Movements, Survival, and Habitat Use of the Threatened Eastern Indigo Snake (*Drymarchon couperi*) in Southeastern Georgia

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Executive summary

The U.S. Fish and Wildlife Service listed *Drymarchon couperi* (eastern indigo snake) as threatened in 1978 under the Endangered Species Act, because of population declines caused primarily by habitat loss and degradation. The current range of the species is limited to extreme southeastern Georgia and Florida. Across its range, *D. couperi* occupies a wide variety of habitat types including longleaf pine-turkey oak sandhills, pine and scrub flatwoods, dry prairie, tropical hardwoods, freshwater wetlands, and coastal dunes. These required habitats are declining in quality and area because of development, fire exclusion, certain forestry practices, and agriculture. We conducted a radiotelemetry study of *D. couperi* from 2002-2004 to investigate habitat use, survival, movements, and home ranges in southeastern Georgia. We tracked 32 snakes (19 M, 13 F) at sites on Fort Stewart and adjacent private property. We determined home ranges using two estimates of home range size, (minimum convex polygons, MCP, and kernel density analysis, KD) at 3 scales: cumulative (total radiolocations), annual, and seasonal. We analyzed intraspecific differences in annual home range size through a series of *a priori* hypotheses, using repeated measures regression analysis, evaluated with an information theoretic approach. We used known-fate modeling to estimate survival over time and as related to individual covariates. We generated *a priori* hypotheses based on previous work on snake survival and from *D. couperi* natural history information. Candidate models tested for effect of time, sex, size, and overwintering site on survival. Habitat analysis was performed using compositional analysis at 3 spatial scales on standardized Gap Analysis Program land cover categories. Annual home ranges were large (MCP: $\bar{x}_{male}$ = 510 ha; $\bar{x}_{female}$ = 101 ha). Models for annual home range size

estimates suggested a positive correlation with body size, negative influence of sex (being female), and negative home range size association with habitat undergoing restoration opposed to areas used for commercial timber production. Annual survival for 2003 was 0.890 (SE = 0.074, n = 25) and 0.723 (SE = 0.088; n = 27) in 2004. Survival analysis suggested an effect of size (body length), as standardized by sex, as the strongest predictor of adult *D. couperi* survival with larger males and larger females more at risk than smaller adults of each sex. Snakes used the highest diversity of habitats in late spring and summer as they moved from dry upland winter and early spring habitats to wetter, lowland summer ranges; however, snakes continued to periodically use upland xeric habitats throughout warmer months. Habitat use analyses suggested nonrandom use, with positive selection of wetland, evergreen forest, pine-hardwood mixed forest, and field habitats and an avoidance of roads, urban areas, and deciduous forests. Snakes maintained close association with underground shelters. We recorded most fall and winter locations at gopher tortoise burrows, with less reliance on these burrows in spring and summer. In Georgia, we believe that conservation of large tracts of relatively undisturbed land is potentially the most important factor for conservation of this species; however, it is also as important to restore habitat to include appropriate sheltered retreats (gopher tortoise burrows) for *D. couperi* populations in southeastern Georgia.

Introduction

Description

  Drymarchon couperi, named for its bright bluish black coloration, is the longest North American snake species (Holbrook 1842). This large, stout-bodied, nonvenomous snake can obtain maximum lengths of 2.6 m and is uniformly blue-black dorsally with reddish or cream-colored areas around the gular region (Wright and Wright 1957, Conant and Collins 1998). Throat and head coloration is highly variable in both extent and hue and may be correlated with geographic location (Moler 1992). Ventrally, and posterior of the head, the snake has a light bluish slate color also described as a whitish black iridescent coloration (Holbrook 1842, Conant and Collins 1998). Scales are large and smooth in 17 scale rows at midbody and the anal plate is undivided. Adult males may have 1 to 5 middorsal scale rows lightly keeled (Layne and Steiner 1984). The antepenultimate supralabial scale does not contact the temporal or postocular scales, as found in the Texas indigo. Young *D. couperi* are similar in appearance to the adults; however, some may show a blotched dorsal pattern and more reddish color on the head and anterior portion of the ventral side.

  Holbrook, in 1842, originally described this species as *Coluber couperi*, with the type locality as a dry pine hill lying south of the Altamaha River, Georgia (Holbrook 1842). In 1853, Baird and Girard reassigned the species to genus *Georgia*. Cope transferred it to genus *Spilotes* in 1860 and relegated it as a subspecies of *Spilotes corais* in 1892. In 1917, Stejneger and Barbour resurrected the genus name *Drymarchon*, (*Drymarchon corais*; Daudin 1827), designating the species as *Drymarchon corais couperi* which remained stable until 2000 (McCraine 1980). Throughout most of the

twentieth century, genus *Drymarchon* was considered monotypic, *Drymarchon corais*, with multiple subspecies ranging from the Coastal Plain of the southeastern United States, extreme southern Texas, and further southward to Northern Argentina.

Recently, it was proposed that the Eastern Indigo Snake be raised to full species status because of consistent differences in head scalation and large geographic separation compared to the Texas Indigo Snake (*Drymarchon corais erebennus*; Collins 1991). This designation has been provisionally accepted by the Society for the Study of Amphibians and Reptiles (SSAR; Crother 2002). Currently, the United States Fish and Wildlife Service (FWS) has not adopted the Eastern Indigo Snake's designation to full species status and continues to use *Drymarchon corais couperi*.

Distribution

Drymarchon are primarily tropical, ranging from the southeastern United States to northern Argentina. Two forms are found in the United States: *D. couperi* and *D. corais erebennus* (Texas Indigo Snake). Historic accounts report that *D. couperi* maintained a relatively continuous geographic distribution along the Coastal Plain from South Carolina to southern Louisiana (Smith 1941). By 1957, reports indicated that distribution information from Alabama, Mississippi, and Louisiana was uncertain, with extirpation of populations in these areas likely (Wright and Wright 1957). The last known valid record from South Carolina was in 1954 (Jasper County, Diemer and Speake 1981); however, this record may have been a false identification.

Status of the species in Alabama is currently unknown, despite documentation of the species in western parts of the Florida panhandle (Moler 1992). From 1976 until about 1990, D.W. Speake (Alabama Cooperative Fish and Wildlife Research Unit),

released *D. couperi* to 19 sites in Georgia, Alabama, Florida, South Carolina, and Mississippi (D.W. Speake, personal communication). A recent survey of most of the 9 Alabama release sites found no new *D. couperi* records during the surveys (Hart 2003). However, since 2000, there has been an apparent increase in number of reported *D. couperi* sightings, with 9 potential sightings in Alabama since 1986, 3 of which were at release sites from Speake (Hart 2003). Although evidence suggests that most of the releases failed to establish breeding populations of *D. couperi,* some of the sites may have populations remaining (D.W. Speake, personal communication).

An investigation into *D. couperi* distribution in Georgia, using mailed questionnaires, museum records, and recent sightings, found evidence of *D. couperi* in 52 of the 94 counties in the Coastal Plain (Diemer and Speake 1983). A similar study investigating the distribution of the species in Florida, examining historical, museum, and current records, found the species in all but three Florida counties (Gulf, Lafayette, and Union; Moler 1985a). Remaining viable natural populations of *D. couperi* likely occur only in southern Georgia and Florida (Lawler 1977) and are considered uncommon to rare where populations remain.

Habitat associations

Across its range, *D. couperi* occupies a wide variety of habitat types including longleaf pine-turkey oak sandhills, pine and scrub flatwoods, dry prairie, tropical hardwoods, freshwater wetlands, and coastal dunes. *D. couperi* may show seasonal shifts in habitat occupancy, wintering on sandhills but moving to adjacent, more mesic habitats during summer (Speake et al. 1978). This pattern may be more pronounced in the more northern portions of its range (Speake et al. 1978).

In Georgia, *D. couperi* is primarily associated with Miocene and Plio-Pleistocene marine terrace sand deposits in middle and lower Coastal Plain located primarily on north or northeastern sides of major Coastal Plain streams (Lawler 1977, Wharton 1977). These sand deposits composed of xeric well-drained, deep sandy soils (such as Kershaw and Lakeland soils) often support populations of gopher tortoises (*Gopherus polyphemus;* Speake et al. 1978, Speake et al.1982, Diemer and Speake 1983). Longleaf pine (*Pinus palustris),* scrub oak (*Quercus* spp.) and turkey oak (*Q. laevis*), with occasional live oaks (*Q. virginiana*) dominate these Georgia upland habitats (Diemer and Speake 1983).

Warm season habitat use by *D. couperi* in Georgia is not well understood; however, evidence suggests that in Georgia the snakes move seasonally into more mesic and hydric habitats and may prefer xeric sandhill uplands adjacent to or near tupelo or bald cypress wetlands, river bottoms, or large pine flatwood tracts (Lawler 1977, Speake et al.1981, Diemer and Speake 1983). Although habitat use may be more diverse in late spring and summer months as snakes move from their winter and early spring breeding and overwintering habitats into summer ranges, snakes during these warmer months may continue to use sandhill habitats (Speake et al. 1978).

Evidence suggests that habitat preferences are more general in the southern portion of *D. couperi's* range. In Florida, the species associates with a wide range of xeric to hydric conditions, including mangrove swamps, wet prairies, xeric pinelands, hydric hammocks, and scrub (Lawler 1977, Moler 1992). Apparent geographic differences in habitat use between northern and southern portions of the snake's range may be attributable to the more stable thermal environment further south and the snake's winter behavior (Speake et al. 1982, Moler 1992).

Throughout their range, during cooler periods, *D. couperi* requires sheltered retreats from winter cold and desiccating conditions. These shelters may include active or inactive gopher tortoise burrows or other animal burrows, stumps, logs, and debris piles (Lawler 1977, Speake et al.1978). When occupying areas with gopher tortoises, *D. couperi* regularly associate with tortoise burrows, using them for shelter from temperature extremes and desiccation, protection from predation, and possibly as nest sites (Holbrook 1842, Speake et al. 1978, Landers and Speake 1980, Speake et al. 1981, Speake et al. 1982). Laboratory experiments suggest that *D. couperi* are highly susceptible to desiccation (Bogart and Cowles 1947). In more mesic habitats lacking gopher tortoises, *D. couperi* may take shelter in hollowed root channels, rodent burrows, armadillo burrows, hollow logs or crab burrows (Lawler 1977, Moler 1985b). Speake et al. (1978) found 108 shelter sites used by *D. couperi*. Of these, 77% were located in active or inactive gopher tortoise burrows, 18% under decaying logs and stumps, and 5% under plant debris.

Life history

Diet

D. couperi actively forages diurnally on a wide variety of prey and will consume most vertebrates small enough to overpower. Juveniles may consume invertebrates (Rossi 1994). The species is not a constrictor, but instead uses its strength and size to subdue and consume prey, usually alive. While rare, *D. couperi* may also climb trees or shrubs to flee or to capture prey (Anonymous 1999; D. Stevenson, unpublished data).

Movement

Reported *D. couperi* home ranges vary between 4.8 to >300 ha (Speake et al.

1983; Moler 1985b; R. Bolt, personal communication). The species is almost exclusively

diurnal (Moulis 1976, Steiner et al. 1983, Moler 1985, Moler 1992) and can be active

year round on days $\geq 11^{\circ}$C (Speake et al. 1978).

