

## Lizard Distributions and Reproductive Success in a Ponderosa Pine Forest

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**ABSTRACT.**—We assessed relative abundance, demographic, and reproductive success data for two lizard species in a Northern Arizona ponderosa pine forest, a fire-dependent system unnaturally modified by fire suppression over the past century. During May to October 1997–1999, we employed up to 70 pitfall arrays to sample lizards over 6990 array-days. At each array, we described macro-vegetative cover, stand, and microhabitat characteristics. *Sceloporus graciosus* responded to habitat variation at all three spatial scales. Adult *S. graciosus* were widely distributed among cover and stand types. However, reproductive success and hatchling abundance were highest in the most open cover (meadow) and stand (savannah) types, and lowest in pure ponderosa cover and dense ponderosa stands. Adult females replaced themselves annually only in meadows, savannahs, and forest with a deciduous component. *Eumeces skiltonianus* adults and juveniles were least abundant in meadows, but females replaced themselves each year in meadow and ponderosa-pinyon-juniper vegetative cover and in savannahs. Hatchlings were least abundant in intermediate- and high-density ponderosa stands, whereas juveniles of both species were most abundant in areas containing a deciduous tree component. Both species were present in plots having lower percent duff groundcover than at plots containing no lizards. Increased tree densities, canopy closure, and litter accumulation influenced distributions of both lizards. Furthermore, abundance and reproduction in these lizards were generally optimized in habitat with features most similar to that present prior to fire suppression activities and in areas containing a deciduous tree component.

Ponderosa pine (*Pinus ponderosa*) forest is the most common montane vegetative cover type in the southwestern United States, covering 3.4 million ha in Arizona and New Mexico alone (Brown, 1994), and providing habitat for over 280 native vertebrate species (New Mexico Game and Fish Department, 2000). Historically, the physical structure and floral composition of these forests were maintained by periodic, low intensity fire recurring roughly every four to 36 years (Swetnam and Baisan, 1996), periodic drought, and grass-seedling competition (Covington et al., 1997). Thus, ponderosa forests were heterogeneous at multiple temporal and spatial scales (Cooper, 1960; White, 1985) and were generally dominated by low tree densities with vegetative understories in various stages of seral maturation depending on local fire frequency.

Human fire suppression and logging activities over the past ~125 years in the American southwest have caused most ponderosa pine forests to become unnaturally dense and fire-prone (Covington and Moore, 1994; Fulé et al.,

1997; Swetnam et al., 1999). In modern southwestern ponderosa forests, tree densities are up to 8.5 times greater than circa 1883 (Fulé et al., 1997) and are characterized by increased canopy closure, decreased sunlight penetration to ground level, a replacement of herbs and grasses with deep beds of flammable organic litter (Kolb et al., 1994; Covington et al., 1997), and a concomitant loss of habitat heterogeneity at the microhabitat, forest stand, and landscape scales. As these conditions have intensified, biodiversity in ponderosa forests is believed to have decreased over the past several decades (Noss et al., 1995).

Studies in other regions of the United States have demonstrated that lizard populations can decline in the absence of natural disturbance regimes such as fire (Greenberg et al., 1994; Ballinger and Watts, 1995). In this paper, we report on a three-year study of the species composition, spatial distributions, relative abundance, and reproductive success of lizards in a ponderosa pine forest that has been fire-suppressed for ~125 years (Moore et al., 1999). We first described forest habitat conditions at three spatial scales, since knowledge of patterns of habitat selection at different spatial scales is vital to successful management and conservation of species (Johnson, 1980; Block and Brennan, 1993). We mapped the current distribution of distinct vegetative cover types, grouped forest

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stands into classes based on structural and floristic characteristics and described ground-cover-substrate composition. We then compared hatchling, juvenile, and adult abundance and female reproductive success of two locally common lizards (Sagebrush Lizard, *Sceloporus graciosus*; Western Skink, *Eumeces skiltonianus utahensis*) among vegetative cover, forest stand, and microhabitat types.

