all species were represented on all plots. Saturation (ratio of marked lizards to the number removed on each plot) was significantly different between the first and all other post-manipulation census periods. There was no significant difference in saturation among the second (1 yr), third (15 mo) and fourth (27 mo) census periods, suggesting asymptotic saturation within 1 yr of the perturbation. The pattern of colonization by resident lizards was similar to that of all lizards (residents and transients). There was no difference in saturation among species, but there were significant habitat and census period differences in saturation.

There is a resurgence of interest in the processes that determine the limited membership of species in ecological communities. Current efforts focus on rules of assembly (Drake 1991, Law and Morton 1993, Luh and Pimm 1993) that permit the accumulation and determine the post-colonization sorting of species. Mechanisms that influence assembly formation include founder or priority effects, differences in invasion rates, and the vagaries of colonization history (Sutherland 1974, Robinson and Dickerson 1987, Robinson and Edgemon 1988, Drake 1990, 1991). Strong competitive interactions among species (Gilpin et al. 1986) have been shown to affect species richness and composition and, in theory, diversity trajectories (Yodzis 1989). Both habitat selection (Meffe and Sheldon 1990) and environmental disturbance (Kingsolving and Bain 1993) have clear effects on assembly recovery following perturbations. In addition, the approach of community fabrication has revealed the significance of dominance-based assembly rules in determining fitness (Alford and Wilbur 1985, Wilbur and Alford 1985) and species richness and composition (Gilpin et al. 1986, Robinson and Dickerson 1987, Robinson and Edgemon 1988, Drake 1991) in small-scale experimental systems.

The current status of experimental research on assembly rules appears to lag behind the conceptual and theoretical basis of assembly dynamics (Law and Morton 1993, Luh and Pimm 1993). For example, although priority in establishment has been demonstrated in small-scale arenas, its significance in natural assemblies remains largely unknown. One question is the extent to which mechanisms of community assembly operate at
the scale of habitat patches large enough to support several individuals and species. Community recovery and assembly rely on colonization and the spatial and temporal scales at which it operates (Gilpin and Hanski 1991). In spite of the attention directed to colonization on a geographic scale (Ricklefs and Schluter 1993), little is known about colonization among local populations. Voids in our knowledge of the process make it difficult to distinguish unsuccessful colonization attempts from cases in which colonization has never occurred (Robinson and Dickerson 1987).

In this paper we utilize a study system in which we have observed lizard species richness to vary within some habitats over short intervals of time. Some species occasionally disappear from habitats, perhaps due to stochastic extinctions in small populations. Subsequent to these extinctions the species recolonize the habitats by dispersal from surrounding source populations. We wanted to know more about colonization especially differences among lizard species in colonization, differences in colonization among habitat types, and the temporal pattern of colonization. Because lizard species richness does vary, and recovery requires colonization, we conducted an experimental reduction in the numbers of four iguanid lizard species to create density sinks in different habitats. We then examined the response of lizards to this perturbation for a period of 27 months.

Methods and study system

Study area

The field research was conducted at the Colorado National Monument, Colorado, (elevation 1750 m), and combined an experimental reduction of lizard numbers with mark and recapture surveys of lizards. The dominant habitat is pinyon pine (Pinus edulis) and juniper (Juniperus utahensis) woodland which is often dissected by rocky washes and narrow canyons. We distinguish three habitats in this study: pinyon-juniper woodland with sand substrate and numerous tree falls, and two types of canyon habitat. One canyon habitat is narrow and rocky, with exposed ledges and deeply eroded washes. Pinyon pine and juniper flank these narrow canyons. The second canyon habitat is wider and steep-sided but the canyon floor is dominated by sandy substrates and pinyon-juniper woodland.

Study plots

Within the three habitats we constructed eight study plots. Four were in pinyon-juniper woodland (Window Rock), two were in rocky canyon habitat (Fruita Canyon) and two were in sand-substrate canyon (Independence). The four replicates in pinyon-juniper woodland (compared with two in each of the other habitats) reflect the prevalence of this habitat type on the Colorado Plateau. The three habitats formed the apices of a triangle with a total area of 0.9 km². The distance between Fruita Canyon and Window Rock was 1.1 km, between Window Rock and Independence 1.9 km, and between Fruita Canyon and Independence 1.6 km. Within each of the three habitats, study plots varied from 50 to 120 m apart. We constructed the plots using natural landmarks (rock ledges, tree falls), and the plots varied in area and shape. Given the terrain, we could not standardize plot area, but rather we surveyed habitats containing structural features likely to be included in lizard territories and home ranges (M'Closkey and Heenar 1994). These included tree falls and rock ledges.