Reproduction and growth

Information on reproductive behavior of *D. couperi* populations is sparse, with

most of the information from captive observation (Hallam et al. 1998). Breeding occurs

from October to March (Groves 1960, Speake et al. 1978, Steiner et al. 1983, Moler

1992), and possibly though April in Georgia (Moulis 1976). A single clutch of 4 to 12

eggs (Steiner et al. 1983) is laid during May and June (Moler 1985b, Moulis 1976,

Steiner et al. 1983). There is little information available on nesting locations, but there

are at least two reports of egg deposition sites located in gopher tortoise burrows (Moulis

1976, Speake et al. 1978). Females may be capable of reproduction annually (R. Bolt

and D. Stevenson, personal communication). Eggs hatch after approximately 3 months,

with peak hatching activity from August through September (Groves 1960, Wright and

Wright 1957, Smith 1987). Hatchlings are 45 to 61 cm in length (Moler 1992). Sexual

maturity may be reached in 3 to 4 years (Speake et al. 1978). Delayed fertilization

(female sperm storage) may be possible (Carson 1945). Adult male *D. couperi* may be

territorial, at least during the breeding season, resulting in combat and possibly

cannibalism (Waide and Thomas 1984, Moler 1992, Stevenson 2003).

Ecdysis in *D. couperi* occurs frequently (every 30-45 days). Prior to shedding,

snakes may be inactive for 10-14 days. Estimates of *D. couperi* inactivity because of

ecdysis span up to one third of their life (Moler 1985b, 1992). This may have important implications for surveying; especially those conducted over a short time period, as is often done for determining the presence/absence of the species at a particular site. The sex ratio of wild populations has not been shown to differ significantly from 1:1 (Moulis 1976, Steiner et al. 1983). No information is available on individual longevity in the wild. Maximum reported captive longevity is 25 years and 11 months (Shaw 1959).

Status and threats

In 1978, the FWS designated *D. couperi* as threatened according to the Endangered Species Act of 1973. The species is also state listed as threatened in Florida (1971) and Georgia (1977; Johnson et al. 1999), and endangered in Mississippi, South Carolina, and Alabama. Protective status at federal and state levels was enacted because of population declines caused primarily by commercial pet trade collection and extensive habitat loss across the southeastern geographic range of the species (United States Fish and Wildlife Service 1978). Other threats include wanton killings, highway fatalities, and residual pesticide exposure (Lawler 1977). In a recent Florida telemetry study, vehicles caused 40% of in-field mortality (R. Bolt, unpublished data). An additional threat to the species is attributable to its association with diamondback rattlesnakes (*Crotalus adamanteus*). Gassing, the practice of introducing gasoline into animal burrows, such as gopher tortoise burrows to expel rattlesnakes, is most often fatal to *D. couperi* (Speake and Mount 1973, Speake et al. 1978) and may be a limiting factor in portions of the range where "rattlesnake roundups" are held (Lawler 1977). Federal and state protection prevents commerce in the pet trade and has effectively curtailed commercial collecting and its impact on natural populations (Lawler 1977).

Currently, habitat loss, fragmentation, and degradation may be the primary threats to the continued survival of *D. couperi*. Xeric habitats, such as upland longleaf pine forests, are rapidly declining in quality and area because of encroaching construction, development, agriculture, livestock farming, and some forestry practices (Lawler 1977). Although the species is able to use a wide array of habitats, winter survival, especially in its northern range, is dependent on availability of appropriate winter shelters. In Florida, practices such as removing tree stumps for resin wood have drastically reduced availability of winter shelters in areas where gopher tortoises are in low numbers (Moler 1992). In Georgia, similar trends may have occurred.

Longleaf pine forests covered >90 million acres across the southeastern United States at the onset of European settlement. Currently, there are <3 million acres of this habitat remaining (Landers et al. 1995). These structurally and biologically diverse systems, following moisture gradients from xeric sandhills to mesic flatwoods, create a natural mosaic of upland and lowland habitats that are similar in fire regime and some dominant vegetative species. Degradation of these forests occurs through fire suppression, poor management, and use of off-road vehicles (Lawler 1977). Fire suppression leads to an increase in ground litter cover and tree density resulting in lower wiregrass growth, which is essential forage for gopher tortoises (Lawler 1977).

Problem statement and justification

Despite federal protective status of *D. couperi*, insufficient information exists in the literature to adequately address habitat assessment techniques to ensure a sufficient amount of land is conserved to sustain *D. couperi* populations (Hallam et al. 1998). This

lack of basic natural history and survey information inhibits the development of conservation and endangered species management plans for the species.

Speake et al. (1982) developed a formal endangered species recovery plan for *D. couperi*, detailing steps necessary for protection, recovery, and removal of the species from federal protection. These steps include delineating, maintaining, and protecting existing populations. The authors emphasized the need to determine habitat requirements and conduct studies on population ecology, movements, and food habitats. Other steps in the plan included reestablishing populations where viable and improving public attitude towards the species (Speake et al. 1982). The recovery plan revision (Speake 1993), recommends continued federal protection of the species. In the revision, Speake supports this recommendation primarily as a means to continue protecting the species from commercial pet trade collection and as encouragement to land owners and managers to continue management practices that benefit *D. couperi*.

Although previous research has been conducted on *D. couperi* in Georgia, additional investigations into the snake's natural history will help ensure successful conservation of the species (Speake et al. 1982, Hallam et al. 1998). Prior research on the species in Georgia (e.g., Speake et al.1978, Diemer and Speake 1983, Smith 1987) is limited because of its relevance primarily to captive and relocated snakes and shorter tracking durations (range: 5 to 176 days; Speake at al.1978).

In addition, since Georgia presently constitutes the northern extent of the genus, results from studies in Florida may not be valid for Georgia populations. Therefore, despite a recent radiotelemetry study in Florida, it is important to have reliable data from Georgia populations for comparisons and management within the state.

We initiated this research in 2002 to investigate movements and habitat use of *D. couperi* in southeastern Georgia. Our objectives were: (1) to determine habitat use and to examine changes in habitat use over time; (2) to determine home ranges and movements, including seasonal shifts in movement patterns and home ranges; (3) to estimate survival; and (4) to determine seasonal shifts in underground shelter use.

Methods

Site descriptions

We conducted this research on Fort Stewart Military Reservation and tracts of adjacent private property, located in Bryan and Liberty Counties, Georgia. Fort Stewart encompasses ca. 111,600 ha (279,568 acres) located in the Atlantic Coastal Plain of southeastern Georgia spanning portions of Evans, Tattnall, Long, Liberty, and Bryan counties. In this region, extensive sand ridges, likely originating from strong winds during the late Pleistocene Period (Wharton 1977), exist along north and northeastern banks of many streams. Interspersed with sand ridge habitats are various wetland habitats, such as blackwater swamps, bottomland hardwood forests, bay swamps, shrub bogs, Carolina bays, cypress and gum ponds, and impoundments including man-made ponds and lakes. Additional upland habitats include mixed pine-hardwood forests and mesic and dry pine flatwoods (Stevenson 1999).

Management activities within the study areas on Fort Stewart centered on restoration and conservation of native habitats, including longleaf pine forests. Management activities include: prescribed burning, wiregrass seeding, longleaf pine planting, turkey oak control and removal, and thinning pine plantations. There were no paved roads within the Fort Stewart study site, only maintained and non-maintained unpaved roads.

We conducted part of this study on private property north of Fort Stewart. The site contained a single, uninterrupted block of land (ca. 6000 ha). All landowners gave consent for access to their land. Specific management activities varied by landowner; however, most tracts were managed for pine timber production, with habitat management for game species, primarily *Odocoileus virginianus* (white-tailed deer) and *Meleagris gallopavos* (wild turkey). All private property tracts were bounded on one side by a paved road and with no paved roads within tracts. The tracts had long histories of fire exclusion until recently when many landowners begun burning for timber and game management.

In areas where native sandhill vegetation communities have been left relatively undisturbed, fire exclusion lead to increased canopy cover and reduced native ground cover because of turkey oak dominance in absence of fire. Although there are no flatwoods habitats on the area of Fort Stewart that we used for this study, extensive flatwoods habitats historically existed on private property sites. During this study, these areas were maintained for short-rotation timber production with clear-cutting, bedding, and windrow creation. Some cypress ponds remained within the plantations and clear cuts. Extensive wetlands along the Canoochee River remain largely intact on private property sites; however, a majority of lowland areas adjacent to river wetlands currently exist as mature loblolly pine plantations, with dense canopy and midstory shrub cover.

Telemetry

We captured snakes by hand on xeric upland sandhill habitats on the Fort Stewart and private property sites during late fall to early spring. To ensure only adults were included in the study, we did not implant snakes with snout-vent length (SVL) <125 cm.

After this minimum size was established, we selected snakes for implantation based on sex and site of capture to represent the study areas and sexes as evenly as possible.

Cold season radio implantations in snakes have been implicated in increased mortality risks. Rudolph et al. (1998), reporting on late fall implantations of 10 *Crotalus* in Texas, found that 4 of the snakes died 1 to 4 months following surgery and release, which was significantly higher than mortality in snakes implanted in warmer months. Speculation regarding the cause of increased mortality included surgery complications, hypothermia, and predation; however, even upon necropsy, the authors could not determine causes of death in these cases. Currently, the only known reliable method of locating *D. couperi* in Georgia is during late fall and winter breeding period while snakes are associated with xeric uplands and gopher tortoise burrows in these habitats (Stevenson et al. 2002). Therefore, we worked closely with T. Norton, DVM, Wildlife Conservation Society, to develop surgical and care protocols that reduced risks to the animals from implantation procedures.

We used temperature sensitive radiotransmitters, weighing approximately 16 g, fitted with whip antennas (Holohil Systems, Ltd., Ontario, model SI-2T, 36 mo., 15x37mm, 164.000-164.999 MHz). We also used a lighter and smaller 18-month transmitter in the second year of the study from the same manufacturer. Transmitters were surgically implanted in the coelomic cavity. Isoflurane was administered while the snake was in a plastic clear tube. Once the animal was relaxed, it was intubated with an un-cuffed endotracheal tube and maintained on isoflurane. An ultrasonic doppler was used to monitor anesthesia, while snakes were manually ventilated throughout the procedure. Transmitters were implanted ca. 2/3 from the anterior and the antenna was

threaded subcutaneously anteriorly of the transmitter (Reinert and Cundall 1982, T. Norton, personal communication).

Following surgery, PITs (passive integrated transponder) were implanted subcutaneously approximately 20 scale rows anterior of the snake's vent to provide an additional means of individual identification. Also following surgery, while still anesthetized, individuals were weighed, measured (snout-vent and tail length), and sexed by cloacal probing. To facilitate healing, snakes were held in captivity for 10 to 16 days post-operatively at elevated temperatures (21-27 C thermogradient) to allow for recovery. We released snakes at their point of capture during late morning, on days with forecasted maximum temperatures >15.5 C and lows >4 C. In spring 2004, we used ultrasound on 7 of the 10 females in the study at that time. At study completion, we recaptured most snakes and surgically removed transmitters. Removal procedures and snake care were identical to those used for implantation.

Radiotracking began approximately 24-hours after release. We tracked snakes on foot using homing techniques. At each location we recorded the snake's activity, visibility, body position, and use of structural habitat features. Visual sightings were obtained only when disturbance to individuals could be minimized. We determined coordinates of each location using a global positioning system (GPS) in Universal Transverse Mercator (UTM) units according to North American Datum 83 (NAD 83) for use and analysis in ArcView GIS software (Environmental Systems Research Institute 1998). If an animal had not changed position since its previous location, we used coordinates previously recorded for that location to ensure identical GPS coordinates.

