Seasonal Shifts in Shelter and Microhabitat Use of *Drymarchon couperi* (Eastern Indigo Snake) in Georgia

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Drymarchon couperi (Eastern Indigo Snake), a threatened species of the southeastern Coastal Plain of the United States, has experienced population declines because of extensive habitat loss and degradation across its range. In Georgia and northern Florida, the species is associated with longleaf pine habitats that support *Gopherus polyphemus* (Gopher Tortoise) populations, the burrows of which *D. couperi* uses for shelter. The extent that *D. couperi* uses these burrows, in addition to the use of other underground shelters and the microhabitat features associated with these structures is largely unknown. From 2003 through 2004, we conducted a radiotelemetry study of *D. couperi* (*n* = 32) to examine use of shelters and microhabitat in Georgia. We used repeated measures regression on a candidate set of models created from *a priori* hypotheses using principal component scores, derived from analysis of microhabitat data to examine microhabitat use at underground shelters. Proportion of locations recorded underground did not differ seasonally or between sexes. In winter, we recorded >0.90 of underground locations at tortoise burrows. Use of these burrows was less pronounced in spring for males. Females used abandoned tortoise burrows more frequently than males year-round and used them on approximately 0.60 of their underground locations during spring. Microhabitat use at underground shelters was most influenced by season compared to sex, site, or body size. Females in spring and summer used more open microhabitat compared to males, potentially in response to gestation. Our results suggest that the availability of suitable underground shelters, especially *G. polyphemus* burrows, may be a limiting factor in the northern range of *D. couperi*, with important implications for its conservation.

T HE spatial pattern of landscape component use by a species may reflect the arrangement of necessary resources such as prey, mates, refuge, and appropriate thermal conditions (Gibbons and Semlitsch, 1987; Macartney et al., 1988). These resources are often spatiotemporally variable, thus affecting spatial patterns of habitat use throughout the year (Gregory et al., 1987). Therefore, measurement of specific use of habitat components and spatial patterns of use over time can be used to understand individual or population level resource requirements, potentially leading to more effective conservation efforts.

Thermally stable, humid shelters are critical habitat components for many wildlife species, often required for hibernation, reproduction, and protection from environmental extremes (Kinlaw, 1999). Accessibility, size, and structure of shelters affect their suitability for different species (Beck and Jennings, 2003), and availability of appropriate shelters may be a limiting resource for some wildlife populations (Huey, 1991). This can be especially true for non-excavator ectotherms, including most snake species, which rely on naturally existing shelters, such as root channels and animal burrows (Pringle et al., 2003; Webb et al., 2004). For example, decline of *Hoplocephalus bungaroides* (Broad-headed Snake) in Australia has been linked to loss of suitable shelters (Shine et al., 1998) and an increase in vegetation density which negatively affected thermal conditions (Pringle et al., 2003). Although many snake species require shelters for survival, the identification and detailed measurement of these resources is often lacking.

Drymarchon couperi (Eastern Indigo Snake), a threatened species of the southeastern Coastal Plain of the United States (United States Fish and Wildlife Service, 1978), has experienced population declines because of extensive habitat loss, fragmentation, and degradation across its range (United States Fish and Wildlife Service, 1998). In Georgia and northern Florida (northern portion of the range), the species is associated primarily with Longleaf Pine (*Pinus palustris*) and Wiregrass (*Aristida stricta*) upland communities, especially during the fall–winter breeding season, and is found in association with *Gopherus polyphemus* (Gopher Tortoise) populations that inhabit these xeric habitats. *Drymarchon couperi* requires shelters for protection from environmental extremes including fire and predation and is a known commensal of *G. polyphemus* where it occurs (Holbrook, 1842; Landers and Speake, 1980; Speake and McGlincy, 1981; Smith, 1987; Speake et al., 1987). *Gopherus polyhemus*, a keystone species (Eisenberg, 1983; Jackson and Milstrey, 1989), is a primary excavator, creating burrows averaging 3–6 m long and 2 m deep (Smith and Green, 2005). Availability of shelters for *D. couperi* varies locally and regionally as habitats and climatic conditions change and, in addition to burrows of *G. polyphemus*, can include woody debris, windrows, stump and root channels, small mammal and armadillo burrows, and hollow logs (Lawler, 1977; Speake et al., 1978; Smith, 1987; Moler, 1992; Stevenson et al., 2003). Although *D. couperi* is known to use burrows of *G. polyphemus* for shelter, details of this use (e.g., seasonality, use of other shelters, and microhabitat features) are not well understood.

