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Relationships Between Green Anoles (*Anolis carolinensis*) and Shrub-level Vegetation in Fire-maintained Longleaf Pine (*Pinus palustris*) Forests of Eastern Texas

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Abstract - We examined habitat use by *Anolis carolinensis* (Green Anole) at perch heights ≤5 m, particularly in relation to woody shrub-level vegetation, in fire-maintained *Pinus palustris* (Longleaf Pine) forest stands on the Angelina National Forest in eastern Texas. We surveyed Green Anoles in 2 stands, within 20 established plots per stand with varying shrub densities, during June (breeding season) and August (post-breeding season) for 3 years. An unforeseen prescribed fire in 1 stand provided an opportunity to examine the effects of fire on anoles and their habitat. Only adults were found during June. Adult detections decreased substantially, and juveniles predominated during August. The number of Green Anole detections was positively correlated with the number and volume (m^3) of shrub-level plants. Also, anoles selected shrub-level plants with greater than average width, height, and volume. Larger shrubs provide more display perches and escape routes as well as greater protective cover from predators, and perhaps greater availability of arthropod prey.

Introduction

Anolis carolinensis Voigt (Green Anole) is the only member of its genus native to the United States, and is found from North Carolina, south through Florida, and west to southeastern Oklahoma and central Texas (Conant and Collins 1998). The Green Anole is most closely related to *Anolis porcatus* Gray (Cuban Green Anole) of western Cuba (Glor et al. 2005, Nicholson et al. 2012). Direct overseas dispersal by an ancestral species from Cuba to the continental United States, possibly during the late Miocene–Pliocene, and subsequent speciation produced the Green Anole of the southeastern United States (Glor et al. 2005).

Anolis species, primarily those of the Greater Antilles, preferring similar microhabitats and possessing similar morphological and behavioral attributes, have been assigned to one of several ecomorph classes based on their habitat niche (Losos 2009; Williams 1972, 1983). Like its close Cuban relative, the Green Anole is a member of a clade of "trunk-crown" ecomorphs belonging to the *carolinensis* subgroup (Losos 2009, Poe 2004, Williams 1983). Williams (1983) states that these ecomorph categories can be strictly applied only to the anole communities of the Greater Antilles. However, ecomorphological radiation has been demonstrated for mainland *Anolis* as well (Irschick et al. 1997, Velasco and Herrel 2007). The Green Anole of the southeastern United States evolved in the absence of congeneric

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competition, resulting in ecological release, which allowed the Green Anole to broaden its habitat use and occupy a variety of microhabitats from terrestrial levels to the upper canopy (Campbell 2000, Irschick et al. 2005, Jenssen and Nunez 1998, Jenssen et al. 1995, Losos 2009). Thus, while retaining many of the trunk-crown ecomorph attributes of its Cuban ancestor, the Green Anole of the southeastern United States has been described as a habitat generalist using a wide variety of perch substrata and diameters (Jenssen et al. 1995, 1998).

Our interest in the habitat preferences of the Green Anole arose from our studies involving *Falco sparverius* L. (American Kestrel) foraging and nestling provisioning. These studies show Green Anoles to be the most common prey item delivered to American Kestrel nestlings (R.R. Schaefer, unpubl. data). Green Anoles are abundant in the open, fire-maintained *Pinus palustris* P. Mill. (Longleaf Pine) forests inhabited by breeding kestrels in the West Gulf Coastal Plain.

Extensive wild fires in the southeastern United States are now rare and have been replaced by well-controlled prescribed fires. Woody shrub-level and herbaceous ground vegetation are much more susceptible to fire than mid-story and canopy trees. Herbaceous ground vegetation typically recovers during the growing season following a fire, but woody shrub-level vegetation may take 2 or more years to attain pre-fire densities. The temporary loss of the woody shrub layer is the most drastic vegetative change immediately following a prescribed fire in regularly burned Longleaf Pine forests. For this reason, we focused our attention on anole use of woody shrub-level vegetation. The shrub layer provides a refuge for hatchling Green Anoles (Campbell 2000) and likely supports an abundance of prey due to close proximity to the ground and leaf litter where many arthropods originate (Campbell 2000, Collins et al. 2002, Hanula and Franzreb 1998). Green Anole response to fire and the temporary loss of shrub-level vegetation is unknown.

Our objective was to determine habitat preferences of Green Anoles in the lower vegetative strata (≤5 m) in fire-maintained Longleaf Pine forests of eastern Texas. Specifically, we wanted to examine relationships between woody shrub-level vegetation and Green Anoles. Therefore, with the notable exception of shrub density, the general vegetative structure of our research plots was similar within each of our 2 study stands. Although the application of fire was not part of the study design, an unforeseen prescribed fire in one of our stands provided the opportunity to examine the effects of fire on anoles and their habitat.

Field-Site Description

Study areas were located in open, mature pine forest with a canopy dominated by fire-dependent Longleaf Pine on the Angelina National Forest in eastern Texas. Other canopy species, present in much smaller numbers, included *P. echinata* P. Mill. (Shortleaf Pine), *P. elliottii* Engelm. (Slash Pine), *P. taeda* L. (Loblolly Pine), and *Quercus falcata* Michx. (Southern Red Oak). Overall, Longleaf Pine was also the dominant mid-story species within our plots. Certain hardwood species such as *Liquidambar styraciflua* L. (Sweetgum) and *Ilex vomitoria* Ait. (Yaupon) were prevalent mid-story species in some plots. Numerically, some of the more common shrub species were *Sassafras albidum* (Nutt.) Nees (Sassafras), Sweetgum, *Morella cerifera* (L.) Small (Wax Myrtle), and *Rhus copallina* L. (Shining Sumac).

We randomly chose 2 stands (333 Road and Boykin) and 20 plots within each stand for a total of 40 plots. Each plot measured 5 m x 20 m and was separated from the nearest plot by at least 50 m. Based on other studies, this distance of separation suggests that overlap in home ranges of anoles in neighboring plots was unlikely (Jenssen and Nunez 1998, Nunez et al. 1997).

During the second year of the study (2006), one stand (333 Road, n = 20 plots) was prescribe burned by national forest personnel in an effort to diminish wildfire threats through fuel reduction, and to maintain the open character of Longleaf Pine forests favored by the endangered *Picoides borealis* Vieillot (Red-cockaded Woodpecker).