At Window Rock (pinyon-juniper woodland), plots were 1440, 2464, 2912, and 4096 m² in area. At Independence, plots were 3872 and 2280 m², and those at Fruita Canyon were 4776 and 4042 m².

Lizards and field procedures

Four species of iguanid lizard commonly occur on the elevated mesas of western Colorado. All lizard species occur within the three designated habitats, although not necessarily in the same year. Variation in lizard numbers among habitats is substantial with Urosaurus ornatus (tree lizard, mean adult weight ≈ 4 g) and Sceloporus undulatus (fence lizard, ≈ 15 g) reaching highest numbers in rocky canyons and S. graciosus (sagebrush lizard, ≈ 8 g) most common in pinyon-juniper woodland. Uta stansburiana (side-blotched lizard, ≈ 4 g) is found in all habitats but it is uncommon.

During the removal census period (18 May to 6 June, 1992), we captured lizards, measured their snout-vent length (SVL, mm), determined the sex by examination of postanal scales, applied a permanent (toe clip) and temporary (paint) mark, and removed them. Removed lizards were placed in cotton bags and released > 0.4 km from their points of capture and > 1 km from other study plots. The removal census period continued until ≤ 1 lizard was removed. This required seven surveys on each of the eight study plots. The rapid depression of lizard numbers during the removal period is shown in Fig. 1. Following the removals, there were four post-manipulation census periods. These census periods were designed to detect colonization of the plots by lizards. The first was in August 1992 (26 July – 12 August, 40 censuses over all plots), the second was in June 1993 (25 May – 10 June, 33 censuses) following the emergence of lizards from hibernation, the third was in August 1993 (31 July – 18 August, 50 censuses), and the fourth was in August 1994 (3 – 18 August, 48 censuses). Differences in the number of censuses among years reflected the effort required to capture and mark lizards. Census work continued until no new lizards were marked on the
study plots. During the post-manipulation census periods, lizards were handled as described for the removals, but they were released at their point of capture instead of being removed. During a single census each study plot was surveyed by 2–4 researchers twice within the same day. A census on a single plot required 3 to 6 person-hours.

In our analysis we distinguish resident (captured or seen during two or more single censuses) and transient (captured once) lizards. To examine differences among lizard species, habitats, and census periods during colonization we use an index of saturation defined as the ratio of marked lizards on a plot during a census period to the number of lizards removed from each study plot, multiplied by 100. Values of 100 indicate complete saturation by a lizard species, within a habitat, or during a census period, relative to the number of lizards removed. We use the term saturation in the limited sense defined by our experimental results. The index provides a standard by which we assess the recovery of lizards after the removals. We do not imply that the lizard species are at their respective saturation densities (Ks). We analyzed the data by repeated measures ANOVA on the logarithmically transformed index of saturation. In this analysis, lizard species and habitat type were classification variables, and the estimate of saturation was repeated for each of four post-manipulation census periods. For each species the analysis of saturation was conducted on all lizards (residents and transients) and on residents alone. It would have been preferable to compare residents and transients, but limited numbers of transients for some species made the comparison impossible. The next best comparison, one that would at least include transients in the analysis, was the contrast between residents and all lizards.

Our removals successfully prevented juvenile recruitment in 1992 because lizards, with the possible exception of *U. stansburiana*, were removed prior to oviposition. More important, no hatchling lizards were discovered on any of the study plots in August 1992, when juvenile recruitment is readily apparent (Tinkle 1972, 1973, pers. obs.).

Because our study plots varied in area and shape we thought that colonization could be affected by these plot characteristics. To test for this possible bias we regressed saturation for each species against both area and the perimeter/area ratio for the eight plots. Regressions were not significant either for area ($F$'s ranged from 0.05 to 2.4, all $P$'s > 0.1), or for the perimeter/area ratio ($F$'s ranged from 0.18 to 3.3, all $P$'s > 0.1).