To address deficiencies in our understanding of *D. couperi* shelter requirements, we conducted a two-year radiotelemetry study of *D. couperi* to examine, both temporally and spatially, shelter and associated habitat use in the northern portion of its range in southeastern Georgia. Our objectives were to quantify, by season and habitat type, use of underground shelters, types of shelters used, and associated

microhabitat characteristics of aboveground areas immediately surrounding shelters.

MATERIALS AND METHODS

Study sites.—We conducted this study on Fort Stewart Military Reservation and tracts of adjacent private land located in the Coastal Plain of southeastern Georgia. The Fort Stewart site covered approximately 8,000 ha of its total 111,600 ha. Private lands covered approximately 6,000 ha adjacent to and continuous with the Fort Stewart site. Upland habitats at the study sites included extensive sandhills (with Longleaf Pine and Wiregrass) and mixed pine–hardwood forests along the banks of streams. Interspersed with uplands were wetland habitats including blackwater swamps, bottomland hardwood forests, cypress and gum ponds, and impoundments (Stevenson et al., 2003). Neither site contained paved roads, but did have maintained and non-maintained unpaved roads. Paved roads bounded two sides of the private lands site. Both sites supported populations of *G. polyphemus*.

Approximately 17% of the Fort Stewart site and 14% of the private lands site contained *G. polyphemus* burrows (Hyslop, 2007; Hyslop et al., 2009). Areas in the private lands with *G. polyphemus* included approximately 50% sandhills, 11% Sand Pine plantation (*P. clausa*), 21% pine plantations less than ten years old (primarily *P. palustris*), <1% in pine plantations greater than ten years old (primarily *P. taeda*), and 18% actively managed hay fields. All sites supporting *G. polyphemus* on Fort Stewart were managed for wildlife with some timber extraction and no agricultural activities in more than ten years.

Radiotelemetry.—We captured *D. couperi* by hand on sandhill habitats occupied by *G. polyphemus* on Fort Stewart and private lands (Hyslop, 2007). We implanted 20 snakes (7 females, 13 males) with transmitters between December 2002 and April 2003, with 12 additional snakes (6 females, 6 males) added between October 2003 and March 2004. We used 16 g radiotransmitters in the first year (model AI-2T, 15 × 37 mm; Holohil Systems, Ltd., Ontario, Canada) and smaller 9 g transmitters in the second year of telemetry (SI-2T, 11 × 33 mm). Transmitters were surgically implanted in the coelomic cavity (Reinert and Cundall, 1982) by a wildlife veterinarian. We tracked snakes on foot and by vehicle using homing techniques (Mech, 1983) 2–3 times per week from January 2003 through December 2004.

Shelter use.—We classified radiolocations in burrows, root/stump channels, under logs or woody debris, within windrows (debris piles created during timber harvest and site preparation), in burrows of *Dasypus novemcinctus* (Armadillo), or burrows created by mammals other than armadillos as underground. Tortoise burrows used by *D. couperi* were classified as active/inactive or abandoned based on external characteristics, including signs of recent tortoise activity, structural characteristics of the burrow, and amount of litter and vegetation around the burrow opening (Auffenberg and Franz, 1982; McCoy and Mushinsky, 1992; Smith et al., 2005). Snake locations recorded on the surface, under litter, under vegetation, or those in trees, were classified as surface locations. We used repeated measures ANOVA on arcsine-transformed data to examine influence of sex and season (winter: 15 December–14 March; spring:

15 March–14 June; summer: 15 June–14 September; fall: 15 September–14 December) on proportion of locations recorded underground versus surface. At each underground location, we recorded shelter type and surface linear distance from snake location to shelter opening (nearest 0.5 m).