Methods

Habitat surveys

We conducted a complete census of all shrub, mid-story, and canopy plants within each plot once during the growing season (June–August) of each year. We categorized woody vegetation based on height: ground cover (<0.5 m), shrub (≥0.5 m and <3 m), mid-story (≥3 m and below the canopy), and canopy. We measured the height (m) and width (m) of each live, woody shrub-level plant (shrubs and vines) and calculated volume (height x width^2). We used a clinometer to measure the height (m) of the canopy, calipers to obtain diameter at breast height (cm) for all mid-story and canopy stems, and a spherical densiometer to determine canopy closure (%). At the center point of each plot, we estimated percent ground cover of woody vegetation, herbaceous vegetation (combined grasses, forbs, and ferns), and bare ground/leaf litter within a 1-m^2 subplot; and used a one-factor (1.0 m^2/ha) prism to measure basal area of pine canopy, hardwood canopy, pine mid-story, and hardwood mid-story.

Green Anole surveys

We conducted Green Anole surveys during 4–17 June and 10–24 August of 2005, 2006, and 2007. These June and August dates overlap a portion of the Green Anole breeding season and post-breeding season, respectively (Jenssen et al. 1995). We recorded temperature (°C) and cloud cover (%) at the first, middle, and last plots within each stand during surveys. All surveys were conducted within a shaded temperature range of 26.5–38.0 °C and a cloud cover range of 0–100%.

Anole surveys were intended to be complete counts of all exposed anoles present on plots. Surveys were done by 2 people jointly and coincidently. The same 2 observers surveyed each plot 4 times per month (June and August) annually by simultaneously walking the length of the plot. We reversed the stand and plot order at each visit to vary the daily time and temperature at each plot surveyed. June and August surveys began no earlier than 1153 CDT and 1039 CDT and ended no later than 1633 CDT and 1555 CDT, respectively. Search time at each plot was dependent on vegetation density. Observers thoroughly searched all possible perch sites

≤5 m above ground. The upper portions of canopy and tall mid-story trees (>5 m above ground) were not included in the searches since the observers could not adequately locate anoles above that height. For each Green Anole observation, we recorded perch height (m) where first sighted, perch substrate (live shrub, canopy pine bole, etc.), perch-site plant species, and a visual estimate of age based on body size (1 = adult, 2 = adult/juvenile, 3 = juvenile). Approximate snout–vent length (svl) measures for each body size category are >50 mm for adults, 40–50 mm for adult/juvenile, and <40 mm for juveniles (Irschick et al. 2005, Lovern 2000). Both observers had previous experience measuring anole svl and felt confident in visually assigning individuals to these svl categories. Anoles assigned to size category 2 were either large juveniles or small adults, and accounted for only 1.0% ($n = 1$) and 2.7% ($n = 6$) of total anole detections during June and August, respectively. We eliminated them from all analyses since we were unsure of their age. Few adults were detected during August ($n = 27$ detections for the 3 years combined) and were eliminated from analyses due to small sample size with the exception of adult and juvenile perch-height comparisons. We envisioned that in many cases individual anoles would need to be captured to properly determine sex. Since plots would be surveyed multiple times per month each year, and because sex determination was not critical for this study, we chose not to determine sex in an effort to minimize disturbance to anoles, which could possibly decrease detectability during subsequent surveys. We used a 1-m pole marked with 0.1-m increments to measure the width (m) and height (m) of all live shrub-level plants on which Green Anoles were observed, and subsequently calculated the volume (height x width^2) of each plant.

Data analyses

We calculated habitat variables by plot and year: shrub volume (total and by species), shrub numbers (total and by species), canopy height, total number of canopy trees, total number of mid-story trees, percent canopy closure, percent ground cover (woody vegetation, herbaceous vegetation, and bare ground/leaf litter), and basal area of pine canopy, hardwood canopy, pine mid-story, and hardwood mid-story. We used a repeated measures analysis of variance to test each habitat variable for differences between years and stands. Because all plots on 1 stand were burned in 2006, the effects of stand and fire were confounded in 2006. We tested for fire effects using the interaction between stand and year.

Within each stand, season, and year, we determined the maximum number of anoles detected at each plot among the 4 surveys. We assumed the maximum number of anoles detected at each plot during any 1 survey represented the minimum number of anoles present on that plot. This maximum number of detections was used in calculating the mean number of anoles per plot for each stand.

We used Spearman correlation coefficients to determine relationships between the number of shrub-level plants and anole detections in each stand, with the plant and anole numbers averaged across years on each plot. We used Wilcoxon rank-sum tests to compare the width, height, and volume of woody shrub-level plants available to anoles and those used by anoles within each stand, season, and year. For these tests, we used the subset of plots where anoles were detected.

Although anole surveys were intended to be complete counts, the number of detections varied within years among surveys for individual plots. Therefore, we used *N*-mixture models to estimate abundance on each plot, incorporating estimates of detectability from replicated counts (Royle 2004). We used all 40 plots to create the models. Although we were not directly interested in determining anole abundance, these models allowed us to evaluate the relationships among environmental variables and estimates of anole abundance (Royle 2004). We analyzed data by year and separated June and August. All anole detections during June pertain to adults, and all August detections pertain to juveniles. We standardized all continuous habitat and weather variables to unit variance.

We considered temperature and cloud cover to be survey-specific factors influencing anole movements, which would affect the probability of being seen by the observers. We created models using the Royle option for repeated count data in program PRESENCE 5.7 (Hines 2006) for each season and year, evaluating the effects of all combinations of temperature and cloud cover on detection rate. We used the detection variables in the model with the lowest Akaike's information criterion for small sample sizes (AIC_c; Burnham and Anderson 2002) in models estimating abundance. Habitat variables that differed between stands or among years, or reflected use by anoles (width, height, and volume of shrubs, both total and by species) were included as site-specific covariates. We included stand and the confounding effects of the 2006 fire as a categorical variable (stand: 333 Road = 1, Boykin = 0). The abundance models and a null model (constant detection and abundance) were compared utilizing ΔAIC_c (Burnham and Anderson 2002, MacKenzie et al. 2006). We considered models within 2 units of AIC_c to provide information on the relationship between the covariates and anole abundance. To further evaluate the models, we constructed 95% confidence intervals around the beta estimates for the covariates. If the confidence intervals included zero, indicating the covariate was not significantly associated with abundance, we discarded the model.