Trapping

In December 2002, we constructed and installed 18 drift fences at Fort Stewart (12) and at the private property sites (6) on sandhill uplands with known *D. couperi* populations. Each fence had a 1.2 x 1.2 x 0.3 m box trap with four funnel entrances and 15 m of 1-m high silt fencing radiating at 90° from each funnel. Trap design was adapted from traps used on *Pituophis melanoleucus* (pine snakes) in Texas, Tennessee, and southern Alabama (C. Rudolph and M. Bailey, personal communication). In March 2003, we modified this design with the addition of a "shelf" radiating over each funnel entrance to potentially reduce the chance that large snakes would climb over the box trap. We checked fences and traps daily and activate them only when overnight temperatures were above 5 C and daily temperatures were not over 33 C.

Home range and activity centers

To investigate the area used by the snakes in this study, we used the minimum polygon method (Mohr 1947) of delineating home ranges with convex polygons (MCP; Southwood 1966) and kernel density analysis (KD; Worton 1987, 1989) to estimate utilization distributions. We calculated all home ranges using Animal Movements Extension (Hooge and Eichenlaub 1997) to ArcView GIS with Spatial Analyst (Environmental Systems Research Institute 1998). MCP analysis included all radiolocations (100% MCP). To calculate KD, we used fixed kernel method, with least squares cross validation smoothing parameter (h) based on Silverman (1986, Hooge and Eichenlaub 1997, Seaman and Powell 1996). KD analyses were conducted at the 95% isopleths, representing a complete range, comparable to100% MCP method, and at 50% isopleths representing core areas of activity.

We calculated home ranges at three temporal divisions. Cumulative home ranges were calculated for snakes tracked for ≥ 9 months. These ranges represent total, or cumulative, range for that individual during the study. Cumulative ranges were not compared, but are presented for conservation and reserve planning purposes. We calculated annual home ranges from winter to winter, using breeding season and associated return to breeding and overwintering areas as the annual cut-off (December 15- December 14). We also examined home range by season: winter (December 15- March 14), spring (March 15- June 14), summer (June 15- September 14), and fall (September 15- December 14).

We used 2 data sets for home range estimations. We maintained a relatively consistent tracking effort throughout the study; however, seasonal variations in snake activity and movement lead to differences in days between successive telemetry locations. Therefore, we used the complete data set for the MCP range estimates and an abbreviated data set for estimation of utilization distributions (KD). For this abbreviated data set, we retained only novel radiolocations and removed repeated use locations, to alleviate potential bias in tracking frequency caused by seasonal variations in snake activity and movement (Hemson et al. 2005).

To address possible sample size biases in using the MCP method to estimate home and seasonal ranges, we used bootstrap analysis to examine sample size-home range area relationships. We performed the bootstrap analyses using the Animal Movements extension to ArcView (Hooge and Eichenlaub 1997), with 500 iterations per sample size. If incremental area curves visually reached asymptote, we included the home range in analyses.

Home range modeling

We analyzed home and seasonal ranges using linear regression to examine biological and ecological correlates of intraspecific range size variation. Home range data were natural-log transformed to approach normality. Model selection was performed using an information theoretic approach (Burnham and Anderson 2002), in which Akaike's Information Criterion (AIC; Akaike 1973), corrected for small sample sizes (AICc; Hurvich and Tsai 1989) was the metric used for model comparison. Linear regression was performed on a candidate set of models created from *a priori* hypotheses. Because of repeated measures within our data set (individuals tracked over successive years), and an unbalanced design, we used mixed, or hierarchical, modeling for the linear regression (PROC MIXED, SAS Institute Inc, Cary, NC, Version 9.01). We also used AICc to objectively choose the appropriate covariance structure for the data. Model averaging is not appropriate with repeated measures designs (J. Peterson, personal communication). Instead, we report Akaike weights for all model parameters in addition to parameters estimates for models in our 90% confidence set.

We used slightly different, but comparable, *a priori* hypotheses and modeling for examining MCP and 95% KD annual home ranges, 50% KD activity centers (AC), and MCP seasonal ranges. Exceptions occurred due to differing data structures and home range estimation techniques. We modeled seasonal ranges only using the MCP method because both home range techniques gave similar range estimates. Parameters used in annual models included: sex (dummy variable coded for female, Sex), snout-vent length (Size), interaction term (Sex*Size), overwintering location (Site), and number of radiolocations (Locations). The overwintering site variable is dichotomous, indicating

overwintering on Fort Stewart versus private property. The locations variable was not used in KD and AC models because of the data set used for those analyses. Modeling for seasonal home ranges also did not include an overwintering site variable, instead, we used a continuous variable for the proportion of locations, by season, that were recorded on private property or Fort Stewart (Site%).

We hypothesized that sex influences intraspecific variation in annual range size, with males maintaining larger ranges than females. We also hypothesized that home range size may not be affected by sex, but that an apparent sexually dimorphic pattern emerges because of differences in size between males and females. *D. couperi* is a sexually dimorphic species, with larger males; however, in this study, there was overlap in size of males and females, with some large females and some smaller males. Because larger animals have higher metabolic needs and therefore resource needs, we hypothesized that males will have larger annual and seasonal ranges than females. We also hypothesized that snakes overwintering in assumed lesser-quality habitat available at the private property sites will require larger ranges to meet their basic needs for survival. For annual KD and AC and seasonal ranges, this hypothesis predicts that snakes with higher proportions of radiolocations in private property will require larger home ranges than snakes with higher use of areas in Fort Stewart.

By setting a minimum tracking duration for inclusion of individuals into annual and seasonal range analyses, in addition to bootstrap analyses, we assume that home and seasonal ranges included in these models are relatively stable with sufficient radiolocations; however, there may be residual sample size impact on home range size with increasing number of radiolocations. Therefore, we also incorporated this

possibility into our modeling by including number of radiolocations collected per individual in our modeling.

Patterns of movement

To investigate patterns of movement, we compared movement frequency and distance by sex, season, and year. We calculated frequency of movement as the proportion of tracking days that an individual altered its location. To examine movement frequency, we divided both years of the study into 14-day periods, and calculated proportion of days moved compared with number of days tracked within that 14-day period. We used this method to standardize tracking effort across all seasons and individuals. We retained the animal as the sampling unit, and deleted records for snakes with only 1 location in the 14-day period.

To determine average distance moved per day, or daily movement index, we calculated straight-line distances between successive locations as an index of minimum distances traveled (Animal Movements Extension, Hooge and Eichenlaub 1997). Calculations were based on number of days in each season that individual snakes were located. We again used 14-day periods, summing distance moved over the period and dividing by 14 for an average daily movement in each period.

For both sets of movement analyses, we completed repeated measures analyses of variance (ANOVA; SAS 9.1). We calculated movement frequency and mean daily movement distance as a function of sex, season, and year.

Survival analysis

We used known-fate modeling within program MARK (White and Burnham 1999) to estimate survival over time and as related to several individual covariates for radio-tagged *D. couperi* tracked in this study. The known-fate model estimates probability of survival (S) and is analogous to the Kaplan-Meier product limit estimator (Kaplan and Meier 1958), allowing for staggered entry of individuals (Pollock et al. 1989). Although daily radiotracking ended in December 2004, we continued monthly tracking through June 2005 as we captured snakes to remove transmitters; therefore, survival analysis covers January 2003 through June 2005. We divided the study period into 30, 1-month sections for survival analysis. We included four individual covariates in the data structure: sex, overwintering site (site; private property or Fort Stewart), size at capture (size; snout-vent length), and size scaled by sex (size, standardized). Because *D. couperi* is sexually dimorphic with, on average, larger males, we standardized size by sex using residuals of size versus sex regression as a covariate in our survival models. Individual covariates were standardized and logit link functions were used for all models.

We generated a set of a *priori* hypotheses based on previous work on snake survival (e.g., Bronikowski and Arnold 1999) and from *D. couperi* natural history information. Candidate models tested for effect of time, sex, size, and overwintering site on survival. We hypothesized that survival would be time dependent, with higher mortality in late winter and early spring than in other periods. Larger movement distances, such as seen with males, may decrease survival probability by increasing encounters with predators, humans, and other hazards. Lower quality habitats available at private property sites may also impact survival probability by not providing sufficient

resources for long-term survival. There were no models incorporating both sex and size independently due to possible correlation between these parameters. We did not include home range size as an individual covariate in survival models because of strong correlations between home range size and sex. We used an information-theoretic approach to assess candidate models and to select the best approximating confidence set of models for inference (90% confidence set; Burnham and Anderson 2002).

Habitat association analysis

Landscape level habitat use analyses identify broad environmental factors, vegetation coverage, and hydrology important to a population's use of an area (North and Reynolds 1996). The concept that a habitat component is used more or less than its availability is important in understanding habitat use of a species (Johnson 1980). For this study, we delineated available habitat as the collective extent of the snakes' observed locations for the duration of the study. This method uses biologically relevant markers to define the boundaries of the site, although it may underestimate available habitat since boundaries are set at snake locations.

Landscape-level habitat types at the site, as delineated by Gap Analysis Program land cover data (GAP), included: roads and urban areas (roads); open water, forested, and non-forested wetlands (wetlands); agricultural and other fields (field); clear-cuts and other habitats with sparse canopy cover (CC/sparse); forests with at least 75% deciduous trees (deciduous); forests with at least 75% evergreen trees, including managed pine plantations (evergreen); and pine-hardwood mixed forest, including shrub/scrub habitats (mixed).

To examine habitat use, we used compositional analysis (CA; Aitchison 1986,

Aebischer et al. 1993) as computed with bycomp.sas (Ott and Hovey 1997). CA, through examination of use and availability of habitat types, assesses if habitat use differs significantly from random. Selective use occurs when components are used disproportionately to their availabilities. A component used significantly more than availability would predict is considered preferred (Johnson 1980). If use is determined to be nonrandom, paired t-tests are used to compare all habitat types, which produce a ranking of habitats based on preference and significance of their use versus availability. Compositional analysis regards the animal as the sampling unit to eliminate problems associated with non-independence of sequential data taken on the same individual. The method examines all habitat types simultaneously and takes the log-odds ratio of habitat proportions to compensate for inter-relatedness of habitat use data (Aebischer 1993).

Habitat selection may vary with scale; therefore, we examined habitat use hierarchically (e.g., Johnson 1980). The broadest scale encompasses geographical distribution of an organism across the landscape. At finer scales are areas the animal is found in a particular locality (home range), and its actual position within the habitat (within home range). We evaluated habitat use at the two finer levels of this hierarchy. We analyzed home range selection by comparing the landscape-level habitat composition of the 100% MCP home ranges of individuals to the habitat composition of the study area. Site use was evaluated by comparing habitat at radiolocations to the 100% MCP home ranges. An additional level of analysis was included, comparing habitat at individual radiolocations with proportion of habitats available at the study site (overall selection; McClean et al. 1998b). Based on preliminary examinations of the data, we did not have reason to suspect that sex or year impacted habitat use; therefore, we combined

year and sex for compositional analyses.