We also recorded general habitat type at shelter locations based on hydrology, land use, management, and vegetation. Habitat categories included sandhill (uplands with Longleaf Pine overstory; tortoise burrows present), clearcut (primarily harvested mesic pine flatwoods with windrows; bedding for Loblolly Pine planting), field (old-field, hay fields, and food plots), plantation (planted pine trees in rows; may or may not contain tortoise burrows), miscellaneous uplands (uplands with pine–hardwood mixed overstory composition; may or may not contain tortoise burrows), and wetlands (isolated upland wetlands and bottomlands; no tortoise burrows). Individual snakes were retained as the sampling unit for shelter and general habitat use analyses.

Microhabitat use.—Microhabitat analysis focused on identification of vegetation and structural conditions immediately surrounding areas of use (North and Reynolds, 1996; Morrison et al., 1998). We collected these data on 3-m diameter circular plots centered on openings to underground shelters associated with individual radiolocations. Microhabitat data included percent vegetated understory cover (<150 cm in height), percent vegetated canopy cover (>150 cm in height), substrate composition, and tree basal area. We used a modified version of the James and Shugart (1970) method for measuring microhabitat vegetation and substrate in forest and shrub habitats (Martin et al., 1997). We used visual estimation (ocular tube) at 20 points within 3-m diameter plots to measure percent vegetation cover to the nearest 5%. Understory cover categories included total vegetation; forbs, grass, sedge, and rush (grass and forbs); and woody shrub, vine, and palmetto (woody vegetation/palm). Substrate composition was measured as percent cover of bare ground, litter, and course woody debris including litter cover. We recorded basal area of the surrounding habitat from the center of each 3-m sampling plot using an angle gauge. We collected microhabitat variables at all underground radiolocations from January 2003 to January 2004 (427 novel locations). From February 2004 to December 2004, we randomly selected a subset of underground locations to collect microhabitat data, averaging one location per individual per week (192 novel locations).

At our sites, there was no reliable means to determine availability of underground shelters because of uncertainties in determining the subsurface structure of potential shelters or their suitability for *D. couperi*. Therefore, we analyzed patterns of use within our sample as a function of selected ecological factors. We used principal component analysis (PCA; PROC FACTOR, SAS Institute Inc., 2005) to summarize the major dimensions of variation present in microhabitat used by *D. couperi* at underground shelters (619 novel shelter locations). We retained components with eigenvalues ≥1 (Kaiser, 1960). Correlations between variables within factors (factor loadings) were interpreted as strong if >0.50.

We used the resulting principal component scores as dependent variables in repeated measures linear regressions, with individual animals retained as the sampling unit, to examine ecological correlates of microhabitat use (PROC MIXED, SAS Institute Inc., 2005). Regression was performed
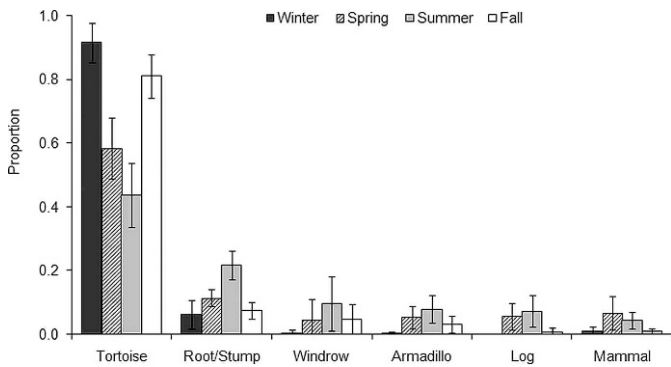
Fig. 1. Underground shelter ($\bar{x}$, 95% CI) use by *Drymarchon couperi* radiotracked in winter ($n = 30$), spring ($n = 32$), summer ($n = 28$), and fall ($n = 26$), 2002–2004, Georgia. Shelter types: burrows of *Gopherus polyphemus* (tortoise), root and stump channels (root/stump), debris piles created during timber harvest and site preparation (windrow), armadillo burrows, shelters associated with fallen woody debris (log), and burrows created by mammals other than armadillos (mammal). Values are mean proportion of underground locations, with individuals retained as the sampling unit.