Results

Habitat characteristics

Canopy height, pine canopy basal area, and pine mid-story basal area were similar between 333 Road and Boykin (Table 1). Hardwood canopy trees were rare in both stands. Hardwood mid-story trees were more prevalent at 333 Road. Canopy closure, number of canopy and mid-story trees, number of shrub-level plants, and percent of bare ground/leaf litter were greater at 333 Road. Percent of herbaceous ground cover was greater at Boykin. However, a significant interaction between stand and year suggested that fire affected the volume of shrub-level plants and percent of woody ground cover.

Within each stand, mean volume of shrub-level plants/plot varied across years (Boykin: $P = 0.002$; 333 Road: $P = 0.009$). At Boykin, the volume increase from 2005 (9.8 m^3, SE = 1.8) to 2006 (16.3 m^3, SE = 3.1) was not statistically significant ($P = 0.092$), but volume subsequently declined ($P = 0.002$) sharply by 2007 (5.2 m^3, SE = 0.9). In contrast, at 333 Road (burned in March 2006), mean shrub volume/

plot declined significantly ($P = 0.011$) from 2005 (70.4 m^3, SE = 13.3) to 2006 (26.8 m^3, SE = 4.4), and recovered by 2007 (63.2 m^3, SE = 10.9).

Green Anole surveys

Ninety-seven adult Green Anoles were detected during June (breeding season) surveys over the 3-year study. During August (post-breeding season) surveys, juveniles (n = 186) predominated and few adults (n = 27) were detected. Mean maximum anole detections per plot were greater at 333 Road than at Boykin during June 2005 and 2007, and August 2007; and were similar during June 2006, and August 2005 and 2006 (Fig. 1). Survey plots at 333 Road (n = 20) were prescribe-burned on 1 March 2006. Mean maximum adult detections during June dropped at 333 Road from 2005 (9 months pre-fire) to 2006 (3 months post-fire), and then increased in 2007. Juvenile detections at 333 Road during August showed a similar pattern. Detection declines for both June adults and August juveniles were noted at the 20 unburned plots at Boykin from 2005 to 2006, and further declined in 2007.

Habitat use

Perch substrata and heights. Green Anoles were observed on shrub-level plants ("live shrub" or "re-sprouting shrub") more often than any other perch substrate during June and August of each year, at both 333 Road and Boykin (Figs. 2, 3). For the combined 3 years, 76.5% of adult (June) anole detections at 333 Road, and 55.2% at Boykin, were on shrub-level plants. Mid-story hardwoods (7.4%) and pine canopy

Table 1. Comparison of habitat variables measured at *Anolis carolinensis* (Green Anole) survey plots, in 2 *Pinus palustris* (Longleaf Pine) forest stands (333 Road and Boykin) in eastern Texas (n = 3 years, average of 20 plots/stand/year). Int. = interaction of stand and year.

	333 Road[A]		Boykin		P[B]		
Habitat Variable	Mean	SE	Mean	SE	Stand	Year	Int.
Canopy height (m)	26.37	0.00	26.49	0.00	0.8404	1.0000	1.0000
Pine canopy basal area (m^2/ha)	22.94	0.21	20.81	0.23	0.0711	0.9995	0.8675
Pine mid-story basal area (m^2/ha)[C]	1.52	0.18	1.28	0.03	0.3743	0.7115	0.5554
Hardwood canopy basal area (m^2/ha)	0.46	0.11	0.02	0.02	<0.0001	0.2419	0.4641
Hardwood mid-story basal area (m^2/ha)	1.23	0.13	0.28	0.02	<0.0001	0.6874	0.8029
Canopy closure (%)	77.81	0.19	68.65	0.33	<0.0001	0.8277	0.9863
Number of canopy trees/plot	1.97	0.02	1.40	0.00	0.0255	0.9956	0.9956
Number of mid-story trees/plot	2.33	0.35	0.52	0.02	<0.0001	0.2089	0.2664
Number of shrub-level plants/plot[D]	82.53	6.73	15.13	1.53	<0.0001	0.7200	0.4512
Bare ground/leaf litter (%)	50.45	6.58	35.15	5.41	<0.0001	<0.0001	0.1592
Herbaceous ground cover (%)	20.23	4.21	52.75	5.28	<0.0001	<0.0001	0.8658
Woody ground cover (%)[E]	29.33	2.99	12.10	1.88	<0.0001	0.5649	0.0194
Volume of shrub-level plants (m^3)	53.47	13.49	10.45	3.21	<0.0001	0.0414	0.0011

[A]Prescribe burned on 1 March 2006.
[B]Repeated measures analysis of variance, with stand and year as the effects.
[C]Mid-story = vegetation ≥3.0 m in height and below canopy.
[D]Shrub = woody vegetation ≥0.5 m and <3.0 m in height (including vines)..
[E]Ground = vegetation <0.5 m in height.

boles (24.1%) followed shrub-level plants as the most commonly used perch substrata by adults during June at 333 Road and Boykin, respectively. Large males were typically found at such sites. Juvenile (August) anoles were observed on shrub-level plants 89.6% and 78.8% of the time at 333 Road and Boykin, respectively. Mid-story hardwoods (5.2%) and grass (11.3%) followed shrub-level plants as the most commonly used perch substrata by juveniles during August at 333 Road and Boykin, respectively. Only juveniles were found on grass and herbaceous dicots, with all observations occurring in 2005 when overall anole numbers were greatest. We do not know the frequency of anole use of upper canopy tree boles (>5 m above ground) and canopy crowns since we limited our observations to heights ≤5 m.