In addition to our habitat use analyses performed on standardized GAP habitat categories, at each snake radiolocation we also noted habitat type based on hydrology, land use, management, vegetation, and gopher tortoise presence. These habitat categories included: sandhill (xeric uplands with longleaf pine overstory and gopher tortoise burrows), clear-cut, field (includes old-field, minimally maintained hay fields, and food plots), plantation (any habitat planted by rows in pine trees, may or may not support gopher tortoise population), slope forest (transitional habitat between xeric uplands and wetlands), miscellaneous uplands (xeric uplands with pine-hardwood mixed overstory composition), and wetlands (isolated upland wetlands and bottomlands, no gopher tortoise populations). Mesic pine flatwood habitats are often associated with the Coastal Plain of southeastern Georgia; however, we have not included this habitat type in our classification because there were no snake locations recorded in intact mesic pine flatwoods. These areas existed primarily as large clear-cuts characterized by extensive windrows, planting beds, with occasional isolated wetlands interspersed. We include this additional habitat use summary here primarily to distinguish between sandhill and plantation areas, which are combined within the evergreen GAP category. Also, within GAP categories, some sandhill habitats are classified within mixed and CC/sparse categories. In all habitat use analyses the individual was retained as the sampling unit.

Shelter use

Throughout its range, *D. couperi* requires shelter from temperature extremes, desiccating conditions, and predation. In northern portions of *D. couperi*'s range (southeastern Georgia), these shelters often include gopher tortoise burrows, woody

debris, and stump holes (Lawler 1977, Speake et al. 1978). To examine shelter use by *D. couperi* radiotracked in this study, we categorized all radiolocations as underground or surface. We classified locations such as those in a burrow or stump hole, in addition to locations found under logs, woody debris, and within windrows as underground. Locations on the ground, under litter, under vegetation, or those in trees, were categorized as surface locations. Windrows, constructed after pine plantation harvesting during site preparation for the next planting rotation, were composed primarily of a mixture of woody debris and soil. Vegetation often grows on and around windrows, adding another dimension to the structure. We recorded windrow locations as underground when snakes were under woody debris or under the soil in an animal burrow or other opening. If the snake was exposed, under living vegetation, or under litter, we recorded it as a surface location.

Categories used in this study to describe underground shelters include: gopher tortoise (GT) burrows, root and stump openings (root/stump), debris piles created during timber harvest and site preparation (windrows), shelters associated with fallen woody debris (log), armadillo burrows (*Dasypus novemcinctus*), and burrows created by mammals other than armadillos (mammal). We separated armadillo burrows because they are reliably identifiable from other mammal burrows and for comparisons with other studies (e.g., Lawler 1977, Moler 1985, Layne and Steiner 1996).

Gopher tortoise burrows are regularly 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). Here, we define

active gopher tortoise burrows as those with intact structural integrity of the burrow opening and with signs of tracks and/or shell markings. We denoted burrows as inactive if there was no evidence of recent use and the entrance not obscured with debris. Abandoned burrows (abandoned) were classified as those with compromised structural integrity of the burrow opening, no sign of gopher tortoise tracks or shell scrapings, and litter and vegetation obstructing the opening. Because of documented difficulties in accurately classifying gopher tortoise burrows, especially with burrows that appear to be inactive (Smith et al. 2005), for the purposes of analyses, we combined active and inactive burrows into a single category (active).

Results

Telemetry

We began fieldwork 1 March 2002 and captured a female during the first week. Implantation was successful; however, the snake died a day after surgery. A necropsy completed by T. Norton, DVM, Wildlife Conservation Society, revealed a high internal parasite load and significant skin lesions over the body. Histopathology reports completed at the University of Georgia's College of Veterinary Medicine, Athens Diagnostics Laboratory, indicated that the snake's death was related to a septic infection that was likely caused by skin and/or internal lesions (N.L. Stedman, unpublished report A2-046010). Internal lesions were attributable to gastric nematode and migrating immature pentastome activity. Opportunistic bacteria, possibly introduced by pentastomes, also infected the sites of activity. Stedman suspected several species of bacteria involved in the skin lesions, indicating that infection was opportunistic

secondary to another compromising factor such as high environmental humidity. In Georgia, researchers find similar skin lesions on *D. couperi* throughout winter (D. Stevenson, personal communication); however, concentration of lesions on this indigo snake was higher than normally encountered.

Twenty snakes (7 F, 13 M) were captured and implanted with transmitters between 12 December 2002 and 11 April 2003. Twelve additional snakes (6 F, 6 M) were added between 10 October 2003 and 1 March 2004 (Table 1). We recorded field search effort for the first 18 *D. couperi* captured. We limited field searching data collection to the first 18 captures because our effort shifted from searching for snakes to tracking snakes (with incidental captures). NLH conducted most searches; Fort Stewart fish and wildlife biologists (primarily D. Stevenson) and other intermittent field help conducted additional searches. Between 1 December 2002 and 12 March 2003, we searched for snakes on 43 days for 249 person-hours. We found 13 individual *D. couperi* sheds (19.2 person-hours/shed) and 18 *D. couperi* adults (13.8 person-hours/snake).

Of the 20 snakes captured and implanted December 2002 through April 2003, 11 snakes (6 F, 4 M) were censored before the end of the study because of mortality, transmitter malfunction, and unknown fates. We censored 3 (1 F, 2 M) of 12 snakes added between October 2003 and March 2004. To our knowledge, we lost one snake because of tracking failure. We tracked this individual from October 2003 through April 2004 when we lost the signal until early September 2004. Over both years of the study, we censored 12 snakes that died. Of these, one death was directly attributable to human causes. This snake was hit by a vehicle on an unpaved road in private property. We found the remaining 10 individuals in the field, dead from unknown causes. Necropsies

were performed by T. Norton on all snakes found dead with significant body tissue remaining; however, all were inconclusive as to cause of death.

We collected 4993 radiolocations for 32 snakes tracked between January 2003 and December 2004 (Fig. 1). Individual snakes were tracked between 89 to 711 days ($\bar{x}$ = 420) resulting in 39-254 locations per individual (Table 1). We tracked 30 snakes >6 months and 18 of these for >12 months.

Trapping

From 15 December 2002 to April 2004, we opened 18 traps for 847 trap-days (47 days). Although traps were successful at capturing a variety of reptiles, amphibians, and small mammals common to uplands in the region, no *D. couperi* were captured until fall 2003 and after we modified the traps. We captured 6 *D. couperi* in traps in October and November 2003 (ca. 140.5 trap-days per *D. couperi* capture). One capture, an adult, was included in telemetry study; 4 were sub-adults; and 1 was a yearling. Two captures were on Fort Stewart (12 traps used) and 3 were on the private property site (6 traps used) in an open, young plantation with a high density of gopher tortoise burrows.

Construction, installation, and maintenance of traps took approximately 360 person-hours from fall 2002 when trap construction began to December 2003 when trap maintenance was no longer necessary. Construction was the least time consuming activity (68 person-hours), followed by installation (120 person-hours) and maintenance (172 person-hours), which included clearing vegetation from the traps prior to prescribed burns. Each day of trapping, we spent about 1 person-hour activating and/or checking traps, or ca.160 person-hours from December 2002 through April 2004.

From 15 December 2002 to 26 March 2003 we ran traps for 306 trap-days (61

person-hours activating and checking traps). No *D. couperi* were captured in traps during

this period. We activated traps only sporadically through most of spring and summer

2003 because of lack of assistance and high temperatures (above maximum for activating

traps). Traps were modified by adding a shelf parallel to the ground and over the trap

entrance in fall 2003. From 28 September 2003 to 21 November 2003 we ran traps for

363 trap-days (70 person-hours activating and checking traps). Between 6 October 2003

and 12 November 2003 traps captured 6 individual *D. couperi* (details above). Trapping

effectiveness, including time spent constructing, installing, maintaining, and checking

traps, for the period which we ran traps was ca. 86.8 person-hours per *D. couperi*

captured (including traps used first year, which may have been ineffective in capturing

large snakes). Excluding time spent constructing, installing, and maintaining traps,

overall trapping efficiency was 26.8 hours per *D. couperi* capture (both original and

modified traps). For the trapping period when *D. couperi* were successfully captured

(September 2003 – November 2003), trapping efficiency was ca. 11.7 hours per *D.*

couperi captured excluding trap construction, installation, and maintenance (in second

year, traps were modified for more effective capture of large snakes). With construction

installation, and maintenance included in the estimate, trapping efficiency for this period

was ca. 71.7 hours per *D. couperi* captured.

Home ranges and activity centers

Bootstrap analysis of 100% MCP annual home ranges calculated for snakes

tracked ≥9 months yielded area curves that approximated asymptotes, suggesting the

existence of definable home ranges for snakes in this study and a sufficient number of

radiolocations for each individual in the annual home range analyses. Bootstrap analysis

of 100% MCP seasonal home ranges for snakes tracked for a complete season also yielded area curves that approximated asymptote, again suggesting definable seasonal ranges and a sufficient number of radiolocations for each individual in seasonal home range analyses. There were insufficient novel radiolocations per individual in the winter to complete bootstrap analysis on the winter ranges.

Fifteen males and 12 females met the criterion for calculating cumulative home ranges (tracked $\geq$9 months). Mean cumulative MCP home range was 381 ha (range = 35-1800). The 95% KD home ranges of males and females were similar to MCPs (individual's MCP area divided by 95% KD area, $\bar{x}$ = 1.1). Cumulative 95% KD home ranges for snakes tracked $\geq$9 months averaged 397 ha (range = 35-2385 ha; Table 2).

Eighteen snakes in 2003 (11M: 7F) and 20 snakes in 2004 (13M: 7 F) were used for annual home range calculations. Males, on average, had larger annual home ranges (2003 MCP $\bar{x}$ = 538 ha, range = 164-1528; 2003 95% KD $\bar{x}$ = 762 ha, range = 178-2385; 2004 MCP $\bar{x}$ = 481 ha, range = 140-1433; 2004 95% KD $\bar{x}$ = 552 ha, range = 113-2136) than females (2003 MCP $\bar{x}$ = 126 ha, range = 32-354; 2003 95% KD $\bar{x}$ = 173 ha, range = 51-459; 2004 MCP $\bar{x}$ = 77 ha, range = 36-124; 2004 95% KD $\bar{x}$ = 79 ha, range = 34-150 (Fig. 2). KD analysis at the 50% isopleths for annual ranges yielded 1 to 3 distinct regions of core habitat use for each snake. Male snakes, on average, had larger annual activity centers ($\bar{x}$ = 94.1 ha) than females ($\bar{x}$ = 14.9 ha). The activity centers (50% KD) averaged ca. 12% of the area calculated for 95% KD ranges.

For seasonal data analysis, we removed snakes with incomplete seasons of telemetry data. Winter 2002-2003 and 2003-2004 seasonal MCP ranges were relatively small for males and females (Fig. 3). On average, males had the largest mean seasonal ranges in

both summer seasons. Average female seasonal home ranges were of similar area in the spring and fall (Fig. 3).

Home range modeling

MCP, 95% KD, and 50% KD annual home range global models confirmed adequate goodness of fit ($P < 0.05$). Residual normality plots of natural-log transformed data supported normality of transformed data in annual range estimates. Autoregressive covariance structure was most appropriate for our data when using AICc on the global model for home range analyses. The annual MCP home range model with sex, size, and overwintering site ranked highest ($\omega = 0.824$) and was 6.2 times more likely than the next best approximating model (Table 3). The 90% confidence set of models contained 3 of 10 candidate models (Table 4).

For annual 95% KD home ranges, the model ranked first included sex, size, and proportion of locations on Fort Stewart versus private property ($\omega = 0.58$) and was ca. 2.5 times more likely than the second ranked model (Table 5). The second ranked model contained sex and size ($\omega = 0.23$) and was ca. 2 times more likely than the third best approximating model. The 90% confidence set of models contained 3 of 9 candidate models (Table 6).