Fig. 2. Seasonal *Gopherus polyphemus* burrow use for male and female radiotracked *Drymarchon couperi* at active/inactive (unshaded bars) and abandoned (shaded bars) burrows ($\bar{x}$, 95% CI, $n = 32$) in 2003–2004, Georgia. Values are the mean proportion of underground locations, with individuals retained as the sampling unit.

on a candidate set of models created from *a priori* hypotheses and selected using Akaike's Information Criterion (Akaike, 1973; Burnham and Anderson, 2002) corrected for small sample sizes (AICc; Hurvich, 1989). We also used AICc to select a covariance structure for the data. Model averaging may be inappropriate with repeated measures designs (Reiman et al., 2006); therefore, we report Akaike weights for model parameters. Our global model included the parameters sex, snout–vent length (size), over-wintering location (site; Fort Stewart or private lands), and season. We selected model confidence sets for weights within 0.10 of the highest weighted model (90% confidence set; Burnham and Anderson, 2002).

We expected variation in microhabitat use to be influenced primarily by season because of seasonal shifts in habitat use (Hyslop, 2007). We also expected sex to influence microhabitat use, with females using more open canopy patches, especially during gestation in spring, to meet thermoregulatory requirements associated with reproduction (Blouin-Demers and Weatherhead, 2001). Alternatively, we hypothesized that size, not sex, may instead influence microhabitat use (i.e., availability of suitable underground shelters decreased with increasing body size because large shelters may be limited). We also predicted that land use differences between Fort Stewart and private lands would influence microhabitat use because of differences in proportions of land with tortoise burrows in timber production and in field habitats. Lastly, we expected that microhabitat use may also be a function of site and season (i.e., habitats used seasonally may not be available on each site in each season).

RESULTS

Radiotelemetry.—Males averaged 158 cm SVL (range 120–191 cm) and 2.2 kg (range 0.72–4.3 kg) at capture; females averaged 138 cm SVL (range 110–156 cm) and 1.5 kg (range 0.55–2.3 kg). The proportion of radiolocations at novel locations varied by season (repeated measures ANOVA; $F_{3,70} = 61.1$, $P < 0.001$) but not by sex ($F_{1,30} = 2.8$, $P = 0.10$), with a sex by season interaction ($F_{3,70} = 5.73$, $P =$
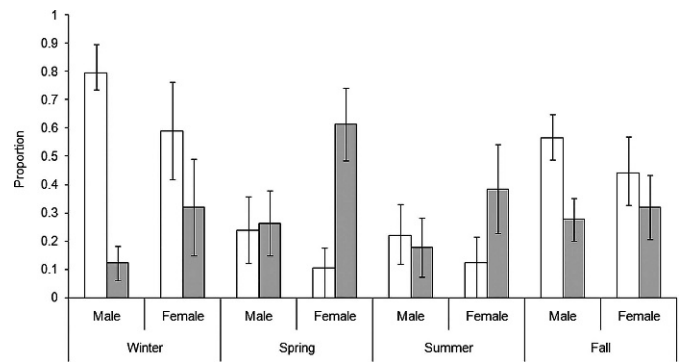
0.002). Differences in least square means (95% CI) indicated males had higher use of novel locations than females in spring ($\bar{x}_M = 0.54$, 0.49–0.589; $\bar{x}_F = 0.45$, 0.39–0.51; $t_{70} = 2.27$, $P = 0.023$) and fall ($\bar{x}_M = 0.63$, 0.58–0.68; $\bar{x}_F = 0.48$, 0.41–0.54; $t_{70} = 3.6$, $P < 0.001$), but no difference in proportion of novel locations between males and females in winter ($\bar{x}_M = 0.28$, 0.22–0.33; $\bar{x}_F = 0.30$, 0.24–0.36; $t_{70} = 0.60$, $P = 0.550$) or summer ($\bar{x}_M = 0.63$, 0.58–0.68; $\bar{x}_F = 0.69$, 0.62–0.76; $t_{70} = 1.57$, $P = 0.121$). Although individual degrees of fidelity to specific shelters varied, all snakes tracked in fall and winter 2004–2005 returned to at least four specific shelters they used the preceding year.