Adult anole perch height averaged 0.88 m (SE = 0.06, n = 97) in June and 1.14 m (SE = 0.15, n = 27) in August (P = 0.054). This difference may well have been

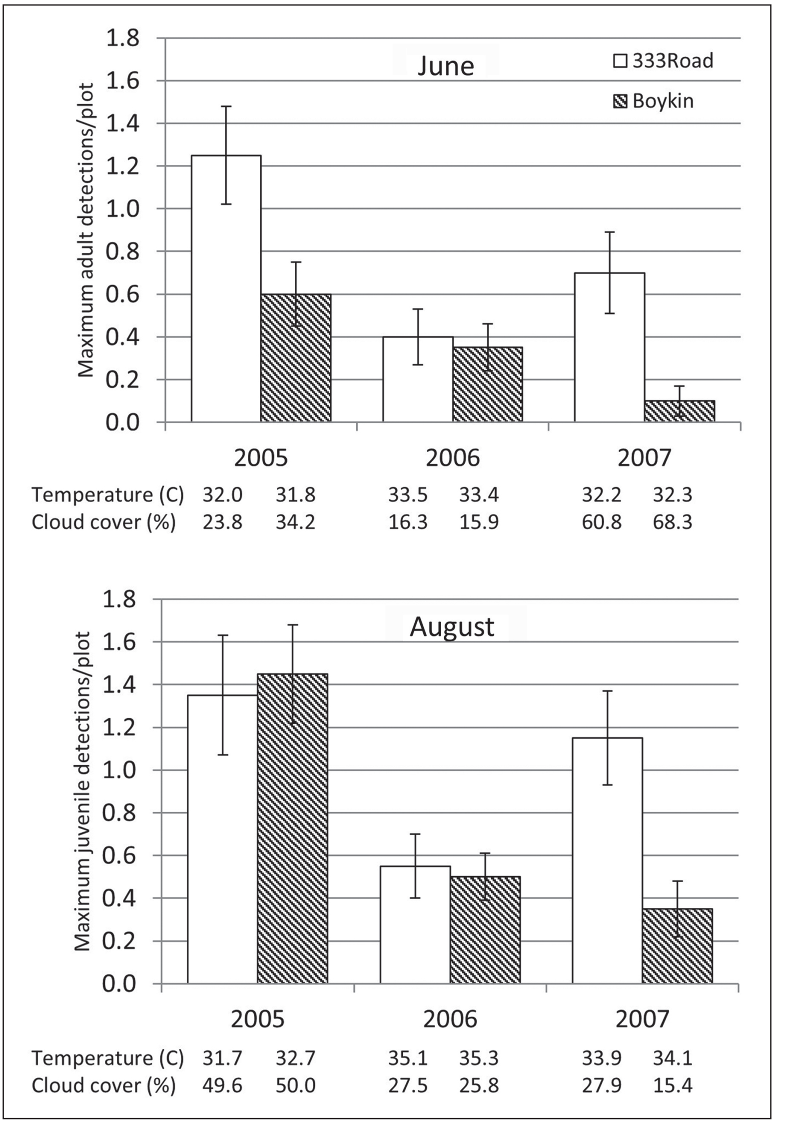

Figure 1. Mean maximum *Anolis carolinensis* (Green Anole) detections per plot at 333 Road (n = 20) and Boykin (n = 20) stands during June (adults only) and August (juveniles only), in open *Pinus palustris* (Longleaf Pine) forest in eastern Texas. A prescribed fire burned all plots at 333 Road on 1 March 2006, three months prior to the start of June surveys for that year. Mean temperature and and cloud cover is given for each stand and year during June and August.

greater had we been able to survey upper portions of canopy trees. During August, adult perch height was significantly greater (Z = 3.35, P = 0.001) than juvenile perch height (mean = 0.71 m, SE = 0.03, n = 186).

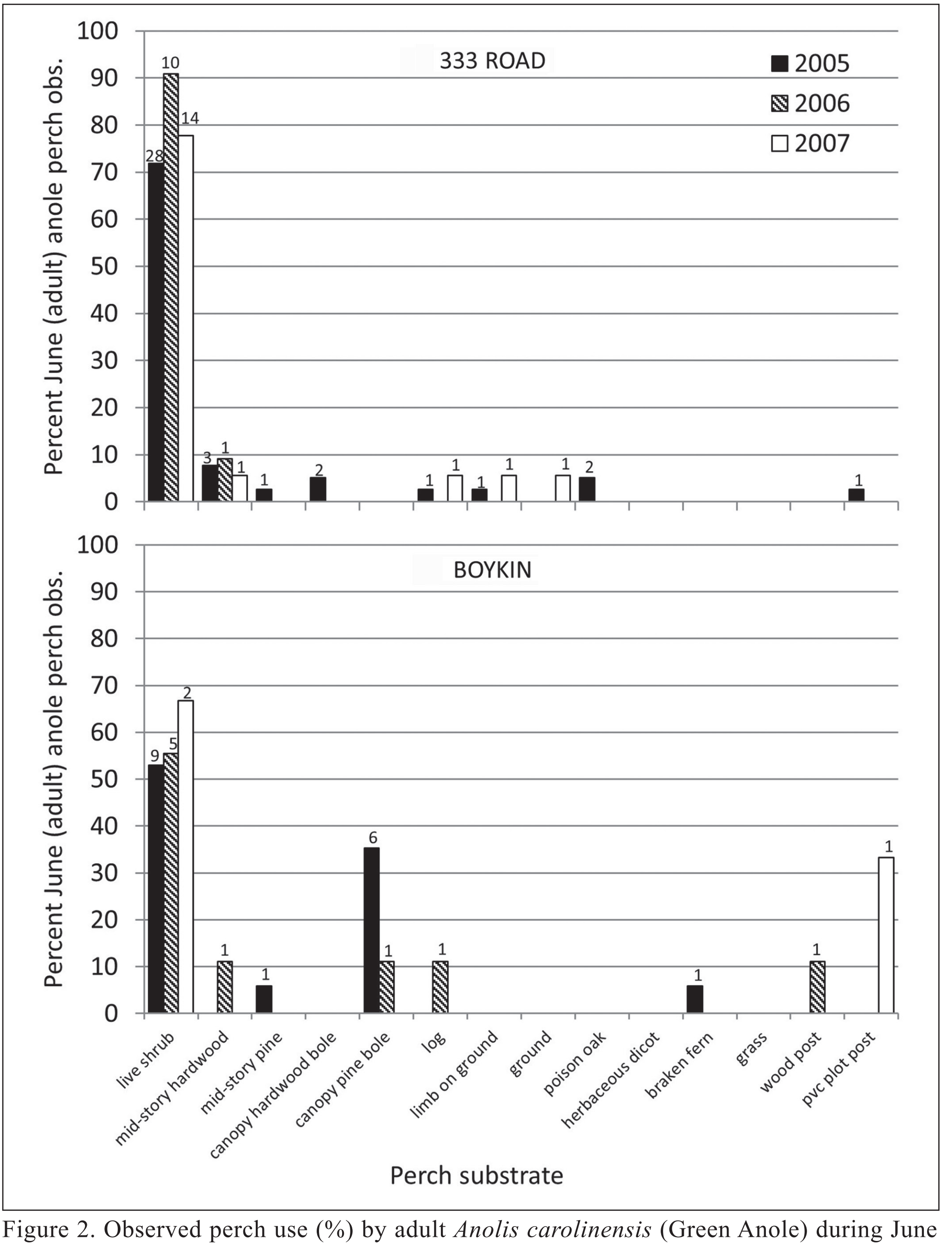

Figure 2. Observed perch use (%) by adult *Anolis carolinensis* (Green Anole) during June (breeding season) of 2005, 2006, and 2007 in 2 stands (333 Road, Boykin) of open *Pinus palustris* (Longleaf Pine) forest in eastern Texas. The number of anole observations on each perch substrate is shown at the top of the bars.