We recognize the possibility that the number of lizards removed in 1992 may not be representative of lizard abundance over a greater period of time. Therefore, as a validation of our estimate of saturation, we used surveys of lizards marked and released on the study plots in 1991. These surveys were one year before the initiation of the experiments and during the same period as the removals (late May to early June). If the numbers removed were typical of lizard numbers on the plots, then we expect a positive correlation between the abundance of lizards in 1991 and the number removed in 1992. The results for the three species for which we

Fig. 1. Number of lizards removed from four study plots in pinyon-juniper woodland (Window Rock), two study plots in narrow canyon with sand substrate and woodland (Independence), and two study plots in narrow, rocky canyon (Fruita Canyon), June, 1992.
have sufficient data support this prediction (U. ornatus, $r = 0.90$, $P < 0.01$; S. gracilisus, $r = 0.94$, $P < 0.01$; S. undulatus, $r = 0.85$, $P < 0.01$; all Ns = 8).

**Results**

Surveys we conducted before 1992 revealed spatial and temporal variation in species richness. Even at the same site, diversity varies from two to four lizard species. This variation could have been due to difference among species in local extinction and colonization rates. Lizard species contributing to the gains and losses had either low overall abundance (U. stansburiana), or abundance that varied among habitats (S. gracilisus).

**Lizard diversity and numbers**

The number of lizards removed and the number of subsequent colonists for all plots within the three habitats are shown in Figs 2, 3, and 4. Over all habitats, 83 tree lizards, 50 sagebrush lizards, 65 fence lizards, and 18 side-blotched lizards were removed. It is likely that a few lizards escaped our detection and remained on the study plots after the removal period. But the primary goal of the manipulation was to create density sinks, and the removal of 216 lizards among the eight plots certainly fulfilled that objective (Fig. 1). Colonization by all species was rapid and each was present in the three habitats by June 1993. Sceloporus gracilisus and U. stansburiana were absent at Independence in the August 1992 census which was only 2 mo after the removals.

After the removals there was a more or less steady build-up of lizards within habitats (Figs 2, 3, and 4). The first opportunity to detect colonization occurred in the first post-manipulation census period (August 1992), and responses of the lizards were variable. Sceloporus undulatus at Fruita Canyon eventually reached the number initially removed (Fig. 4). The same high level of colonization was apparent for S. gracilisus at Fruita Canyon and Window Rock, and to a lesser extent for U. ornatus at Fruita Canyon and Window Rock, and S. undulatus at Window Rock (Fig. 2). It is difficult to reach definitive conclusions about U. stansburiana because of its low abundance on the study plots.

It is also obvious that some habitats were colonized more quickly and completely than others. Overall, Fruita Canyon was colonized by more lizards and Independence by the fewest relative to the numbers removed. Window Rock was intermediate. It also appears that by August 1994, there were fewer lizards compared to the peak colonization in 1993 for S.
Table 1. Analysis of the saturation of 3 habitats by 4 lizard species over 4 post-manipulation census periods (27 mo) by repeated measures ANOVA.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Sum of squares</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lizard (L)</td>
<td>2.29</td>
<td>3</td>
<td>1.60</td>
<td>0.224</td>
</tr>
<tr>
<td>Habitat (H)</td>
<td>7.90</td>
<td>2</td>
<td>8.29</td>
<td>0.003</td>
</tr>
<tr>
<td>Census (C)</td>
<td>5.87</td>
<td>3</td>
<td>7.70</td>
<td>0.000</td>
</tr>
<tr>
<td>L × H</td>
<td>3.66</td>
<td>6</td>
<td>1.28</td>
<td>0.315</td>
</tr>
<tr>
<td>C × L</td>
<td>0.86</td>
<td>9</td>
<td>0.38</td>
<td>0.942</td>
</tr>
<tr>
<td>C × H</td>
<td>0.45</td>
<td>6</td>
<td>0.29</td>
<td>0.937</td>
</tr>
<tr>
<td>C × L × H</td>
<td>3.83</td>
<td>18</td>
<td>0.84</td>
<td>0.653</td>
</tr>
<tr>
<td>Error</td>
<td>13.74</td>
<td>54</td>
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</tr>
</tbody>
</table>

graciosus and S. undulatus at Window Rock, S. undulatus at Independence, and S. graciosus at Fruita Canyon.

Recovery of lizards

We analyze the colonization of lizards and habitats by using an index of saturation which compares the number of lizards during each post-manipulation census period to the number removed in June 1992. There were significant differences among habitats and census periods (Table 1). Differences in mean saturation among lizards varied from approximately 44 to 62 (Fig. 5), although differences among species were not significant, and therefore unplanned contrasts were not performed. Differences in mean saturation among habitats were significant (Fig. 6, Table 1) as were 2 of 3 pairwise contrasts (Tukey’s HSD test). Narrow canyons with extensive rock exposure (Fruita Canyon) reached higher levels of saturation (74) than woodland restricted to canyons (Independence, P < 0.001). Pinyon-juniper flatland (Window Rock) is intermediate in saturation (58) between the two canyons and is also significantly different from Independence (P = 0.001).