Shelter use.—We recorded snakes in underground shelters on 3,825 of 4,993 total locations collected for the 32 radiotracked snakes. Proportion of locations recorded underground ($\bar{x} = 0.76$, 95% CI = 0.74–0.78) did not differ between seasons (repeated measures ANOVA; $F_{3,70} = 1.29$, $P = 0.284$) or sexes ($F_{1,37} = 0.36$, $P = 0.551$), but did indicate a potential interaction ($F_{3,70} = 2.96$, $P = 0.053$). In winter, shelter use was primarily restricted to tortoise burrows for both males and females (>90% underground locations). In spring, snakes used tortoise burrows less ($\bar{x} = 0.58$ of underground locations) and used more root and stump openings ($\bar{x} = 0.12$). In summer, use of tortoise burrows was lowest ($\bar{x} = 0.44$), with root and stump use higher than in any other season ($\bar{x} = 0.22$). In fall, underground shelter use was similar to use in winter (i.e., high tortoise burrow use and lower use of all other categories; Fig. 1).

Drymarchon couperi use of underground shelters varied with habitats used. In sandhill habitats, snakes predominantly used tortoise burrows for underground shelters ($\bar{x} = 0.84$ of underground locations in sandhill habitat). *Drymarchon couperi* also used tortoise burrows in plantation ($\bar{x} = 0.92$), and field habitats ($\bar{x} = 0.72$). Wetlands did not contain tortoise burrows; in these habitats, snakes predominantly used hummocks of soil and roots ($\bar{x} = 0.65$) and woody debris ($\bar{x} = 0.28$) for shelter. Underground shelter use in clearcuts was largely restricted to windrows ($\bar{x} = 0.81$). In other types of upland forests, snakes most often sought shelter in root/stump channels ($\bar{x} = 0.56$), mammal burrows ($\bar{x} = 0.11$), and under woody debris ($\bar{x} = 0.11$). Regardless of habitat type, armadillo burrows were used on less than 0.06 of underground locations.

Table 1. Seasonal Microhabitat Characteristics Associated with Underground Shelters Used by *Drymarchon couperi* Relocated 2003–2004, Georgia. Values are non-transformed proportions of cover in 3-m diameter circular plot centered at entrances of shelters used by *D. couperi*. Basal area (m²/ha) was collected from a single point at the center of each 3-m diameter plot.

Variable	Winter			Spring			Summer			Fall		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
Understory	0.34	0.02	102	0.48	0.02	164	0.54	0.03	117	0.44	0.02	236
Canopy	0.09	0.02	102	0.18	0.02	164	0.22	0.03	117	0.12	0.01	236
Woody debris and litter	0.45	0.02	102	0.42	0.02	164	0.33	0.03	117	0.41	0.02	236
Woody understory/palm	0.15	0.02	102	0.32	0.02	164	0.38	0.03	117	0.22	0.02	236
Grass and forbs	0.18	0.02	102	0.16	0.01	164	0.15	0.02	117	0.20	0.01	236
Basal area (m²/ha)	4.28	0.35	91	6.66	0.50	144	6.12	0.55	97	19.41	1.23	211

Types of tortoise burrows used by *D. couperi* differed by season and sex (Fig. 2). In winter, males used a higher proportion of active/inactive burrows and females used an equal proportion of active/inactive and abandoned ones. During spring, approximately 0.60 of female underground locations were in abandoned burrows compared to approximately 0.24 of male underground locations as males started using shelters other than tortoise burrows. In summer, *G. polyphemus* burrow use was lowest for males and females, although females continued to use abandoned burrows (0.40 of underground locations). In fall, males and females used similar proportions of both burrow categories.