#### MATERIALS AND METHODS

*Study Area.*—We conducted this study at the Mt. Trumbull Resource Conservation Area (RCA) in the southern portion of the Unikaret Plateau on the Arizona Strip, north of the Colorado River and west of the Kaibab Plateau. Our study area (N36°214.488', W113°104.254') lay between Trumbull (2448 m) and Logan (2398 m) Mountains in a broad saddle shaped by volcanic activity. Lizards and vegetation were sampled between 1980 and 2196 m elevation. The major vegetative communities within the study area included pure ponderosa pine forest and ponderosa-deciduous forest, which included both Gambel oak (*Quercus gambelii*) and New Mexican locust (*Robinia neomexicana*). Pinyon (*Pinus edulis*) and juniper (*Juniperus osteosperma*) occurred sporadically throughout the RCA and dominated the south-facing slopes and lower elevations.

The Mt. Trumbull area has a bimodal pattern of precipitation with peaks during winter and summer; spring and fall are relatively dry. Annual precipitation at Nixon Spring (1982 m, north end of the study area) averaged 32.9 cm/year, based on a 30-year average ending in 2000 (WRCC, 2000).

Euro-American settlement of the Mt. Trumbull area occurred in 1870 and logging of the area began two years later. Small, portable sawmills were used nearly continuously until the 1960s (J. H. Altschul and H. C. Fairley, unpubl. data). Cattle grazing also began in the 1870s and continues today. Typical of the American southwest, the Mt. Trumbull area has been under active fire suppression for the past century (Moore et al., 1999; Ecological Restoration Institute, unpubl. data).

*Sampling Design.*—We collected lizard relative abundance and demography data using pitfall traps (Jones, 1986; Bury and Corn, 1987). We installed 70 pitfall arrays on a 300-m grid system overlaid on the study area, resulting in proportional stratification among vegetative cover types but randomness with respect to stand and microhabitat features. Arrays consisted of four buckets, three equally spaced about a center bucket. Periphery buckets were 7.6 m from the center bucket and were connected by a 15-cm high drift fence. Buckets rims were elevated ~2.5 cm above substrate surface and ramped

with soil to allow access by lizards while preventing flooding, shaded by an elevated (2.5–5.0 cm) lid and had a thin layer (2–4 cm) of litter in the bottom to reduce trap-related mortality. At each array, two 1.2 × 1.2-m plywood basking substrates were placed on the ground in random directions 10 m from the central bucket. Each time arrays were visited, lizards at basking substrates were captured using long-handled butterfly nets. Arrays remained open >20 days/month during June to September in 1997 and May to September in 1998 and 1999. We checked traps every two to three days to minimize trap mortality. We collected data simultaneously at all sites, employing 38 arrays in 1997, 70 arrays in 1998, and 56 arrays in 1999.

*Lizard Variables.*—All lizards captured received a unique toe clip identification, allowing us to tally the relative abundance of each lizard species at each array. We recorded snout-vent length (SVL; mm), girth (mm), and mass (g) of all lizards, and used these data to assign lizards to hatchling, juvenile, and adult age class categories. Three age class categories are readily identifiable during the active season for *S. graciosus*, with little or no overlap in size (Mueller and Moore, 1969; Tinkle, 1973). Our assignments were also guided by descriptions of minimum SVL at maturity from 14 studies on *S. graciosus* reported in Tinkle et al. (1993). Although similar published data do not exist for *E. skiltonianus*, scatterplots of size class data for this species segregated into three groups that we ascribed to hatchling, juvenile, and adult age classes. Finally, we indexed reproductive success of lizards among arrays within each year as:

$$\begin{aligned} & (\text{no. hatchlings}) / [(\text{no. adults} + 1) \\ & \times \text{proportion adult } \text{♀s}] \end{aligned}$$

for *S. graciosus* because gender of this species is easily determined (Stebbins, 1985) and

$$(\text{no. hatchlings}) / [(\text{no. adults} + 1) \times 0.5]$$

for *E. skiltonianus*, since gender can not be determined for this species in the field.