Differences in saturation among census periods were significant (Table 1, Fig. 7), and reflect the slow initial colonization in August 1992 (saturation = 25) followed by a rapid immigration of lizards in the first full season of activity (1993) following the experiments (saturation = 66–67). Overall saturation in August 1994 (59) was slightly, but not significantly, less than the saturation in 1993. Unplanned contrasts between censuses revealed significant differences in saturation between August 1992 and the early summer (P = 0.001) and late summer (P = 0.002) periods of 1993 (Fig. 7), and 1994 (P = 0.004). There was no significant difference in saturation either between June and August 1993 (P = 0.998) or between August 1993 and August 1994 (P = 0.994), suggesting that much of the eventual colonization of the plots had been achieved by June 1993, one year after the manipulations.

Resident lizards

Our analysis of colonization by lizards ignores the distinction between lizards that establish residence and those that move through a habitat and do not establish residence. We repeated the analysis of saturation by resident individuals of 4 lizard species over 4 post-manipulation census periods (27 mo) by repeated measures ANOVA.

Table 2. Analysis of the saturation of 3 habitats by resident individuals of 4 lizard species over 4 post-manipulation census periods (27 mo) by repeated measures ANOVA.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Sum of squares</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lizard (L)</td>
<td>0.72</td>
<td>3</td>
<td>0.37</td>
<td>0.774</td>
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<tr>
<td>Habitat (H)</td>
<td>11.76</td>
<td>2</td>
<td>9.05</td>
<td>0.002</td>
</tr>
<tr>
<td>Census (C)</td>
<td>4.88</td>
<td>3</td>
<td>7.33</td>
<td>0.000</td>
</tr>
<tr>
<td>L × H</td>
<td>3.82</td>
<td>6</td>
<td>0.98</td>
<td>0.466</td>
</tr>
<tr>
<td>C × L</td>
<td>3.05</td>
<td>9</td>
<td>1.53</td>
<td>0.162</td>
</tr>
<tr>
<td>C × H</td>
<td>0.89</td>
<td>6</td>
<td>0.67</td>
<td>0.677</td>
</tr>
<tr>
<td>C × L × H</td>
<td>6.80</td>
<td>18</td>
<td>1.70</td>
<td>0.068</td>
</tr>
<tr>
<td>Error</td>
<td>11.98</td>
<td>54</td>
<td></td>
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</tr>
</tbody>
</table>
separating the resident lizards (captured or observed more than once) from the total number marked. Resident lizards constitute the majority (77%) of those marked. The index of saturation was computed as previously described for all lizards on a study plot. The results of the ANOVA are given in Table 2. The results of this analysis are qualitatively the same as the results for all lizards (Table 1). There are no significant differences in saturation among species but there are significant differences among habitats and among census periods. Pairwise contrasts between habitats and census periods also matched the results of all lizards, with the exception that all 3 pairs of habitats were significantly different in saturation by resident lizards (Tukey's HSD test).

The role of lizard density
The removal plots may differ in the number of potential colonists that are available. Territorial behavior and crowding within source populations may provide the impetus for movement away from other individuals, and lizards encountering a density sink may establish residence. It is possible that colonization of the different plots was dependent on the density of lizards surrounding the plots. We do not have estimates of lizard density surrounding the removal plots, so we used the density of removed lizards as a surrogate. The key assumption is that the density of lizards removed from plots is similar to the density of lizards in the vicinity of the plots. These lizards would be the likely source of initial colonization. We tested for the effects of density in the saturation of habitats by regressing saturation of each plot in June 1993 against the number of lizards removed per ha from each of the eight plots in June 1992. This was done separately for each lizard species. With the small number of study plots there is limited power to detect any but the strongest effect of density in colonization. However, no regression was significant and F's were <2.92 (P: 0.138 to 0.505).

Discussion
The results of our experimental investigations on colonization by lizards revealed several interesting features of the study system. In the context of this experiment, we use “saturation” as an operational criterion to assess the recovery of each lizard species and habitat relative to the number of individuals removed. This use differs from the familiar context of saturation of communities by species. Lizard species do not differ significantly in saturation, either by all individuals (Fig. 5, Table 1) or by resident lizards (Table 2). However, there were significant differences among habitats in saturation by lizards (Fig. 6). Significant differences among census periods revealed rapid colonization within the first year of the removals with no additional increase in saturation up to 27 mo (Fig. 7).