Linear, horizontal distances of *D. couperi* locations in tortoise burrows to burrow openings ($\bar{x}$ = 2.7 m, 95% CI = 2.6–2.9; 9 m maximum) varied seasonally ($F_{3,153}$ = 21.2, P > 0.001), by tortoise burrow category ($F_{1,150}$ = 26.7, P > 0.001), and between sexes ($F_{1,26}$ = 4.26, P = 0.490), with no interaction. Snakes remained farther back in burrows in fall and winter and closer to entrances in spring and summer. On average, snakes were closer to active/inactive burrow entrances and farther back in abandoned ones.

Microhabitat use.—Patterns of microhabitat use at underground shelters differed seasonally for most variables (Table 1). Microhabitat use in winter corresponded with the lowest cover values for canopy, understory vegetation, woody vegetation, and palm. Basal area ranged from 0.0–40.2 m²/ha and was lowest, along with canopy cover, in fall and winter. In spring and summer, snakes, on average, used areas with higher canopy cover, basal area, woody understory, and palm cover. Use of microhabitat with higher

Table 2. Summary of Principal Components Analysis of Microhabitat Variables for Underground Shelter Use for Radiotracked *Drymarchon couperi*, 2003–2004, Georgia. Boldface type indicates loadings >0.50.

Variable	Component		
	PC1	PC2	PC3
Understory cover	**0.962**	−0.040	0.076
Canopy cover	−0.074	**0.822**	−0.215
Woody debris and litter cover	**−0.874**	0.184	−0.256
Woody vegetation/palm cover	**0.789**	0.028	**−0.589**
Grass and forbs cover	0.152	−0.089	**0.962**
Basal area	−0.063	**0.874**	0.082
Eigenvalue	2.347	1.485	1.380
Percent total variance	39.1	24.8	23.3

proportions of grass/forbs and woody debris/logs was lowest in summer.

Principal component analysis extracted three orthogonal components with eigenvalues >1 accounting for 0.87 of the common variance among six microhabitat variables (Table 2). Principal component 1 (PC1) had positive loadings for percent understory cover, woody vegetation, and palm cover, and a negative loading for course woody debris and litter cover (Table 2). We interpreted locations with high PC1 scores as plots dominated by woody vegetation and palm cover and mostly void of other vegetation. Principal component 2 (PC2) had positive loading for basal area and canopy cover suggestive of areas of denser, more closed canopy forest (Table 1). Principal component 3 (PC3) had negative association with woody understory vegetation cover and positive association with grass/forbs. We interpreted these locations as patches dominated by grass and forb understory cover (Table 2).

Global models for all three components confirmed adequate goodness of fit (P < 0.001). AIC_c analyses on global models suggested the autoregressive covariance structure as most appropriate for modeling. The 90% confidence set of models for PC1 included 1 of 12 candidate models, which contained season as the only model parameter (ω = 0.91; Table 3). Coefficient estimates for effect of season on use of PC1 suggested highest use of PC1 patches in summer. The 90% confidence set of models for PC2 included 1 of 12 candidate models, which included season and sex (ω = 0.98; Table 3). Coefficient estimates for effect of season on use of PC2 suggested highest use of PC2 patches in spring and summer and a strong negative influence of sex (being female) on use of PC2 throughout the year. The 90% confidence set of models for PC3 included 2 of 12 candidate models. The model with most support included season, sex, and site (ω = 0.60; Table 3) and was 1.58 times more likely than the next approximating model, given the data and candidate models. Coefficient estimates for the top-ranked model suggest a higher use of these patches in all seasons except winter, a strong negative association with private lands, and an unclear effect of size. The second-ranked model included season and site (ω = 0.38). Coefficient estimates for the effect of season also suggested higher use of PC3 patches in all seasons except winter and a negative association with private lands.