*Habitat Measurements.*—We interpreted low-elevation, high-resolution aerial photographs taken in 1997 to classify the entire study area into major vegetative cover types. We drew polygons delineating vegetative cover types on photographs and then digitized them in Arc/Info. We then field-checked points randomly located in all cover type assignments, and assessed our accuracy in an error matrix (authors, unpubl. data).

At the forest-stand scale, we collected habitat data at each array using methods modified from Noon (1981) and Clawson et al. (1984). Stand-scale habitat data were collected in 0.2 ha

(25-m radius) plots centered on each pitfall array. Slope and aspect were determined at plot center. All trees within a 6-m wide belt extending north to south and east to west across the diameter of the plot were tallied by species and diameter at breast height. Tree canopy closure (cc) was tallied along 40 points spaced equidistant along the four cardinal directions. We used point-quarter sampling (Smith, 1980) to estimate volume ( $m^3/ha$ ) of logs (>2.5-cm, >3-m length), surface area ( $m^2/ha$ ) of rocks (>30-cm high), and indexed presence of natural basking substrates as log volume plus rock surface area.

We estimated percent ground surface covered by duff (dead, organic, nonwoody and <2.5-cm diameter woody material), logs, rocks, shrubs, grass, forbs, and bare soil along line transects running north to south, east to west, northeast to southwest, and northwest to southeast, totaling 160 m distance. Ground surface variables were measured at all arrays in both 1998 and 1999 but were not collected in 1997.

*Data Analysis.*—We recorded array locations with a Trimble® GPS receiver and superimposed them on the GIS map of vegetative cover types. We then visually compared 90% confidence intervals (CI) describing abundance of hatchling, yearling, and adult lizards, and of reproductive success, among vegetative cover types (Zar, 1996). Prior to comparisons, abundance and reproductive success data were log-transformed to improve distributions and variance homogeneity. To determine whether there was annual replacement of female adult lizards in different cover types, we examined 90% CI about values of reproductive success using raw data; intervals that overlapped or exceeded one indicated annual reproductive replacement by females, whereas intervals <1 demonstrated failure of adult females to replace themselves.

To identify natural groupings in and variation among forest stands we submitted canopy closure, and ponderosa and deciduous tree density data from all arrays to a cluster analysis (Systat vers. 9, SPSS Inc., Chicago, 1999). We standardized the data, and chose Pearson correlation as a distance metric to remove the influence of differences in scale among variables. We chose these three variables because they are the primary metrics of a presettlement restoration prescription proposed for this area. Once array membership within clusters was identified, we compared relative abundance and reproductive success of lizards among forest stand types in the same manner as for vegetative cover types.

Finally, to identify relationships between groundcover-substrate descriptors and lizards, we grouped arrays by presence/absence for each lizard species and tested for differences in ground cover variables using Mann-Whitney *U*-tests.

## RESULTS AND DISCUSSION

*Lizard Assemblage.*—We sampled lizards over 6990 array-days during 1997–1999 (1238, 3943, and 1809 days/yr, respectively). We documented a five-species lizard assemblage numerically dominated by *S. graciosus*, which comprised 65, 81, and 85% of sampled individuals, and occurred at 22/38, 61/70, and 44/56 arrays each year, respectively. *Eumeces skiltonianus* comprised 34, 18, and 12% of captured individuals and occurred at 19/38, 39/70, and 22/56 arrays each year, respectively. *Sceloporus undulatus*, *Cnemidophorus velox*, and *Phrynosoma douglasii* accounted for the remaining 1–3% of lizards sampled each year.