Characteristics of lizards
Although the lizard species differed in total abundance, the lack of difference among species in saturation indicates that lizards colonized to the same relative pre-removal levels. This resilience (Sutherland 1990) and persistence (Rahel 1990) suggest that colonization was not constrained by differences among species in available recruits or their relative dispersal ability from source habitats. The initial colonization (June–August 1992) may have been by individuals that were unsuccessful in acquiring territory or home range space in adjacent habitat. In June 1993, there was another group of successful colonists that quickly settled as residents on the study plots.

The initial colonization of habitats in August 1992 was not by recruitment of juveniles from within the study plots because removals of lizards, with the exception of *U. stansburiana*, were completed before oviposition. In addition, we did not observe hatchlings of any lizard species in August 1992, when recruitment occurred and was apparent outside of the boundaries of the study plots. Others have shown that life history differences may affect the initial stages of community assembly. Alford and Wilbur (1985) and Wilbur and Alford (1985) have demonstrated significant interspecific competitive effects in experimental amphibian communities as a result of order of hatching or introduction. In a sense, our results are paradoxical in that differences among species in life history characteristics (Tinkle and Hadley 1975, Stamps 1983a) might be expected to be associated with differences in dispersal and colonization. For example, the large home ranges
Saturation of habitats

We estimated the peak saturation of lizards at \( \approx 67 \) in June 1993 (Fig. 7), but there was variation among species ranging from 44 for tree lizards to 62 for fence lizards. This estimate of saturation is probably conservative because the lizards removed in June 1992, would have included both residents on the study plots and a few individuals moving onto the plots as the removals were in progress.

Why do habitats differ in their recovery? The two canyon habitats are the most different pair in terms of saturation, with overall values at \( \approx 74 \) for Fruita Canyon and \( \approx 30 \) for Independence (Fig. 6). The three habitats appear to differ in their relative isolation. Window Rock was open to colonization from all sides from pinyon-juniper woodland and rock ledges and walls. Each canyon habitat is \( \approx 0.3 \) km in length, and colonization by lizards into Fruita would have been primarily from the open sides at the mouth of the canyon which was comprised of pinyon-juniper woodland and rock ledges. Independence may be relatively more isolated because the mouth of the canyon is close to an elevated road bed and it has an open, flat wash on one side which is devoid of lizards. Using simulation models of emigration, Stamps et al. (1987) demonstrated how the movement of individuals in patchy habitats is affected by the “permeability” of habitat boundaries. Differences among habitats in the ease of dispersal of potential colonists is consistent with the pattern we observed. Another difference among the plots is that at Window Rock and Fruita Canyon the defaunated area was a relatively small fraction (5% at Window Rock, 10% at Fruita) of the total area available. In these habitats potential colonists would have been adjacent to the removal plots. At Independence, the removal plots constituted a larger fraction (26%) of the total area available. We exercise caution in this conclusion because we reached it after analysis of the data rather than as an a priori prediction about the role of habitat isolation. In the defaunation of stream fish assemblies, Meffe and Sheldon (1990) estimated that the defaunated area was approximately half the total area available, and they concluded that recolonization relied on more distant sources of individuals than those in adjacent habitats.

Priority effects and invasion sequence appear to play major roles in the assembly of small-scale experimental systems (Gilpin et al. 1986, Robinson and Dickerson 1987, Robinson and Edgemon 1988, Drake 1991). In our study system there are differences among habitats in recolonization by lizards, perhaps related to differences in isolation among habitats. However, colonization is rapid and effectively simultaneous for all lizard species. This would seem to limit the potential for space monopolization and founder control as important determinants of assembly formation in lizards at the habitat scale. Although one habitat (Independence, Figs 3 and 6) had significantly lower saturation than the other two, it did regain all four species. The lower saturation was in terms of lizard numbers relative to those removed, and not lower saturation in terms of species richness. Occasional disappearance of lizards from habitats would be countered by the potential for rapid colonization. Therefore, the variation in species...
richness we observed before the experiment would seem to be due primarily to differences among species in local extinction.

Acknowledgements – We thank the Natural Sciences and Engineering Research Council of Canada for continuing support of research to RTM. Special thanks are due Jimmy Taylor, Superintendent Colorado National Monument, for permission to conduct the research. We thank Shirley Crump for her expert preparation of the manuscript copy. We also appreciate help with field work from D. Peterson, D. Petruzzi and A. Schincariol.

References