In all microhabitat modeling, season ranked highest in importance for PC1 and PC2 and second highest for PC3 (0.97). This was the only common variable among the three analyses. Site had the highest importance for PC3 (1.00), but

Table 3. Effects of Season and Individual Covariates on *Drymarchon couperi* Use of Microhabitat Features as Summarized in a Principal Components Analysis. Component 1 (PC1) represents microhabitat patches dominated by woody vegetation and palm cover, mostly void of other vegetation or ground cover. Component 2 (PC2) represents patches with higher basal area and canopy cover, and component 3 (PC3) indicates patches dominated by grass and forb understory cover. Models are listed by Akaike weights in descending order for PC1 only ($n = 31$ snakes).

| | | Component | | | | | | | | |
| | | PC1 | | | PC2 | | | PC3 | | |
Model	K^a	AICc	ΔAICc	w_i	AICc	ΔAICc	w_i	AICc	ΔAICc	w_i
Season	4	4526.34	0.00	0.91	3946.14	42.07	0.00	3609.34	98.79	0.00
Sex, season	7	4532.27	5.93	0.05	3904.07	0.00	0.98	3613.27	102.72	0.00
Size, season	7	4534.07	7.73	0.02	3929.87	25.8	0.00	3618.67	108.12	0.00
Site, season	7	4534.67	8.33	0.01	3954.47	50.4	0.00	3511.47	0.92	0.38
Site, season, size	8	4536.35	10.01	0.01	3933.55	29.48	0.00	3510.55	0.00	0.6
Season, site, season by site	14	4577.65	51.31	0.00	3912.05	7.98	0.02	3551.05	40.5	0.00
Site, size	5	4554.40	28.06	0.00	4006.4	102.33	0.00	3517.6	7.05	0.02
Site	4	4553.74	27.4	0.00	4025.74	121.67	0.00	3518.54	7.99	0.01
Sex	4	4553.14	26.8	0.00	3970.74	66.67	0.00	3613.14	102.59	0.00
Size	4	4553.94	27.6	0.00	4003.74	99.67	0.00	3619.54	108.99	0.00
Sex, season, sex by season	14	4567.45	41.11	0.00	3931.85	27.78	0.00	3634.05	123.5	0.00
Global	23	4713.11	186.78	0.00	4073.51	169.44	0.00	3672.71	162.17	0.00

[a] Number of parameters includes intercept, residual, and random term

lowest for PC1 (0.02) and PC2 (0.02). Size was only important for PC1 (0.20). Sex was important for PC2 (0.98). Neither the site by season or sex by season interaction terms had importance weight for any component.

DISCUSSION

Shelter use.—The degree to which *D. couperi* was found in underground shelters (ca. 0.75 locations) suggests these habitat features are vital to this population. Shelter use in all seasons was closely associated with tortoise burrows, even during warmer months when burrow use was lowest (>0.40 of underground locations; Fig. 1). Snakes used a higher proportion of mesic areas in warmer months and higher proportion of upland areas in cooler months (Hyslop, 2007), thus likely affecting the type and quantity of shelters available. Warm season shelter use by *D. couperi* in Georgia has been previously reported (Speake et al., 1978); however, the study included translocated and captive-reared individuals. Of 108 shelters they described, 0.77 were located in tortoise burrows, 0.08 under decaying logs and stumps, and 0.05 in windrows. These snakes used tortoise burrows an average of 0.88 (December–April), 0.61 (May–July), and 0.82 (August–November); these data were pooled across individuals and sexes. Our results appear to generally agree with those data for winter; however, we cannot directly compare our results to this previous study because of differences in quantitative analysis techniques.

Drymarchon couperi radiotracked in this study, especially females in spring, used abandoned burrows extensively throughout the year. Smith (1987) reported that radio-tracked *D. couperi* females (translocated) released in Florida used abandoned burrows for 0.70 of recorded locations during gestation and following oviposition. Females may use abandoned burrows during this period because of potential disadvantages associated with oviposition in active burrows, such as damage to eggs from tortoise activity. Abandoned burrows are subject to structural degradation from weathering and vegetation growth; however, burrows

may remain structurally intact for decades (Guyer and Hermann, 1997). Activity of *D. couperi* within a shelter also has the ability to modify or reinforce internal structure of shelters, including abandoned tortoise burrows, potentially increasing their longevity (Kinlaw, 1999).