With annual 50% KD activity centers, the model ranked first included only sex and size ($\omega = 0.51$) and was ca. 1.5 times more likely than the second ranked model (Table 7). The second ranked model contained sex, size, and proportion of locations on Fort Stewart versus private property ($\omega = 0.35$). The 90% confidence set of models contained 3 of 9 candidate models (Table 8).

In each annual home range estimate, sex ranked as the most important variable, according to Akaike importance weights; however, size closely ranked second for all estimates. Site ranked third. Number of radiolocations ranked least important in MCP models (Table 9).

The confidence set of models for each home range and activity center estimates suggested a negative influence of sex (being female) and association with Fort Stewart sites on home range size. Home range size correlated positively with body size in all models. Within top ranked models for each range estimate, the 95% confidence intervals of sex and size predictor variables did not span 0, further suggesting that these variables influence intraspecific variation in range size (Tables 4, 6, 8).

Patterns of movement

All snakes tracked >1 year returned to the same sandhill used the previous winter. Of the 20 snakes we captured and implanted the first winter of the study, all that were alive returned to the same overwintering site as the previous 2 winters (n = 9). Individual degrees of fidelity to specific shelters varied; however, all snakes returned to at least one shelter used in the prior year. Most snakes returned to multiple underground shelters that had been used the previous winter.

A few large ranging males in the study (n = 3) traveled 5 to 8 km (linear distance) from overwintering to summer locations. Snakes from the first year traveled primarily to the same areas and used near identical travel corridors the second year. One male used the same travel corridor for two consecutive years, despite clear-cutting of the corridor during winter.

The proportion of radiolocations at novel locations (not previously recorded) 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*season interaction ($F_{3, 70} = 5.73$, $P = 0.002$). Differences in least square means indicated significant difference between males and females, with males showing higher use of novel locations in spring ($\bar{x}_{male} = 0.542$, SE = 0.024; $\bar{x}_{female} = 0.453$, SE = 0.031; $t_{70} = 2.27$, $P = 0.026$) and fall ($\bar{x}_{male} = 0.626$, SE = 0.025; $\bar{x}_{female} = 0.476$, SE = 0.033; $t_{70} = 3.61$, $P < 0.001$), but no difference in proportion of novel locations between males and females in winter ($\bar{x}_{male} = 0.277$, SE = 0.027; $\bar{x}_{female} = 0.302$, SE = 0.031; $t_{70} = 0.60$, $P = 0.550$) or summer ($\bar{x}_{male} = 0.626$, SE = 0.025; $\bar{x}_{female} = 0.691$, SE = 0.033; $t_{70} = 1.57$, $P = 0.121$).

We observed 27 sheds from 17 individual snakes in the field (12 males, 5 females; 1 to 3 sheds per snake). Snakes were inactive for 1 to 3 weeks prior to ecdysis in 16 of 27 shedding events we recorded (14 individuals). Four shedding events were recorded in winter during long periods (> 1 month) of inactivity (4 individuals). We recorded no inactivity prior to ecdysis for 3 of the sheds found (2 individuals). Snakes inactive 1 to 3 weeks prior to ecdysis would rest for 1-2 days, followed by a period of increased activity when foraging behavior was often observed.

Mean daily linear movement distances (Fig. 4), averaged across biweekly periods, varied by sex ($F_{1,30} = 14.7$, $P < 0.001$; repeated measures ANOVA) across seasons ($F_{3,84} = 79.3$, $P < 0.001$), with a non-significant interaction term ($F_{3,84} = 1.8$, $P = 0.16$). Females had smaller daily movement distance than males, regardless of season. Differences in average daily movement (distance) suggested similar average movement between fall and spring for both males ($t_{84} = 1.5$, $P = 0.15$) and females ($t_{84} = 0.9$, $P = $

0.38). Summer average daily movements for males and females were larger than all

other seasons. Winter movements were smaller than other seasons, with no difference

between sexes (t_{84} = 0.1, P = 0.91).

Mean biweekly movement frequency varied by sex ($F_{1, 30}$ = 4.6, P = 0.04;

repeated measures ANOVA) and season ($F_{3, 81}$ = 65.8, $P < 0.001$), with an interaction

effect ($F_{3, 81}$ = 5.9, P = 0.001). Males had larger movement frequency across all seasons

when compared to females; however, this difference was not as large as reported with

movement distance (Fig. 4 and 5). As with the movement distance analysis, difference in

least squares means for mean movement frequency showed similar movement patterns

between fall and spring for females (t_{81} = 0.8, P = 0.44), but a different pattern for males

between spring and fall (t_{81} = 3.3, P = 0.003). We recorded higher movement frequency

in summer compared to all other seasons. Winter movement frequency was smaller than

other seasons, with no difference between sexes (t_{81} = 0.5, P = 0.60; Fig. 5).

Survival analysis

We used 32 radiotracked *D. couperi* in survival analysis. Annual survival for

2003 was 0.890 (SE = 0.074, n = 25). In 2004, annual survival was 0.723 (SE = 0.088; n

= 27). The model-average estimate of monthly survival for snakes tracked between

January 2003 and June 2005 was 0.984 (unconditional SE = 0.006). The model-averaged

estimate of probability of survival for radiotracked snakes during the study was 0.609 (SE

= 0.107).

Five models were included in the 90% model confidence set to evaluate survival

(Table 10). The best approximating model (ω_i = 0.44) included size as standardized by

sex. Survival model-averaged parameter estimates in the confidence set of models

suggested a negative relationship with being female, a positive relationship of overwintering on private property compared with Fort Stewart, and slightly decreasing survival with increasing size (Table 11). Size, as standardized by sex, relative to all other covariates, had a strong negative relationship with survival, suggesting lower survival probability with increasing size within each sex. Our analysis failed to detect a predictive relationship of time on survival. All models that included time or changes over time had little to no support.

Landscape-level habitat use

Landscape-level habitat consisted of 2% road and urban areas, 24% wetlands, 7% agricultural and other fields, 7% clear-cuts and other habitats with sparse canopy cover (CC/sparse), 3% deciduous forest, 51% evergreen forest including evergreen plantations, and 6% pine-hardwood forest. Mean habitat use at radiolocations, with the individual as the sampling unit, averaged 1% on roads, 18% in wetlands, 6% in fields, 20% in CC/sparse, 2% in deciduous forest, 36% in evergreen forest, and 18% in pine-hardwood forest (Fig. 6).

Compositional habitat use analyses suggested nonrandom habitat use at all 3 levels of selection examined (overall selection: $\lambda = 0.229$, $P < 0.001$; home range selection: $\lambda = 0.212$, $P < 0.001$; site selection: $\lambda = 0.324$, $P = 0.011$). Mean differences in proportional use and availability of habitats at 3 levels of selection suggest positive selection for CC/sparse and mixed forest habitat categories (Fig. 7). Rankings for habitat use for overall selection, comparing radiolocations to habitat available from most to least selected included: wetland, evergreen, mixed, CC/sparse, deciduous, roads, and fields. There was no selection difference among the 4 most selected habitats or among the least

3 selected habitats (Table 12). Although wetland and evergreen habitats were used less than available, these habitats were used more than any others, suggesting selection for these areas. Rankings for habitat use for home range selection, comparing habitat composition of the 100% MCP home ranges to habitat available at the study site, from most to least selected included: wetland, evergreen, mixed, field, CC/sparse, roads, and deciduous. Mixed, field, and CC/sparse were tied, with no difference in selection between these habitats (Table 12). Rankings for habitat use for within home range selection, comparing radiolocations to habitat available within respective MCP home ranges, from most to least selected included: evergreen, wetland, mixed, CC/sparse, field, deciduous, and roads. Again, there was little to no selection difference between the 4 most selected habitats or between the last 3 selected habitats (Table 12).

Habitat use, as described by habitat types collected in the field, varied seasonally, corresponding to changes in the amount of area used by the snakes; however, regardless of the season, radiotracked *D. couperi* exhibited high use of sandhills (Fig. 8). Recorded winter habitat use was primarily restricted to xeric uplands with gopher tortoise burrows; 67% of all radiolocations from this period were in sandhills, while 22% were located in young, upland pine plantations with gopher tortoise burrows. All winter plantation locations were recorded in young pine plantations supporting gopher tortoise populations. Habitat use in spring, summer, and fall was concentrated less on xeric upland habitats than observed in winter; however, radiotracked snakes continued to use sandhill habitats throughout the warmer months, with mean use never falling below ca. 35% for any season (Fig. 8). In spring, snakes maintained a strong association with sandhills ($\bar{x} =$ 60% of locations), although mean plantation use dropped from ca. 22% in winter to ca.

8% in spring. Also in spring, mean use of wetlands and clear-cuts increased. Mean use

of sandhill habitats in summer ($\bar{x}$ = 35%) was less than that found in any other season.

Wetland use in summer ($\bar{x}$ = 30%) was higher than recorded in any other season. In fall,

snakes began returning to their overwintering locations, with mean use of wetlands, clear-

cuts, and other uplands less than recorded in summer.

Shelter use

We recorded 76% of all radiolocations in underground shelters. This value

ranged between 70% of locations for females in winter to 82% for males in winter (Fig.

9). Shelter use, in all seasons, was closely associated with gopher tortoise burrows, with

mean use >40%, even in warmer months (Fig. 10). In winter, regardless of sex, >90% of

underground locations were in gopher tortoise burrows. In spring, snakes used gopher

tortoise burrows on an average of 58% of underground locations, with snakes also using

root and stump openings (12%). In summer, use of gopher tortoise burrows was lowest

(44%), while root and stump use was higher than in any other season (22%). In fall,

underground shelter use was similar to that recorded in winter, with high gopher tortoise

burrow use and lower use of all other categories (Fig. 10).

The type of gopher tortoise burrow used on average also varied by season and sex

(Fig. 11). In winter, male and female *D. couperi* shelter use was restricted primarily to

gopher tortoise burrows, with males using a higher proportion of active burrows and

females using a relatively equal proportion of 2 burrow categories. In spring, females

had a higher association with abandoned gopher tortoise burrows while males began

largely using other shelter types. During spring, ca. 60% of female underground

locations were located in abandoned gopher tortoise burrows compared to 24% for male underground locations. In summer, use of gopher tortoise burrows was lowest for both males and females, although females continued to use abandoned burrows an average of 40% of underground locations. Gopher tortoise burrow use in fall was similar between sexes, with males and females using comparable proportions of all burrow categories.

Within landscape-level habitat categories, *D. couperi* tracked in this study used different types of underground shelters as availability of these shelters changed (Table 13). In sandhill habitats, snakes almost exclusively used gopher tortoise burrows. In plantation and field habitats, *D. couperi* also used gopher tortoise burrows to a large extent, and in similar proportions to burrow use seen in sandhill habitats. Wetland habitats did not have gopher tortoise burrows; however, within wetlands there were hummocks of soil, litter, and roots that snakes used. Snakes used root/stump openings on about 65% of underground locations in wetlands, with the remaining underground wetland locations associated with woody debris (28%). Underground shelter use in clear-cuts was restricted primarily to windrows (81%). In uplands and slope forests, snakes most often sought shelter in root/stump openings and in other animal burrows.