*Lizard-Vegetative Cover Relationships.*—The northern half of the study area was covered by ponderosa-deciduous-pinyon-juniper (17 arrays) and ponderosa-pinyon-juniper (7 arrays) mixed forest types, whereas the southern half was covered primarily by pure ponderosa (23 arrays) and ponderosa-deciduous (20 arrays) forest interspersed with pockets of other vegetative types. Small meadows (3 arrays) containing grasses and sagebrush were distributed throughout the study area. Distribution of arrays reflected proportional area of cover types. Only data from 1998 and 1999 are presented for comparisons among vegetative cover types because arrays were not present in all vegetative types in 1997.

*Sceloporus graciosus* abundance varied less among cover types as lizards became older (Appendix 1). In both 1998 and 1999, hatchling *S. graciosus* were more abundant in meadows than in any other vegetative cover type, with no other differences in either year. In 1998, juvenile *S. graciosus* abundance was higher in ponderosa-deciduous forest and ponderosa-deciduous-pinyon-juniper forest than in pure ponderosa forest, with intermediate abundances in ponderosa-pinyon-juniper forest and meadows. In 1999, juvenile abundance was higher in ponderosa-deciduous forest and meadows than in any other vegetative cover, with no other differences (Appendix 1). Adult *S. graciosus* abundance did not differ among vegetative cover types in either year. Reproductive success averaged >3 times higher in meadows than in any forested cover type in both years, differing between meadows (higher) and pure ponderosa forest in 1998 and trending toward this in 1999 (Appendix 1). In addition, female *S. graciosus* replaced themselves only in meadows and ponderosa-deciduous forest.

*Eumeces skiltonianus* responded increasingly to vegetative cover variation with increasing lizard age, and was more abundant in forested cover types than in meadows (Appendix 1). Hatchling *E. skiltonianus* abundance did not vary among vegetative cover types in either year. Juvenile *E. skiltonianus* in 1998 were more abundant in pure

TABLE 1. Vegetation values (mean  $\pm$  1 SE) for forest stands on Mt. Trumbull, Arizona, 1997–1999.

	Stands (N)				
	Ponderosa savannah (8)	Deciduous (20)	Medium density, closed canopy ponderosa (15)	Medium density, medium canopy ponderosa (10)	High density, closed canopy ponderosa (17)
Canopy (%)*	15.6 $\pm$ 4.0	51.3 $\pm$ 3.3	62.5 $\pm$ 2.2	34.3 $\pm$ 3.1	63.2 $\pm$ 1.5
No. ponderosa/ha*	128.5 $\pm$ 51.3	229.6 $\pm$ 33.8	453.9 $\pm$ 60.4	441.5 $\pm$ 36.9	1175.4 $\pm$ 94.5
Avg. dbh (cm) ponderosa	13.8 $\pm$ 5.4	31.1 $\pm$ 1.9	27.6 $\pm$ 1.7	22.5 $\pm$ 2.1	19.2 $\pm$ 1.0
No. deciduous/ha*	93.1 $\pm$ 35.1	518.6 $\pm$ 97.0	86.3 $\pm$ 30.7	23.1 $\pm$ 19.4	69.9 $\pm$ 23.6
Avg. dbh (cm) deciduous	3.0 $\pm$ 1.7	6.8 $\pm$ 0.9	5.3 $\pm$ 1.6	2.1 $\pm$ 1.5	8.1 $\pm$ 1.8
Live ground cover (%)	41.1 $\pm$ 8.8	19.1 $\pm$ 4.2	9.2 $\pm$ 3.4	8.7 $\pm$ 3.1	2.0 $\pm$ 0.5
Basking substrate	604 $\pm$ 235	1310 $\pm$ 254	1898 $\pm$ 733	1660 $\pm$ 517	3309 $\pm$ 1107
Duff (%)	35.5 $\pm$ 7.5	60.5 $\pm$ 3.7	72.4 $\pm$ 3.3	62.0 $\pm$ 4.7	81.3 $\pm$ 1.9
Duff:bare ratio	7.2 $\pm$ 4.8	20.4 $\pm$ 6.3	30.4 $\pm$ 6.6	10.7 $\pm$ 3.2	32.8 $\pm$ 8.0