Microhabitat use.—Microhabitat use at underground shelters was most influenced by season compared to sex, size, or site. In summer and fall, snakes selected areas with higher than average understory vegetation cover, dominated by woody vegetation and palmettos, and higher than average bare ground (PC1) compared to other seasons. PC1 showed no relationship with canopy cover; however, dense shrubs, vines, and palmettos provided shading from direct sun, which would be important for snake thermoregulation during summer. Areas with higher than average basal area and canopy cover (PC2) were used more in spring and summer and less by females than males, supporting our prediction that females used more open patches in spring during gestation. In Georgia, female *D. couperi* usually complete oviposition by late spring to early summer (Moulis, 1976; Speake et al., 1987); therefore, it is unlikely that the inclusion of summer in this model is caused solely by reproductive differences between males and females.

Model results suggested that *D. couperi* use of microhabitat patches dominated by grass and herbaceous understory vegetation cover (PC3) was affected by season, site, and potentially by size. Snakes used these patches less in winter compared to other seasons and exhibited a strong negative relationship to use of these patches on private lands, regardless of season. These results do not necessarily suggest lower use of shelters at these patches in winter, but could be related to different microhabitat characteristics caused by seasonal vegetation composition. The strong negative effect of association with private lands provides support for our prediction that land use on tracts with tortoise burrows may influence *D. couperi* microhabitat use. The effect, if any, of body size was inconclusive and provided no support for our prediction that larger individuals have a limited choice of

underground shelters because of their need for larger structures, given our sites and data.

Conservation implications.—For ectothermic vertebrate species, physiological and survival costs are higher when using thermally unsuitable shelters (Huey, 1991). The availability of certain habitat features, rather than food supply or other factors, may be critical in determining endangerment for some snake species (Shine and Fitzgerald, 1996). *Drymarchon couperi* is considered a diet generalist and will consume most vertebrates small enough to overpower, such as mammals, birds, amphibians, and reptiles, including venomous and non-venomous snakes (Landers and Speake, 1980; Stevenson et al., 2003; Hyslop, 2007). Therefore, it is possible that prey availability may not be a significant limiting resource for this species, even in disturbed areas (Mushinsky and McCoy, 1987). Alternatively, we suggest that appropriate underground shelters, especially *G. polyphemus* burrows, may be a limiting factor for *D. couperi* in the northern portion of the range.

Reduction in suitable underground shelters caused by habitat degradation and loss, which reduces or eliminates populations of *G. polyphemus*, is likely an important factor in extirpation of the species from areas otherwise perceived as suitable habitat. We recommend continuance or adoption of management practices beneficial to *G. polyphemus* in upland habitats, including prescribed burning. Fire exclusion leads to an increase in ground litter cover and tree density, which inhibits growth of shade intolerant forbs and wiregrass (Lawler, 1977), conditions non-conducive for native vertebrates including *G. polyphemus* (Auffenberg and Franz, 1982; McCoy et al., 2006). Declines of *G. polyphemus* have also been detected on protected lands, emphasizing the importance of habitat quality, in addition to land conservation, for this species (McCoy et al., 2006). Additional upland practices that may benefit *D. couperi* include conserving or creating other shelter types, retaining tree stumps, creation of windrows in timber site preparations, and retention of downed woody debris.

Previous investigations of *D. couperi*, especially in the northern portions of the range, have suggested strong ties to tortoise burrows in winter (Speake et al., 1987; Speake, 1993); however, this use has been thought of as opportunistic throughout other times of the year. We suggest that use of *G. polyphemus* burrows is not a casual relationship, but an important requirement for survival in its northern range. We propose that in addition to conservation of large tracts of land (Hyslop, 2007), it is as important to restore and manage lands for *D. couperi* so that, seasonally, adequate shelters are present.

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