Shrub-level vegetation use. A total of 44 and 24 species of woody shrub-level plants were found on the 20 survey plots at 333 Road and Boykin, respectively. Adult anoles were observed on 13 species at 333 Road and 7 species at Boykin

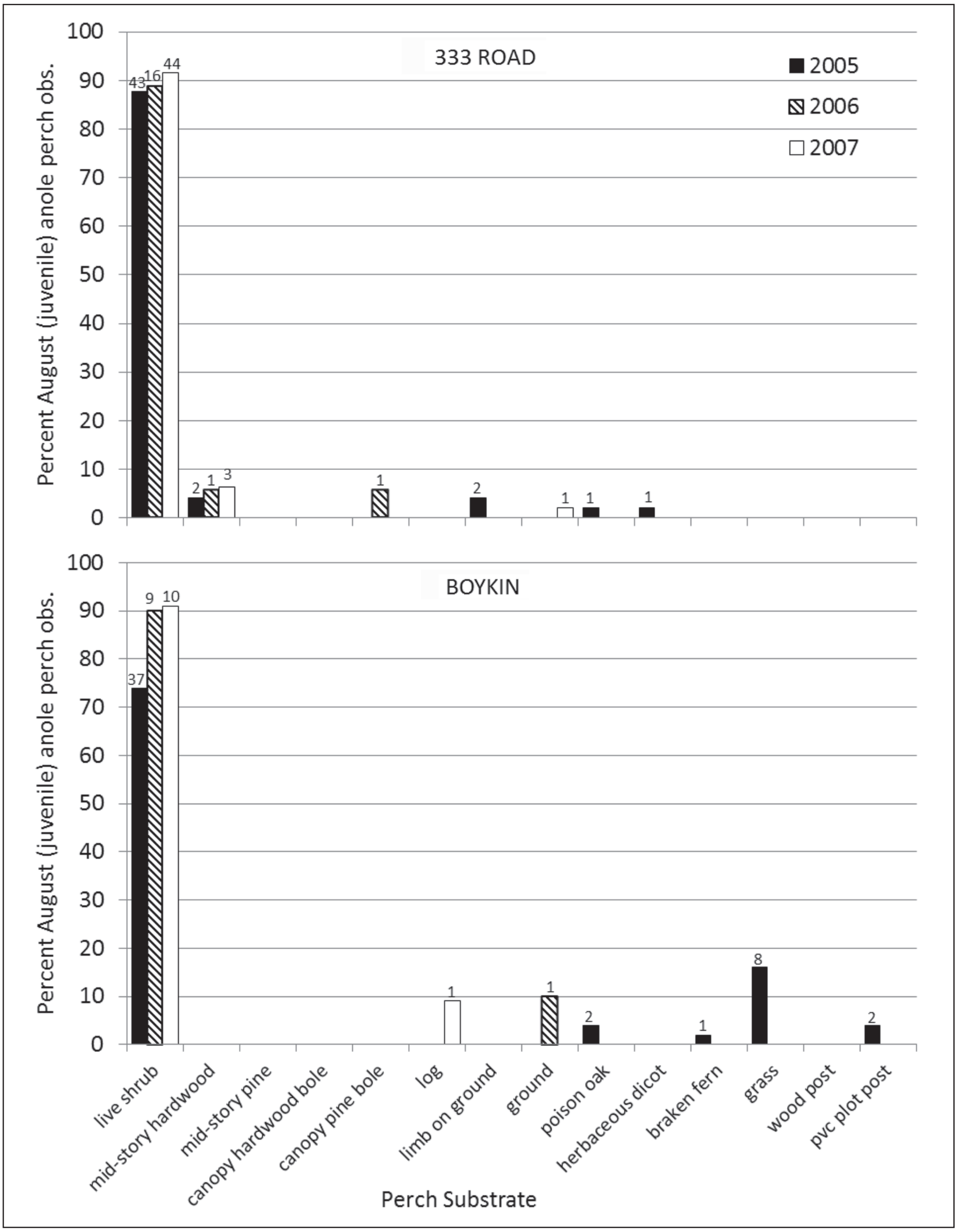

Figure 3. Observed perch use (%) by juvenile *Anolis carolinensis* (Green Anole) during August (post-breeding season) of 2005, 2006, and 2007 in 2 stands (333 Road, Boykin) of open *Pinus palustris* (Longleaf Pine) forest in eastern Texas. The number of anole observations on each perch substrate is shown at the top of the bars.

during June surveys (Figs. 4, 5). Juveniles were observed on 18 species at 333 Road and 13 species at Boykin during August surveys. Within all 40 plots, anoles were not observed on 19 (June) and 19 (August) "other species" of negligible occurrence (mean shrub volume per plot for each species was ≤1%).

Adult anole detections during June were positively correlated with the number of shrub-level plants only at 333 Road (n = 20, r = 0.70, P = 0.001; Boykin: n = 20, r = 0.14, P = 0.550). Similarly, adult detections were positively correlated with the volume of shrub-level plants only at 333 Road (n = 20, r = 0.80, P < 0.001; Boykin: n = 20, r = 0.39, P = 0.089). Juvenile anole detections during August were positively correlated with both the number (333 Road: n = 20, r = 0.59, P = 0.006; Boykin: n = 20, r = 0.54, P = 0.014) and volume (333 Road: n = 20, r = 0.47, P = 0.037; Boykin: n = 20, r = 0.82, P < 0.001) of shrub-level plants at both sites.