\* Denotes variables used to generate clusters.

ponderosa and ponderosa-deciduous forest than meadows but otherwise did not vary. In 1999, juvenile abundance was higher in ponderosa-deciduous-pinyon-juniper forest than in either meadows or ponderosa-deciduous forest. In both years, adult *E. skiltonianus* were more abundant in pure ponderosa and ponderosa-deciduous-pinyon-juniper forest than in meadows, where they were absent (Appendix 1). In 1999, adults were also not detected in ponderosa-pinyon-juniper forest. Although reproductive success did not vary among vegetative cover in either year, adult female *E. skiltonianus* replaced themselves in meadows and ponderosa-pinyon-juniper forest in both years, and also in pure ponderosa and ponderosa-deciduous-pinyon-juniper forest in 1998.

*Lizard-Stand Scale Habitat Relationships.*—The cluster analysis generated five forest stand types based on values of canopy closure and stem density of ponderosa pine and deciduous trees (Table 1). Cluster one contained savannah-like plots with a low density of small diameter ponderosa trees and low percent canopy closure. Cluster two described stands with higher deciduous (oak and locust) composition than coniferous. Cluster three was characterized by high canopy closure, intermediate density ponderosa stands. Cluster four described intermediate canopy closure and ponderosa density, and the lowest deciduous density. Cluster five contained close-canopied, high-density ponderosa stands. Neither slope (Kruskal-Wallis  $P = 0.925$ ) nor aspect (ANOVA  $P = 0.655$ ) differed among clusters.

Relative abundance of all *S. graciosus* age classes and reproductive success were highest in open stand types and decreased as stand density and canopy closure increased (Appendix 2). In 1997, abundance of hatchling *S. graciosus* did not vary among forest stand types. However, in 1998, hatchling *S. graciosus* were more abundant in savannah-like stands than in high-density ponderosa stands, with no other differences. In

1999, hatchling *S. graciosus* were more abundant in savannah-like stands than in deciduous-dominated stands or either of the high canopy-closure ponderosa stand types, and more abundant in deciduous stands than in high-density ponderosa stands (Appendix 2). Juvenile *S. graciosus* were more abundant in deciduous-dominated stands than in high-density ponderosa stands in 1997, and more abundant in savannah-like and deciduous stands than in intermediate-density, high canopy-closure ponderosa stands in either year, and high-density ponderosa stands in 1999 (Appendix 2). In 1997, abundance of adult *S. graciosus* did not differ among forest stand types, whereas in 1998 abundance was higher in deciduous-dominated stands than high-density ponderosa stands. In 1999, adult *S. graciosus* abundance was higher in intermediate-density, intermediate canopy-closure ponderosa stands than in deciduous-dominated stands, intermediate-density high canopy-closure, or high-density ponderosa stands (Appendix 2). *Sceloporus graciosus* reproductive success in 1998 was higher in savannah-like stands than in high-density ponderosa stands. Reproductive success of *S. graciosus* was higher in 1999 in savannah-like stands than in either intermediate-density ponderosa stand types or the high-density ponderosa stands, and was also higher in deciduous-dominated stands than in high-density ponderosa stands (Appendix 2). In both years, adult *S. graciosus* females replaced themselves in savannah-like forest stands; they also replaced themselves in deciduous stands in 1998 but did not in any other stand type in either year. Our data suggest that dispersal from meadows and savannahs into other cover and stand types may be important in maintaining *S. graciosus* in habitat types where reproductive replacement did not occur (Pulliam, 1988). Tinkle (1973), working in a similar ponderosa forest in southern Utah, found *S. graciosus* abundance highest in sagebrush flats. Other

studies have associated *S. graciosus* with open habitat types containing shrubs under which they thermoregulate, escape predation, and hunt (Marcellini and Mackey, 1970; Rose, 1976).