Discussion

Home range

For snakes, like many other wildlife groups, home range size is considered an important trait related to several factors such as body size, energetic needs, and resource availability (Gregory et al. 1987, MacCartney et al. 1988). Annual home ranges from this study (male annual MCP $\bar{x}$ ~ 510 ha, range 140-1528 ha) represent the largest home ranges reported in the literature for a North American snake species. For comparison,

previous studies conducted in Georgia on *D. couperi* report home ranges between ca. 5-100 ha (Speake 1978). In a recent *D. couperi* radiotelemetry study in southeastern Florida, preliminary data show annual home ranges (100% minimum convex polygon, MCP) between 65-300 ha for males ($\bar{x}$ = 118, n = 31) and between 30-115 ha for females ($\bar{x}$ = 41, n = 18; R. Bolt, unpublished data). In another *D. couperi* radiotelemetry study conducted in northeastern peninsular Florida, home ranges for males in the summer ranged from 23 to 281 ha (Moler 1985b).

   D. couperi in this study, on average, occupied their smallest seasonal home ranges in winter, intermediate sized seasonal home ranges in spring and fall, and the largest in summer. Regardless of season, females had smaller home ranges than males except in winter when male and female home ranges were most similar. A previous *D. couperi* telemetry study in Georgia (Speake et al. 1978), using 3 seasons and pooled sexes to calculate home ranges, reported smallest home ranges from December through April (ca. 4.8 ha), intermediate sized from May through June (ca. 42.9 ha), and largest from August through November (ca. 97.4 ha). Radiotelemetry data for these seasonal range estimates were collected from individuals tracked over varying periods, generally less than a season, and 24 of 28 snakes tracked were translocated from other areas in south Georgia (Speake et al. 1978), making comparisons with the present study difficult.

   Home ranges were the smallest for males and females during both winters of the study. Because of smaller movements exhibited during winter, we collected the largest number of radiolocations per snake and recorded the highest re-use of underground shelters; therefore, despite being unable to conduct bootstrap analysis on winter ranges, we were confident that the ranges were adequately recorded during winter.

Home range analyses did clearly identify models explaining potential sources of variation for intraspecific differences in home range size with snakes tracked in this study. Home range model including sex, size, and habitat quality, followed by sex and size model ranked highest in analyses of the 2 home range estimators and estimate of activity centers. Reproductive condition and associated behaviors may account for some differences in home range size between males and females, especially in the spring when the females remained on xeric upland habitats while males began dispersing from their overwintering upland habitats and using lowland areas to a greater extent. There was some evidence to suggest a larger sex effect than size effect influencing home range and activity center size, suggesting intersexual differences instead of just differing resource needs for larger individuals. Numerous studies of snake movements have shown home range size variation by sex (e.g., Gibbons and Dorcas 2004), attributed to differential energetic needs and reproductive differences (e.g., Gregory et al. 1987, Whitaker and Shine 2003). Our home range modeling results support these previous conclusions.

Home range modeling also suggested an effect of habitat quality on home range size. Because of higher timber production, lower gopher tortoise burrow densities, and lower burn frequency, the private property portions of the study area may be of lower quality for *D. couperi*. Our home range models reported an increase in home range size with either overwintering on private property or with an increasing proportion of locations on private property. Individuals overwintering or using private property sites may have to travel further distances to obtain resources to meet their biological needs because of the lower density of suitable habitats in these areas.

Because of the high degree of annual home range overlap recorded, we do not suggest that home range analyses provide evidence of territoriality in *D. couperi* tracked in this study, a conclusion also reached by a majority of snake studies (e.g., Gregory et al. 1987). This conclusion is important because *D. couperi* is thought of as opportunistically cannibalistic (Moler 1992, Gibbons and Dorcas 2004). We did observe combat once between 2 radio-tagged males; however, we did not collect any data that indicated potential cannibalism, nor of strict avoidance behavior of adults outside of the breeding period. In general, male home ranges overlapped less than those of females; however, a common pattern observed was that of single male home ranges overlapping with 2 to 3 female ranges. This pattern was also seen with conspecifics in sheltered retreats, where we observed males and females sharing shelters more often than female cohabitation, with few records of males sharing retreats.

In spring 2004 in-field ultrasounds, 6 of 7 females examined were in poor condition, thin and dehydrated, with multiple crusty skin lesions. Despite their apparently compromised health, ultrasounds showed all 7 females in early stages of egg production. Although we did not conduct ultrasounds of females in 2003, the high proportion of females gravid in 2004 (100% of females examined), in addition to accounts of potential annual reproductive output in the wild (Speake et al. 1987) and in captivity (D. Alessandrini, personal communication), suggest that a number of females tracked in spring 2003 may have also been gravid. Female *D. couperi* tracked in the spring of both 2003 and 2004 exhibited smaller ranges and movements than males, suggesting an influence of reproductive condition on female behavior.

Patterns of movement

    D. couperi followed two general movement patterns during the year. All females

and about half of males maintained association with their overwintering grounds

throughout the year, but most larger-ranging males made directional movements in late

spring, and did not return to their respective overwintering grounds until mid-fall. We

defined these movements as home ranges because of returns to overwintering grounds

and results from bootstrapping analyses.

    Many snake species exhibit larger and more frequent movements during the

breeding season (Gibbons and Dorcas 2004); however, *D. couperi* in this study showed

the opposite activity pattern. The breeding season for *D. couperi* occurs during, or just

prior to the coldest months of the year. Snakes in this study maintained close association

with underground shelters, especially throughout winter. Because these shelters, most

commonly gopher tortoise burrows, are generally concentrated on xeric upland habitats,

the species may have a breeding strategy that exploits this period because of the

concentration of individuals during the winter.

    In seasons other than spring, there was less difference between male and female

movement frequency than seen with movement distance, suggesting similar activity

patterns throughout much of the year but at a reduced spatial scale for females. There

was no difference in degree of site-fidelity to specific locations between males and

females overall; however, in spring and fall, males had higher use of novel locations than

females. Use of novel locations was smallest in winter ($\bar{x}_{male} = 0.34$; $\bar{x}_{female} = 0.39$),

which corresponded to smaller movements also recorded in this season. All snakes

tracked >11 months returned to the same overwintering areas as the previous winter and all snakes also re-used specific shelters from the previous winter.

Reported food items for *D. couperi* include fish, frogs, toads, lizards, turtles, turtle eggs, small alligators, birds, small mammals, and snakes, both venomous and nonvenomous species (e.g., Keegan 1944, Groves 1960, Landers and Speake 1980, Moler 1992, Belson 2000). We observed *D. couperi* (either directly, or indirectly though expelled prey items in captivity) consuming: black racers (*Coluber constrictor*), timber rattlesnakes (*Crotalus horridus*), yellow rat snakes (*Elaphe obsoleta quadrivittata*), eastern hognose snakes (*Heterodon platirhinos*), unidentified water snake (*Nerodia* spp.), unidentified frogs (*Rana* spp.), and gopher tortoise hatchlings. We observed 11 feeding events in the field, 9 of these involved other snakes as prey, 3 of which were timber rattlesnakes.

Survival

Our survival analysis suggested the effect of size (body length), as standardized by sex, as the strongest predictor of adult *D. couperi* survival. This result suggests that within adult *D. couperi* at our study sites, larger males and females were more at risk than smaller adults. Model selection also suggested overwintering site as another potential predictor of adult survival, with higher survival at private property sites. It may be difficult to separate impact of site and larger movements on survival. Home range modeling suggested that snakes that over-wintered on private property sites exhibited larger annual home ranges than those overwintering on Fort Stewart. Larger movements and lower habitat quality, or more dispersed quality habitat, can be associated with lower survival probabilities; however, our survival analysis suggested the opposite for habitat

quality. Because of the observational nature of this study, we cannot exclude the possibility that other factors, such as individual variation, environmental factors, or sample size problems, also influence adult *D. couperi* survival at our study sites.

Habitat use

Compositional analysis of habitat use (GAP categories) indicated that wetlands and evergreen forests were used in higher proportions relative to their availability at three hierarchical levels of selection tested. Clear-cut and/or sparse areas ranked third; however, closer inspection of these areas suggest that the snakes were not preferentially using clear-cuts, but instead may be using, to a high degree, young longleaf plantations with gopher tortoise populations.

Seasonal trends in habitat use may be influenced by thermoregulatory requirements, reproductive condition, and foraging needs. Winter included breeding activities on upland habitats and extended periods of inactivity due to cold temperatures. During spring the males began to move from xeric uplands to surrounding habitats, including wetlands and other non-sandhill habitats. Females remained on sandhill habitats longer in spring. During this period, females associated highly with xeric upland habitats and abandoned gopher tortoise burrows in those habitats; ca. 60% of all female underground locations during the spring were in abandoned gopher tortoise burrows, compared to 28% of male locations during the same season. Females complete oviposition by the beginning of July (Speake et al 1987). Other studies have found similar patterns of earlier male emergence from overwintering compared to female emergence (e.g., Parker and Brown 1980, Whitaker and Shine 2003); however, few studies have been completed on species that are active in cold seasons, such as *D. couperi*.

During the summer, males and females depended less on sandhill habitats, but continued to use upland habitats for resting prior to ecdysis and while digesting prey. In fall, habitat use was transitional, as snakes returned to sandhills to over-winter. During fall, we recorded large (>1 km) and relatively rapid movements in half the male snakes tracked. Males that exhibited this behavior returned to overwintering areas in mid-fall, moving these relatively larges distance to locations not previously recorded during the year.

Comparison to previous *D. couperi* studies suggests geographic variation in habitat use, underground shelter use, and periods of activity. *D. couperi* in southern Florida appears to rely less on gopher tortoise burrows, with more general habitat use than populations found in more northern latitudes of *D. couperi's* range (R. Bolt, personal communication, Moler 1985b, Layne and Steiner 1996).

Trapping and surveying

Our trapping efforts captured 6 individual *D. couperi* during 843 trap-days (140.5 trap-days/capture; 26.8 trap-checking hours/capture; 86.8 total hours/capture, including trap construction, installation, and maintenance). Our burrow searching capture efforts resulted in 18 *D. couperi* captured in 43 days (249 person-hours) from December 2002 to March 2003 of surveying sandhills with gopher tortoise burrows (13.8 person-hours/ capture; ca. 1 capture /2.4 days). Examining just the period where trapping was the most effective (fall 2003) and after traps were modified, we had a trapping efficiency rate of 11.7 person-hours per *D. couperi* capture. Adding trap building, installation, and maintenance into the calculation totaled 71.7 person-hours/snake capture.

Although the large snake traps we installed caught *D. couperi* after the first year and after modification, trapping may be less effective than burrow searches at Fort Stewart sites. Trapping may detect *D. couperi* at a site; however, traps used in this study only detected *D. couperi* on 2 of 4 main sandhills where we placed traps and where *D. couperi* were known to exist. In addition, the relative inefficiency of this method and costs of building and maintaining the traps (especially in areas with prescribed burns) may make it viable only in conjunction with other upland sampling goals. Searching verses trapping needs further research, especially in total costs (labor and materials) per snake captured and in efficient trap designs. In general, winter gopher tortoise burrow surveys for *D. couperi* resulted in few sub-adult captures. Thus, trapping may be a useful tool for determining sub-adult demographics than burrow surveys alone.

The efficiency of burrow searches often relies on the experience of the individual surveyor, their knowledge of the area and gopher tortoise burrow locations, and familiarity with the species and its habits. It took about 2 weeks of searching, surveying, and learning the site to capture the first *D. couperi* for the study. These skills are readily learnable; however, trapping may be more effective for studies where surveyors may change frequently or experienced assistance is not available.