Woody shrub-level plants harboring Green Anoles were generally wider, taller, and greater in volume than all available plants at both 333 Road and Boykin, during June and August of each year (Fig. 6). Sample size for each stand, the number of plots where anoles were observed on shrub-level plants, may have been too small during some years to allow the detection of significant differences in shrub dimensions between available and used shrub-level plants. For example, adult anoles were found on shrub-level plants at 11 plots at 333 Road and 6 plots at Boykin

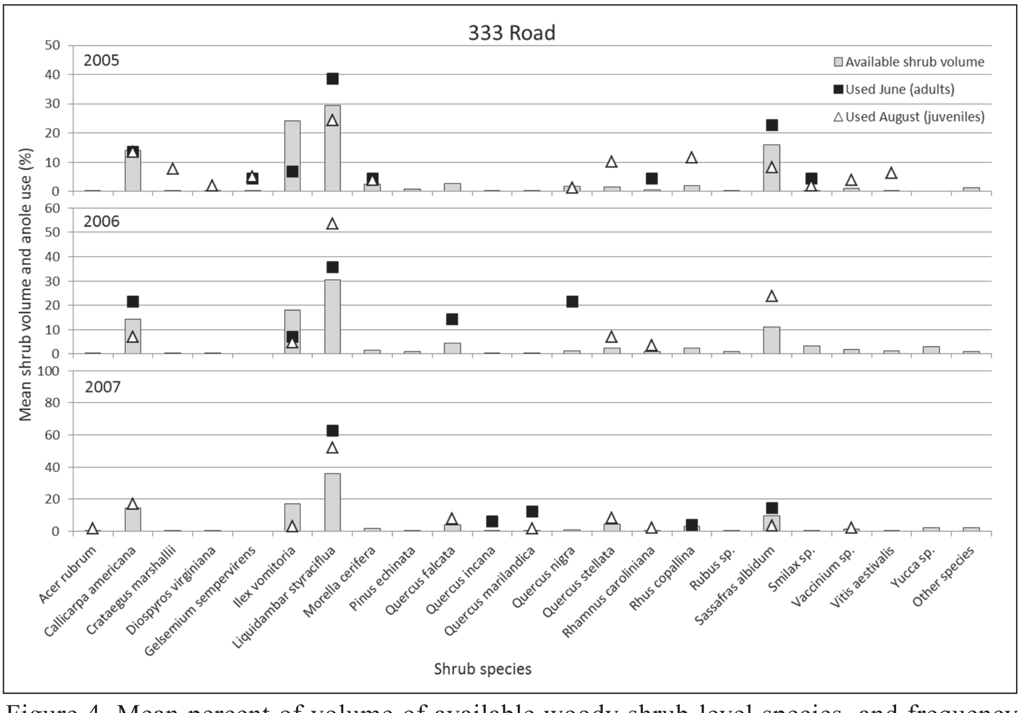

Figure 4. Mean percent of volume of available woody shrub-level species, and frequency of use by *Anolis carolinensis* (Green Anole) during June (adults) and August (juveniles) 2005–2007, at 20 anole survey plots in a stand (333 Road) of open *Pinus palustris* (Longleaf Pine) forest in eastern Texas. "Other" includes species comprising ≤1% of shrub volume and on which anoles were not detected.

during June of 2005. Width, height, and volume of shrubs used by anoles were significantly greater than for all available shrubs only at 333 Road. During August of 2005, juvenile anoles were observed on shrub-level plants at 13 plots at both 333 Road and Boykin. Width, height, and volume of shrubs used by anoles were significantly greater than for all available shrubs at both sites.

Detectability and abundance

In June 2007, anoles were detected at only 12 of 40 plots, and only 3 of the 12 plots had detections in more than 1 of the 4 surveys. Thus, there were too few anole detections to model detectability and abundance during June 2007. There were too few detections of adult anoles in August in any year, so only juveniles were included in August analyses.

Green Anole detectability models including cloud cover and temperature had the lowest AIC_c values in June 2006 and August 2005, but the standard errors of the covariate estimates were high resulting in 95% confidence intervals that spanned zero. Therefore, we discarded these models. For all seasons and years, the constant detectability models had the lowest AIC_c.

Detectability was very low in June 2005 and 2006, and improved in August (Table 2). Cloud cover and temperature were not taken as precisely as they could have been. Had these variables been measured on each plot, they might have improved estimates of detectability.

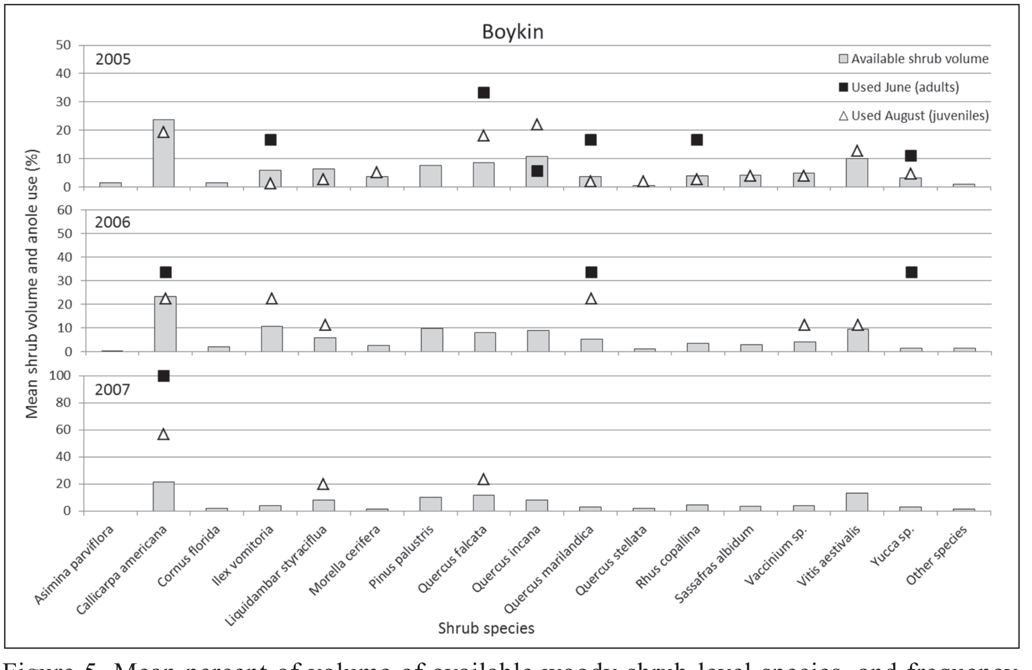

Figure 5. Mean percent of volume of available woody shrub-level species, and frequency of use by *Anolis carolinensis* (Green Anole) during June (adults) and August (juveniles) 2005–2007, at 20 anole survey plots in a stand (Boykin) of open *Pinus palustris* (Longleaf Pine) forest in eastern Texas. "Other" includes species comprising ≤1% of shrub volume and on which anoles were not detected.