Hatchling *E. skiltonianus* abundance differed in 1997 only, being higher in deciduous-dominated stands than in intermediate-density and canopy-closure or high-density ponderosa stands. Juvenile *E. skiltonianus* abundance was higher in deciduous-dominated stands than in high-density ponderosa stands in all three years, and also higher than in either intermediate-density ponderosa stand type in 1998 and 1999 (Appendix 2). Adult *E. skiltonianus* abundance did not differ among forest stand types in 1997 or 1998 but was higher in deciduous-dominated stands than in high-density ponderosa stands in 1999 (Appendix 2).

Reproductive success for *E. skiltonianus* did not differ among forest stands in 1998 or 1999 (Appendix 2). In 1998, *E. skiltonianus* females replaced themselves in savannah-like stands and both intermediate-density ponderosa stand types, whereas in 1999 they replaced themselves only in savannah-like stands and in high-density ponderosa stands. Deciduous stands were the only type in which adult female *E. skiltonianus* did not replace themselves in either year. *Eumeces skiltonianus* forage in and under leaf litter (Behler and King, 1995), and all age classes may have been exploiting high amounts of duff in deciduous stands. Block and Morrison (1998) found a similar positive association between *E. skiltonianus* and California black oaks (*Quercus kelloggii*) in California but did not separate ages or examine reproductive success.

*Lizard-Substrate Habitat Relationships.*—The ratio of organic duff versus bare ground was significantly lower in plots in which *S. graciosus* was present in both 1998 (means =  $19.0 \pm 3.1$  SE vs.  $45.8 \pm 9.8$ ;  $P = 0.003$ ) and 1999 ( $17.2 \pm 3.0$  vs.  $31.5 \pm 11.9$ ;  $P = 0.02$ ). However, *S. graciosus* occurred across the full range of duff:bare ground sampled. In addition in 1998, plots where *S. graciosus* was present had fewer log and rock basking substrates ( $1666.0 \pm 358.3$  vs.  $3577.1 \pm 1118.1$ ;  $P = 0.04$ ), and greater percent ground covered by forbs ( $6.2 \pm 1.2$  vs.  $0.8 \pm 0.5$ ;  $P = 0.04$ ).

Percent ground covered by organic duff was lower in plots where *E. skiltonianus* was present in both 1998 ( $61.3 \pm 2.7$  vs.  $70.7 \pm 3.9$ ;  $P = 0.002$ ) and 1999 ( $58.7 \pm 4.0$  versus  $70.4 \pm 3.1$ ;  $P = 0.013$ ). Percent ground surface covered by organic duff ranged from 3.8–91.3%, however, *E. skiltonianus* was never present in plots containing less than 16.9% or more than 86.9% ground covered by duff. In 1998, the ratio of duff versus bare ground was also lower in plots where *E. skiltonianus* was present ( $18.9 \pm 3.9$  vs.  $27.3 \pm 5.2$ ;  $P = 0.05$ ).

*Conclusions.*—The ponderosa forest we examined was dominated by higher tree densities and less herbaceous ground cover than prior to cessation of natural fire regimes (Fulé et al., 1997; Mast et al., 1999), and tree encroachment into meadows was plainly evident. Greenberg et al. (1994) concluded that the closing of forest stands after fire suppression in Florida served as a major fragmenting agent for lizard populations. Ballinger and Watts (1995) determined that when management prescriptions excluded natural disturbance factors such as periodic fire in Nebraska, lizard species dependent upon disturbed habitats declined or became locally extinct. Comparing burned and unburned coniferous forest in central Arizona, Cunningham et al. (2000) found that average abundance increased  $4.3 \times$  for *Sceloporus undulatus* and  $8.8 \times$  for *Cnemidophorus velox* in burned areas over four years postfire. Both of these species were present but extremely rare on our study area. Comparisons in other fire-dependent ecosystems have documented similar responses by lizards in burned areas (Lillywhite, 1977; Mushinsky, 1985).