The trap design used in this study has been used successfully in multiple large snake (*Pituophis melanoleucus)* surveying efforts across the south (G. Rudolph and M. Bailey, personal communication). Therefore, we cannot comment on potential added capture benefit from our March 2003 addition of a "shelf" radiating parallel to the ground from above each funnel trap entrance. This addition may have aided in making the funnel trap entrances appear less exposed and limit opportunities to crawl over the box trap (30 cm

high with ca. 100 cm high drift fence); however, we do not know if this increased our capture success or if trapping was more effective in fall because of behavioral changes in the snakes. As noted earlier, in fall we observed increases in movement distance (Fig. 4) coupled with increased visits to sandhill habitats compared to summer (Fig. 8). These behavioral factors may have contributed to the increased trapping efficiency we observed in fall 2003 compared to winter 2002-2003.

Previous *D. couperi* trapping efforts in Florida have also captured few individuals. At Avon Park Bombing Range, 15 traps, each consisting of 4 drift fences and 4 funnel traps captured 7 *D. couperi* in 2001 (M. Legare, personal communication). In another Florida study, 1638 trapping days captured 5 individuals using a box trap design with 2 funnel trap entrances and drift fencing for each trap (378 trap days per capture; Layne and Steiner 1996). Another trap design used by Layne and Steiner (1996) in Florida consisted of 7.6 m drift fences radiating from a center with funnel traps placed midway on each side of the fences. This design proved unsuccessful for *D. couperi*, capturing 1 *D. couperi* in 2672 trapping days from 1984 to 1996.

Conservation implications

The specific use of landscape components by a species, as well as the spatial pattern of use, may reflect arrangement of necessary resources such as prey, mates, shelter, and appropriate thermal conditions (Gibbons and Semlitsch 1987, MaCartney et al. 1988). For most mobile animals, including snakes, these resources may be spatiotemporally variable, thus impacting spatial patterns and specific habitat use throughout the year (Gregory et al., 1987). Although measurement and detailed identification of such resources is rarely performed, use measurement of specific

landscape components and spatial pattern of use over time can be used to understand individual or population level resource requirements. This information is vital for formulation of conservation and management guidelines for species-specific conservation efforts.

Our results suggest that temporally, a matrix of heterogeneous habitat types are required for *D. couperi* to meet basic biological needs such as shelter, prey, thermoregulatory requirements, and breeding sites. Although snakes rely heavily upon xeric sandhills throughout winter months, continued use of these upland habitats at such high frequencies throughout the year was unexpected. In addition to the importance of sandhill uplands, wetlands habitats ranked in the top 2 habitat types compared to availability for *D. couperi* tracked in this study. We believe that for Georgia populations, availability of wetland habitats in close association with suitable upland habitats may be necessary for *D. couperi* populations.

Physiographically, sandhill habitats occur naturally as disjunct segments in a scattered distribution over Coastal Plain interspersed with other habitats such as streams and wetlands (Lawler 1977); however, current habitat destruction causes greater fragmentation of sandhills and elimination of natural areas between ridges, which contributes to decline of *D. couperi* populations (Hallam et al. 1998). *D. couperi* requires relatively large tracts of land, especially for a snake species, with dependence on several habitat types throughout the year. Habitat fragmentation and land development, even at low densities, exacerbates *D. couperi* habitat loss because of their large home ranges and movements. The area we used for this study, Fort Stewart and adjacent private property, is one of the largest longleaf pine forests remaining in Georgia. This area potentially

represents one of the last remaining large-scale patches of habitat for the species in the northern half of its range.

We did not record a telemetry location indicating that a snake crossed a paved road. Although we recorded 6 individuals within 100 m of a paved road, all snake locations collected in this study were within boundaries created by paved roads; however, radio-tagged snakes regularly crossed un-paved roads and trails within Fort Stewart and private property. This potential road avoidance behavior we detected may warrant further study, with implications regarding dispersal ability and habitat availability.

Although previous work completed on *D. couperi* suggests strong ties to gopher tortoise burrows during the winter breeding period, use of these shelters has been thought of as opportunistic throughout other times of the year (Speake et al. 1978), with other shelters such as root and stump openings, mammal burrows, and woody debris as suitable alternatives. We suggest this is not a casual relationship, but an integral aspect of the species survival in the northern portion of the range in southeastern Georgia.

In Georgia, we believe that conservation of important habitats is potentially one of the most important factors for maintaining viable *D. couperi* populations; however, it is likely as important to restore land to a state that includes appropriate sheltered retreats (i.e., gopher tortoise burrows), especially for populations in southeastern Georgia. We believe that extensive tracts of undeveloped land including sandhills with gopher tortoise population and adjacent wetland habitats will be needed to maintain sustainable populations of *D. couperi* in southeastern Georgia. Management activities to restore longleaf pine habitats, with an emphasis on also restoring gopher tortoise populations,

such as prescribed burns, longleaf pine planting, wiregrass seeding, and turkey oak removal should benefit *D. couperi* population growth.

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Table 1. Home range and telemetry parameters for *D. couperi* in Bryan and Liberty Counties, Georgia. Home range estimates were calculated from all locations collected per individual throughout the study. Although ranges are displayed for all radiotracked snakes, not all were included in home range analyses (see text).

ID	Sex	SVL (cm)[1]	Total length (cm)	Wt (kg)	Capture date	Site[2]	# Loc-ations	# days tracked	Removed from study	Fate[3]	100% MCP (ha)	95% Kernel (ha)	50% Kernel (ha)
1	M	177	205	3.60	12/17/02	FS	247	711	06/13/05	R	374	193	18
2	M	142	174	1.50	12/19/02	FS	235	705	05/01/05	F	291	258	35
3	M	142	173	1.62	12/29/02	FS	39	180	120/3/03	D	129	229	26
4	M	137	166	1.44	12/29/02	FS	93	380	02/03/04	R	167	171	16
5	F	151	177	1.94	01/09/03	FS	240	609	09/28/04	D	93	99	10
6	M	158	190	1.90	01/10/03	FS	245	669	03/26/05	R	672	729	56
7	F	107	128	0.55	01/20/03	FS	176	508	07/02/04	F	54	53	8
8	F	142	168	1.54	01/21/03	FS	103	390	02/27/04	D	140	132	11
9	F	146	173	1.64	02/02/03	FS	144	490	06/24/04	D	203	256	31
10	M	148	180	1.84	02/02/03	P	226	659	02/22/05	R	712	591	44
11	M	158	183	1.68	02/23/03	P	220	642	02/09/05	R	448	430	77
12	M	191	226	4.26	02/24/03	FS	40	189	09/14/03	D	181	269	76
13	M	156	187	1.72	02/25/03	FS	248	630	12/06/04	R	429	472	28
14	F	124	150	1.20	02/25/03	FS	122	335	02/15/04	D	75	55	5
15	M	152	182	1.60	02/26/03	P	219	626	05/01/05	D	246	134	10
16	M	178	210	2.78	03/09/03	P	44	205	10/17/03	D	1340	2385	602
17	M	182	216	3.16	03/09/03	P	246	626	02/21/05	R	1120	984	133
18	F	130	157	1.20	03/23/03	FS	254	619	05/31/05	R	106	88	18
19	M	169	203	2.60	04/02/03	P	207	605	04/01/05	F	1800	1668	145
20	F	152	181	1.90	04/11/03	P	114	363	04/20/04	D	354	371	38
21	M	180	212	3.66	10/06/03	P	123	289	12/06/04	R	157	164	24
22	M	145	173	1.52	10/06/03	FS	196	416	12/08/04	R	550	364	31
23	M	159	192	2.34	11/11/03	P	150	377	12/08/04	R	334	212	18
24	M	182	217	3.58	11/16/03	FS	66	89	02/29/04	D	10	27	6
25	M	130	157	1.08	11/25/03	FS	122	228	07/29/04	F	254	490	82
26	F	145	175	1.70	11/28/03	P	40	92	03/15/04	D	3	11	2
27	F	146	173	1.78	12/30/03	P	134	322	06/01/05	R	73	95	10
28	M	118	143	0.72	01/15/04	P	132	311	06/01/05	R	141	182	19
29	F	114	136	0.76	020/3/04	FS	150	295	05/01/05	F	36	34	4
30	F	142	169	1.66	020/3/04	P	120	295	06/01/05	R	124	148	14
31	F	156	186	2.28	02/04/04	FS	139	292	07/23/05	F	83	73	6
32	F	140	167	1.56	03/01/04	FS	158	269	06/13/05	R	59	66	11

[1]SVL: Snout-vent length.
[2]Capture site: Fort Stewart (FS); private property (P).
[3]Fate: Dead (D) - Known mortality;
Removed (R) - Transmitter successfully removed and animal released;
In-field (F) - Animal still in field with transmitter, presumed alive.

Table 2. Cumulative 100% minimum convex polygon (MCP) and 95% kernel density

(KD) home ranges, mean of individual MCP and KD ratios, and 50% KD activity centers

for *D. couperi* radiotracked ≥9 months, Liberty and Bryan Counties, Georgia, January

2003 through December 2004.

	100% MCP (ha)	MCP Range	95% KD (ha)	95% KD Range	MCP/ KD	MCP/ KD Range	50% KD	50% KD Range
Male (n = 15)	592	140-1800	617	134-2385	1.1	0.5-1.9	84.1	10-660
Female (n = 12)	117	35-354	122	35-371	1.0	0.8-1.4	27.5	4.4-83
Mean (n = 27)	381	35-1800	397	35-2385	1.1	0.5-1.9	59.0	4.4-660

Table 3. Candidate models for annual MCP home ranges for radiotracked *D. couperi*,
Liberty and Bryan Counties, Georgia, 2003-2004. Models are listed in AICc order by
predictor variables, with number of parameters (K), log-likelihood (Log L), AICc, ΔAICc,
model likelihood, and Akiake weights (ω) for the set of candidate models (*i*).

Model	K	Log L	AICc	ΔAICc	Model Likelihood	ω_i
Sex, Size, Site	6	-49.2	114.60	0.00	1.00	0.824
Sex, Size	5	-52.7	118.26	3.66	0.16	0.132
Sex, Size, Sex x Size	6	-52.6	121.40	6.80	0.03	0.027
Sex, Size, Site, Locations, Sex x Size	8	-49.2	122.40	7.80	0.02	0.017
Sex, Site	5	-61.8	136.46	21.86	0.00	0.000
Sex	4	-67.0	143.82	29.22	0.00	0.000
Size, Site	5	-65.6	144.06	29.46	0.00	0.000
Size	4	-69.4	148.62	34.02	0.00	0.000
Site	4	-82.6	175.02	60.42	0.00	0.000
Locations	4	-87.2	184.22	69.62	0.00	0.000

Model parameters: Sex (being female), Size (snout-vent length), Site (overwintering
location on Fort Stewart versus private property), Locations (number of telemetry
locations).

Table 4. Estimates of fixed and random effects for the 90% confidence set of models for
MCP home ranges for radiotracked *D. couperi,* Liberty and Bryan Counties, Georgia,
2003-2004.

Model	Effect	Parameter	Estimate	SE	Lower 95% CL	Upper 95% CL
Sex, Size, Site	Fixed	Sex (being F)	-0.985	-0.212	-1.423	-0.547
		Size	0.021	-0.005	0.009	0.033
		Site (Winter on FS)	-0.382	-0.199	-0.794	0.029
	Random	Intercept	2.786	-0.891	0.948	4.624
		Residual	0.245	-0.282	0.159	0.938
		Year (repeated)	0.610	-0.159	0.282	0.427
Sex, Size	Fixed	Sex (being F)	-1.050	-0.223	-1.510	-0.591
		Size	0.024	-0.006	0.011	0.036
	Random	Intercept	2.220	-0.887	0.393	4.048
		Residual	0.276	-0.069	0.179	0.482
		Year (repeated)	0.657	-0.146	0.371	0.944

Model parameters: Sex (being female); Size (snout-vent length); Site (overwintering
location on Fort Stewart (FS) versus private property).