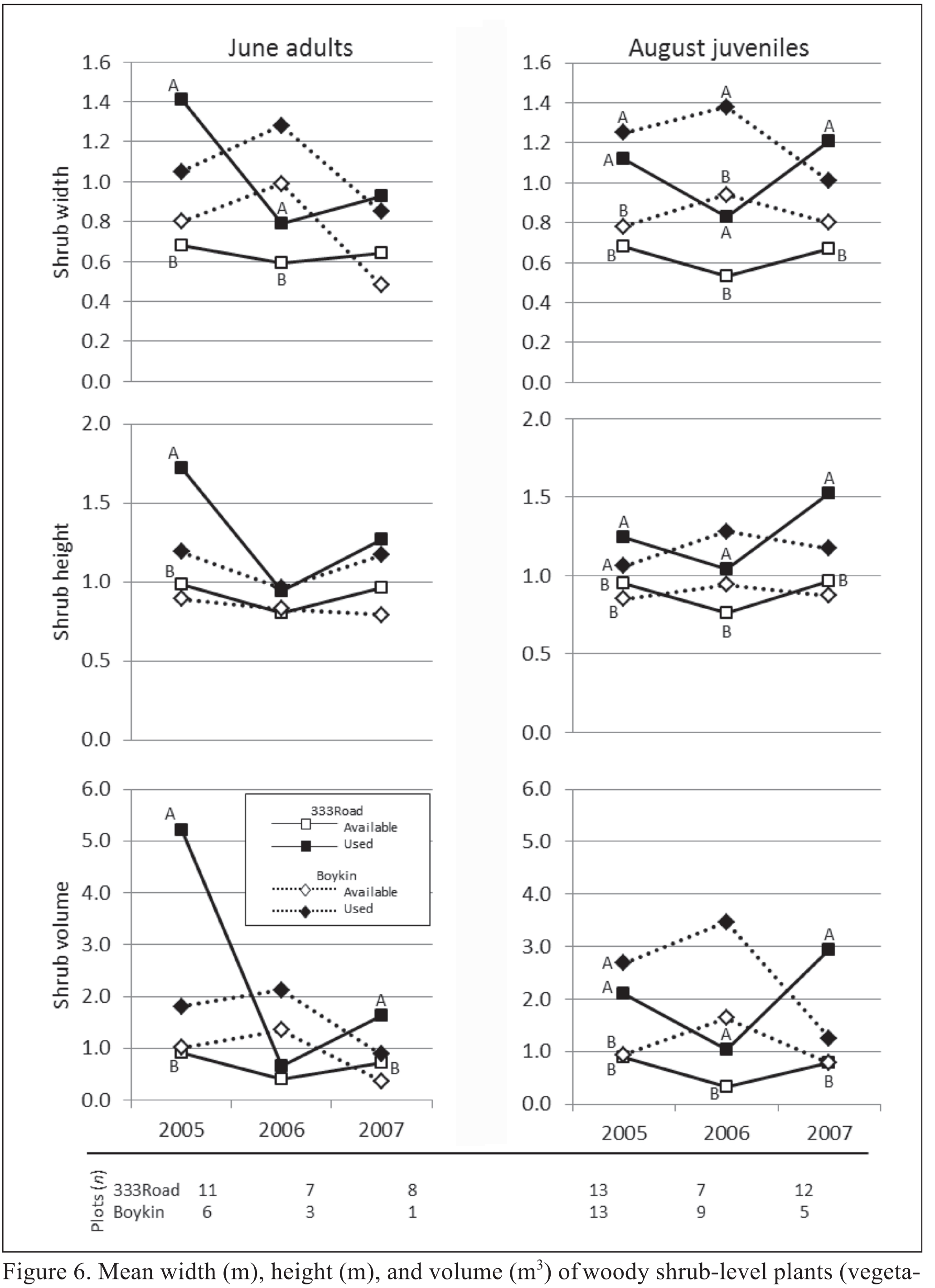

Figure 6. Mean width (m), height (m), and volume (m^3) of woody shrub-level plants (vegetation ≥0.5 m and <3.0 m in height, including vines) available to and used by *Anolis carolinensis* (Green Anole) during June (adults only) and August (juveniles only) in open *Pinus palustris* (Longleaf Pine) forest in eastern Texas. Different letters within stands indicate statistical significance (P <0.05) between available and used means (Wilcoxon rank-sum tests).

We investigated shrub width, height, number, and volume as covariates for abundance. Volume and percent volume of Sweetgum, Sassafras, Southern Red Oak, and American Beautyberry were used as covariates as well because these species were used most frequently (Figs. 4, 5).

Abundance estimates also lacked precision. A 95% confidence interval around the beta estimate for lambda (abundance) did not include zero only in August 2005. However, our objective was not to quantify abundance, but to determine which habitat variables influenced anole numbers. For this reason, we did not average models within 2 units of AIC_c.

Shrub volume was an important positive correlate with anole abundance in June 2005 (Table 2). Interestingly, volume of Sweetgum was positively associated with anole abundance in June 2006. Sweetgum was the most common shrub (14% of shrub numbers) and comprised 18% of shrub-level volume and 27% of anole shrub-level perches. Volume of Southern Red Oak was positively associated with anole abundance in August 2005. Number of shrubs was positively associated with anole abundance in June 2005 and August 2006. In June 2007, the most important correlate with juvenile anole abundance was stand; 333 Road averaged three times as many detections as Boykin (Fig. 1).

Discussion

Recurring fire restricts the growth of woody shrub and mid-story vegetation of non-Longleaf Pine species (Platt et al. 1988, Provencher et al. 2001). In the absence of naturally occurring fire, prescribed fire is commonly used by forest managers

Table 2. *N*-mixture models relating habitat variables to detectability and abundance of *Anolis carolinensis* (Green Anole) in open *Pinus palustris* (Longleaf Pine) forest in eastern Texas during June (adults) and August (juveniles) 2005, 2006, and 2007. Models within 2 units of the lowest AIC_c are presented.