We found lizard reproduction and replacement highest in the most open habitat types present. *Sceloporus graciosus* abundance and reproduction were consistently highest in meadows and savannahs, and lowest in forested cover types, especially high-density ponderosa forest. We found *E. skiltonianus* more abundant in ponderosa and mixed-deciduous forest cover than in meadows, but it became less abundant as stand-scale ponderosa stem density increased and replaced itself in meadows and savannahs in both years. Meadow and ponderosa savannah habitats were most similar to those reported historically common (Fulé et al., 1997; Mast et al., 1999) but were disappearing with long-term fire suppression. These changes may have limited lizard distribution and reproductive success in our study area to a fraction of the area in which they occurred ~125 years ago. If steps are not taken to reverse the trend toward increasing ponderosa density, these lizard species may become further restricted within this ponderosa forest landscape.

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APPENDIX 1. Confidence intervals (90%) describing abundance<sup>1</sup> and reproductive success<sup>1,2</sup> of lizards among vegetative cover types at Mt. Trumbull, Arizona, 1998–1999.

	Cover type				
	Ponderosa	Ponderosa-deciduous	Ponderosa-Pinyon-Juniper	Ponderosa-deciduous-Pinyon-Juniper	Meadow
1998					
<i>N</i> =	23	20	7	17	3
<i>Sceloporus graciosus</i>					
Hatchling	(0.03–0.25)	(0.20–0.59)	(0.02–0.70)	(0.00–0.40)	(1.39–2.05)
Juvenile	(0.33–0.68)	(1.14–1.80)	(0.35–1.30)	(0.71–1.37)	(0.17–2.32)
Adult	(0.49–0.89)	(0.72–1.31)	(0.77–1.63)	(0.56–1.19)	(0.37–2.36)
Repro.	(0.03–0.25)	(0.10–0.52)	(0.02–0.46)	(–0.02–0.38)	(0.32–2.46)
<i>Eumeces skiltonianus</i>					
Hatchling	(0.08–0.35)	(–0.02–0.20)	(0.13–0.78)	(0.11–0.43)	(–0.34–1.53)
Juvenile	(0.03–0.31)	(0.14–0.50)	(–0.09–0.29)	(–0.02–0.18)	0
Adult	(0.08–0.38)	(0.00–0.25)	(–0.05–0.45)	(0.12–0.54)	0
Repro.	(0.11–0.52)	(–0.03–0.26)	(0.12–1.05)	(0.14–0.60)	(–0.48–2.29)
1999					
<i>N</i> =	19	11	7	16	3
<i>Sceloporus graciosus</i>					
Hatchling	(–0.02–0.21)	(0.01–0.45)	(–0.09–0.29)	(0.16–0.50)	(0.57–1.36)
Juvenile	(0.21–0.68)	(1.15–1.93)	(0.27–1.03)	(0.37–0.97)	(1.17–2.12)
Adult	(0.21–0.62)	(0.45–1.04)	(0.34–1.42)	(0.50–1.00)	(–0.75–2.95)
Repro.	(–0.02–0.20)	(0.0–0.37)	(–0.06–0.18)	(0.16–0.57)	(–0.29–2.25)
<i>Eumeces skiltonianus</i>					
Hatchling	(0.06–0.31)	(–0.03–0.28)	(–0.05–0.45)	(–0.02–0.19)	(–0.44–0.91)
Juvenile	(–0.03–0.10)	0	(–0.09–0.29)	(–0.01–0.25)	0
Adult	(0.01–0.21)	(–0.08–0.28)	0	(–0.01–0.25)	0
Repro.	(0.08–0.45)	(–0.04–0.44)	(–0.08–0.71)	(–0.03–0.30)	(–0.70–1.44)

<sup>1</sup> Log-transformed.<sup>2</sup> Number of hatchlings:adult female.