Month/	Detectability[A]			Beta estimates[B]					
Year	Estimate	SE	Model	AIC_c	ΔAIC_c	λ	SE	covariate	SE
June – Adults[C]									
2005	0.11	0.07	Shrubs (volume)	239.59	0.00	1.54	1.07	0.45	0.10
			Shrubs (number)	239.97	0.38	1.60	1.17	0.46	0.10
2006	0.09	0.09	*Liquidambar styraciflua* (volume)	125.40		0.86	1.57	0.42	0.17
August – Juveniles									
2005	0.17	0.07	*Quercus falcata* (volume)	341.18		1.38	0.44	0.25	0.09
2006	0.07	0.07	Shrubs (number)	152.49		3.69	2.35	0.51	0.15
2007	0.36	0.07	Stand	224.61		-0.75	0.41	1.39	0.43

[A]No survey-specific covariates significantly affected detectability; within month and year, detectability was held constant across surveys and plots.
[B]Beta estimates of coefficients from *N*-mixture models (Royle 2004) are in terms of logs and relate to standardized covariate values. Number of parameters estimated is 3 for each model.
[C]There were too few detections in June 2007 to model.

to reduce fuel loads and maintain healthy pine-savanna ecosystems. Canopy trees were not affected by the prescribed fire occurring in 20 of our plots. Most mid-story hardwoods were small in diameter at breast height (dbh) and were killed to ground level by the fire, but immediately re-sprouted during the 2006 growing season. Mid-story pines measured considerably larger in dbh and survived the fire. Most shrubs were killed back to ground level and later re-sprouted into an even-aged shrub layer with dead stems still standing. Plots with less shrub and mid-story vegetation, and less canopy closure, had more sunlight penetrating to ground level, thus allowing for greater herbaceous plant growth (Masters et al. 1996).

The prescribed fire on half of our plots in March 2006 provided an opportunity to observe the effects of fire on Green Anole numbers at our study plots. We expected a drop in anole detections in burned plots, especially during June of 2006 when surveys began just 3 months post-fire. Most shrub-level plants had been killed to ground level by the fire, and relatively little re-sprouting had occurred by the time surveys commenced in early June. In 2006, we did observe a steep decline in anole detections during both June and August. However, declines occurred at both the burned (333 Road) and unburned (Boykin) plots, indicating that the fire was not entirely responsible for the decrease in detections. Anole detections during June of 2007 declined even further at unburned plots, while burned plots showed a modest increase. By August of 2007, when young of the year had emerged, anole detections at burned plots increased to pre-fire (2005) levels, while detections at the unburned plots remained at the low 2006 level. The observed decline in anole detections on both burned and unburned plots suggests that while fire may have been partially responsible for the decline in anole detections at burned plots, other unknown factors must have also played a role. Since we observed an increase in anole detections at burned plots by the second August survey period following the fire, it is possible that fire may benefit anoles. Perhaps fire, while having a short-term negative effect on anole numbers through direct mortality and the immediate reduction of habitat and food resources, has a long-term benefit that is not yet understood.

Green Anole detections among plots were positively correlated with the density and volume of shrub-level plants during both June and August. Only adults were found during June because hatchlings had not yet emerged. During August, the vast majority of anoles found were juveniles, and adult detections were much reduced. Live shrubs, including re-sprouting portions of those killed to ground level by fire, were used by anoles far more often than any other perch substrate surveyed. We do not know how many anoles may have been at heights >5 m because we limited our search to sites ≤5 m above ground. Jenssen and Nunez (1998) found that adult anoles used all available perch heights (0–8 m during May–July) within their study area, though the majority of anoles used perches <5 m.

Although our anole surveys were intended to be complete counts, the number of anoles on each plot varied across replicate surveys. We considered temperature and cloud cover during the surveys to be the variables most likely to affect detectability; however, these variables were not measured at the plot level and did not improve models. Although our anole abundance estimates were not robust, shrub volume or number were important positive correlates in both seasons in 2005 and 2006; shrub volume and number were also correlated with unadjusted estimates of abundance (detections). Interestingly, stand was the most important correlate with juvenile anole abundance in August 2007. Anole detections declined at both stands from 2005 to 2006; detections rebounded in 2007 at 333 Road but not at Boykin. Perhaps the fire in 2006 at 333 Road positively influenced habitat in ways that were not measured in this study, and it is possible that prey abundance was somehow enhanced after the re-emergence of new plant growth at or near ground level.

The number of adult anole observations decreased from 97 detections during June to only 27 during August over the combined 3 years. A similar seasonal decrease in adult numbers was observed by Schaefer et al. (2009) in similar habitat. Did the majority of adults die? Green Anoles are preyed upon by many species (Arndt 1995, Sykes et al. 2007, Yosef and Grubb 1993), but the impact of most predators on anole populations is not well known. The American Kestrel is a major predator of anoles in our region. Green Anoles accounted for 28% of prey items obtained by nesting American Kestrels in open pine forests of eastern Texas and west-central Louisiana (R.R Schaefer, unpubl. data). McMillan and Irschick (2010) found temporal variation in the relative intensity of predatory attacks, most likely from birds, on clay models of male Green Anoles in Louisiana, with predation highest during August–September and March–April (May through July data were unavailable), and lowest during winter months. While predators undoubtedly reduce anoles numbers to some extent, another possible explanation for the reduction in adult detections during August may be a seasonal shift in microhabitat. During the August–September post-breeding season, Jenssen et al. (1995) observed adult male anoles frequenting higher (≥5 m) perch sites more often than they did during May–July of the breeding season. This may partially explain our reduced observations of adult anoles during August. Since we did not search substrata heights >5 m, we may have failed to detect seasonal variation in anole perch height. Adults in our study, males and females combined, tended to occupy higher perches during August (56% of perches at least 1 m) than during June (35% of perches at least 1 m).

Green Anoles were observed on shrub-level plants of greater volume than those generally available in plots. We do not know with certainty why Green Anoles favor shrub-level plants of greater volume, but several possible reasons exist. Larger shrubs may provide more display perches and escape routes. They may harbor more prey, reducing the need to move around as much in search of food. Finally, larger shrubs may provide greater camouflaging cover from predators. Even when discovered, anoles in the interior of larger shrubs may be less accessible and hence more protected from avian predators compared to those in smaller shrubs.

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