APPENDIX 2. Confidence intervals<sup>1</sup> (90%) describing abundance and reproductive success<sup>2</sup> of lizards among forest stand types at Mt. Trumbull, Arizona, 1997–1999.

	Forest stand types				
	Deciduous	Ponderosa			
		Savannah	Medium density closed canopy	Medium density medium canopy	High density closed canopy
1997					
<i>N</i> =	11	4	6	6	11
<i>Sceloporus graciosus</i>					
Hatchling	(0.08–0.74)	(–0.35–1.87)	(–0.06–0.53)	(–0.13–0.82)	(–0.08–0.28)
Juvenile	(0.25–0.90)	(–0.37–1.62)	(–0.06–0.53)	(–0.19–0.55)	(–0.05–0.18)
Adult	(–0.05–0.50)	(–0.47–1.16)	(–0.12–0.35)	(–0.01–1.22)	(–0.05–0.18)
Repro. succ.	—	—	—	—	—
<i>Eumeces skiltonianus</i>					
Hatchling	(–0.05–0.62)	(–0.12–0.82)	(–0.06–0.53)	0	0
Juvenile	(–0.01–0.57)	(–0.47–1.16)	(–0.12–0.35)	(–0.19–0.55)	0
Adult	(–0.03–0.28)	(–0.47–1.16)	(–0.06–0.53)	0	(–0.08–0.28)
Repro. succ.	—	—	—	—	—
1998					
<i>N</i> =	20	8	15	10	17
<i>Sceloporus graciosus</i>					
Hatchling	(0.16–0.53)	(0.36–1.50)	(0.04–0.38)	(–0.06–0.56)	(0.01–0.24)
Juvenile	(0.95–1.56)	(1.04–1.96)	(0.37–0.93)	(0.31–1.42)	(0.45–1.04)
Adult	(0.96–1.39)	(0.73–1.56)	(0.37–0.97)	(0.56–1.59)	(0.35–0.84)
Repro. succ.	(0.10–0.53)	(0.25–1.36)	(0.03–0.28)	(–0.04–0.28)	(0.00–0.23)
<i>Eumeces skiltonianus</i>					
Hatchling	(0.03–0.33)	(0.10–0.70)	(0.08–0.39)	(0.08–0.64)	(0.00–0.29)
Juvenile	(0.26–0.65)	(–0.12–0.40)	(–0.04–0.13)	(–0.06–0.20)	(–0.03–0.11)
Adult	(0.17–0.56)	(–0.06–0.51)	(0.04–0.33)	(–0.03–0.31)	(–0.06–0.22)
Repro. succ.	(0.03–0.43)	(0.13–1.00)	(0.11–0.57)	(0.07–0.85)	(0.01–0.44)
1999					
<i>N</i> =	13	8	12	8	15
<i>Sceloporus graciosus</i>					
Hatchling	(0.09–0.44)	(0.55–1.07)	(–0.05–0.16)	(0.01–0.61)	0
Juvenile	(0.79–1.52)	(1.02–1.91)	(0.20–0.75)	(0.14–1.32)	(0.21–0.78)
Adult	(0.45–0.97)	(0.41–1.38)	(0.25–0.83)	(1.00–1.51)	(0.07–0.54)
Repro. succ.	(0.08–0.52)	(0.46–1.17)	(–0.06–0.20)	(–0.01–0.41)	0
<i>Eumeces skiltonianus</i>					
Hatchling	(0.01–0.31)	(–0.04–0.39)	(–0.05–0.16)	(–0.08–0.25)	(0.08–0.39)
Juvenile	(0.01–0.31)	(–0.04–0.39)	0	0	0
Adult	(0.05–0.44)	(–0.08–0.25)	(–0.05–0.16)	(–0.08–0.25)	0
Repro. succ.	(0.02–0.49)	(–0.07–0.62)	(–0.07–0.27)	(–0.08–0.25)	(0.12–0.61)

<sup>1</sup> Log-transformed.

<sup>2</sup> Number of hatchlings:adult female.