Table 5. Candidate models for annual 95% kernel density home ranges for radiotracked *D. couperi*, 2003-2004, Liberty and Bryan Counties, Georgia. Models are listed in AICc order by predictor variables, with number of parameters (K), log-likelihood (LogL), AICc, delta AICc, model likelihood, and Akiake weights (*ω*) for the set of candidate models (*i*).

Model	K	LogL	AICc	ΔAICc	Model Likelihood	ω_i
Sex, Size, Site%	6	-70.4	157.00	0.00	1.00	0.575
Sex, Size	5	-73.0	158.86	1.86	0.40	0.227
Sex, Size, Private property, Sex x Size	7	-70.1	160.09	3.09	0.21	0.122
Sex, Size, Sex x Size	6	-72.6	161.40	4.40	0.11	0.064
Sex, Site%	5	-76.1	165.06	8.06	0.02	0.010
Sex	4	-80.0	169.82	12.82	0.00	0.001
Size, Site%	5	-81.9	176.66	19.66	0.00	0.000
Size	4	-85.4	180.62	23.62	0.00	0.000
Site%	4	-91.7	193.22	36.22	0.00	0.000

Model parameters: Sex (being female), Size (snout-vent length), Site% (proportion of locations on Fort Stewart versus private property).

Table 6. Estimates of fixed and random effects for the 90% confidence set of models for 95% KD home ranges for radiotracked *D. couperi*, Liberty and Bryan Counties, 2003-2004.

Model	Effect	Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI
Sex, Size Site%	Fixed	Sex (being F)	-1.016	-0.276	-1.585	-0.447
		Size	0.019	-0.007	0.003	0.034
		Site% (on FS)	-0.424	-0.258	-0.956	0.108
	Random	Intercept	3.398	-1.161	1.003	5.794
		Residual	0.416	-0.103	0.270	0.721
		Year (repeated)	0.555	-0.195	0.173	0.938
Sex, Size	Fixed	Sex (being F)	-1.092	-0.284	-1.677	-0.507
		Size	0.021	-0.007	0.005	0.037
	Random	Intercept	2.788	-1.138	0.445	5.132
		Residual	0.451	-0.112	0.293	0.784
		Year (repeated)	0.581	-0.183	0.222	0.940
Sex, Size, Sex x Size	Fixed	Sex	-2.623	-2.230	-7.215	1.968
		Size	0.018	-0.009	-0.002	0.037
		Sex (being F)*size	0.011	-0.015	-0.024	0.045
	Random	Intercept	3.348	-1.374	0.519	6.177
		Residual	0.450	-0.112	0.291	0.786
		Year (repeated)	0.600	-0.179	0.248	0.952

Model parameters: Sex (being female), Size (snout-vent length), Site% (proportion of locations on Fort Stewart (FS) versus private property).

Table 7. Candidate models for annual 50% kernel density activity centers for radiotracked *D. couperi*, 2003-2004, Liberty and Bryan Counties, Georgia. Models are listed in AICc order by predictor variables, with number of parameters (K), log-likelihood (LogL), AICc, delta AICc, model likelihood, and Akaike weights (ω) for the set of candidate models (*i*).

Model	K	LogL	AICc	ΔAICc	Model Likelihood	ω_i
Sex, Size	5	-92.4	197.7	0.00	1.00	0.508
Sex, Size, Site%	6	-91.1	198.4	0.74	0.69	0.351
Sex, Size, Sex x Size	6	-92.4	201.0	3.34	0.19	0.096
Sex, Size, Private property, Sex x Size	7	-91.9	203.7	6.04	0.05	0.025
Sex, Site%	5	-96.2	205.3	7.60	0.02	0.011
Sex	4	-98.6	207.0	9.36	0.01	0.005
Size, Site%	5	-97.6	208.1	10.40	0.01	0.003
Size	4	-99.6	209.0	11.36	0.00	0.002
Site%	4	-107.2	224.2	26.56	0.00	0.000

Model parameters: Sex (being female), Size (snout-vent length), Site% (proportion of locations on Fort Stewart versus private property).

Table 8. Estimates of fixed and random effects for the 90% confidence set of models for 50% KD activity centers from radiotracked *D. couperi*, Liberty and Bryan Counties, Georgia, 2003-2004.

Model	Effect	Parameter	Estimate	SE	Lower 95% CL	Upper 95% CL
Sex, Size	Fixed	Sex (being F)	-1.033	-0.362	-1.778	-0.288
		Size	0.024	-0.009	0.004	0.045
	Random	Intercept	0.175	-1.455	-2.822	3.172
		Residual	0.737	-0.181	0.479	1.277
		Year (repeated)	0.545	-0.199	0.155	0.936
Sex, Size, Site%	Fixed	Sex (being F)	-0.968	-0.359	-1.708	-0.227
		Size	0.022	-0.009	0.001	0.042
		Site% (on FS)	-0.379	-0.335	-1.070	0.312
	Random	Intercept	0.742	-1.513	-2.381	3.865
		Residual	0.707	-0.174	0.461	1.224
		Year (repeated)	0.527	-0.208	0.121	0.934
Sex, Size, Size x Sex	Fixed	Sex	-1.008	-2.854	-6.886	4.871
		Size	0.024	-0.011	-0.001	0.050
		Sex (being F)*size	0.000	-0.020	-0.045	0.044
	Random	Intercept	0.166	-1.761	-3.460	3.792
		Residual	0.737	-0.182	0.479	1.277
		Year (repeated)	0.545	-0.201	0.152	0.938

Model parameters: Sex (being female), Size (snout-vent length), Site% (proportion of locations on Fort Stewart (FS) versus private property).

Table 9. Akaike importance weights for model parameters from annual MCP and 95% KD

home ranges and for 50% KD activity centers for radiotracked *D. couperi*, Liberty and

Bryan Counties, Georgia, 2003-2004.

Model Parameter	Candidate models	Importance weights		
		Annual MCP	Annual 95% KD	Annual 50% KD
Sex	6	1.00	1.00	1.00
Size	6	0.99	0.99	0.98
Site (or Site%)	5	0.84	0.71	0.39
Size x Sex	2	0.04	0.19	0.12
Locations	2	0.02		

Model parameters: Sex (being female), Size (snout-vent length), Site (overwintering
location on Fort Stewart versus private property), Site% (proportion of
locations on Fort Stewart versus private property), Locations (number of telemetry
locations).

Table 10. Candidate models used to evaluate survival of radiotracked *D. couperi*,

Liberty and Bryan Counties, Georgia, January 2003 through June 2005. All models

include an intercept term.

Model	AICc	ΔAICc	ω_i	Model Likelihood	K
Size (standardized)	98.790	0	0.436	1	2
Size (standardized), Site	100.61	1.817	0.175	0.402	3
Sex	101.31	2.516	0.124	0.284	2
Intercept	101.56	2.765	0.109	0.250	1
Size	102.53	3.739	0.067	0.154	2
Sex + Site	103.27	4.477	0.046	0.106	3
Site	103.56	4.764	0.040	0.092	2
Sex(time)	135.39	36.60	0.000	0.000	29
Time	137.69	38.90	0.000	0.000	30
Site (time)	138.38	39.59	0.000	0.000	28
Size (standardized; time)	140.15	41.35	0.000	0.000	30

Model parameters: Sex (being female), Size (snout-vent length), Site (on private property),
Size (standardized; snout-vent length standardized by sex)

Table 11. Survival model-averaged parameter estimates, unconditional standard errors, and confidence intervals for individual covariate effects on survival in radiotracked *D. couperi*, Liberty and Bryan Counties, Georgia, January 2003 through June 2005.

Parameter	Beta	SE	95% Confidence Interval	
			Lower	Upper
Intercept	3.835	1.008	1.860	5.811
Size (standardized)	-0.880	0.429	-1.721	-0.038
Site	0.148	0.265	-0.520	0.520
Sex	-0.070	0.195	-0.382	0.382
Size	-0.030	0.135	-0.265	0.265

Model parameters: Sex (being female), Size (snout-vent length), Site (on private property), Size (standardized; snout-vent length standardized by sex)

Table 12. Log-ratio matrix of differences in preference between pairs of landscape-level habitat types calculated as the log of the ratio between the relative preferences for radiotracked *D. couperi*, 2003-2004, Bryan and Liberty Counties, Georgia. A positive value indicates that the column habitat was used relatively more than the row habitat and a negative value indicates less use. Numbers marked with an asterisk (*) represent significant deviation from random at $P < 0.05$. Rank 6 represents the most important habitat to the study animals when comparing relative use to availability, rank 0 represents the least important habitat.

	Road/Urban		Wetland		Field		Clear-Cut/Sparse		Deciduous		Evergreen		Mixed Forest		
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Rank
Home range selection															
Road/Urban															1
Wetland	-1.13*	0.30													6
Field	-0.01	0.46	0.71	0.45											3
CC/Sparse	-0.64	0.43	0.72	0.40	-0.66	0.51									3
Deciduous	0.14	0.61	1.10*	0.38	0.74	0.51	0.38	0.47							0
Evergreen	-1.17*	0.26	0.05	0.14	-0.92	0.47	-0.67	0.34	-1.05*	0.44					5
Mixed	-0.49	0.56	0.51	0.32	0.16	0.43	-0.22	0.48	-0.59*	0.26	0.46	0.38			3
Within home range selection															
Road/Urban															0
Wetland	-1.51*	0.38													5
Field	-0.45	0.69	1.22*	0.51											2
CC/Sparse	-1.03	0.60	0.31*	0.51	-1.06	0.78									3
Deciduous	-0.31	0.72	1.25	0.49	0.05	0.78	0.94	0.71							1
Evergreen	-1.47*	0.41	-0.04	0.17	-1.05*	0.52	-0.35	0.51	-1.29*	0.48					6
Mixed	-1.12	0.59	0.02	0.43	-0.48	0.75	-0.29	0.56	-1.23	0.67	0.06	0.40			4
Overall selection															
Road/Urban															1
Wetland	-2.89*	0.42													6
Field	0.07*	0.65	2.96*	0.64											0
CC/Sparse	-1.86	0.86	1.03	0.76	-1.93*	0.85									3
Deciduous	-0.54	0.77	2.35*	0.58	-0.61	0.89	1.32	0.82							2
Evergreen	-2.88*	0.45	0.01	0.21	-2.95*	0.67	-1.02	0.75	-2.34*	0.61					5
Mixed	-2.37*	0.90	0.52	0.65	-2.44*	0.98	-0.51	0.90	-1.83*	0.66	0.51	0.71			4

Table 13. Underground shelter use for radiotracked *D. couperi* by landscape-level habitat type, 2003-2004, Liberty and Bryan Counties, Georgia. Values are the average proportion of underground radiolocations, with the snake as the experimental unit.

	GT Burrow	Root/ Stump	Windrow	Mammal	Wood Debris	Armadillo
Sandhill	0.85	0.06	0.00	0.03	0.01	0.06
Plantation	0.92	0.03	0.01	0.01	0.01	0.01
Field	0.71	0.12	0.00	0.11	0.01	0.04
Upland	0.16	0.59	0.01	0.06	0.12	0.06
Slope	0.10	0.40	0.00	0.45	0.00	0.05
Clear-Cut	0.06	0.01	0.81	0.00	0.12	0.00
Wetland	0.00	0.65	0.00	0.03	0.28	0.04
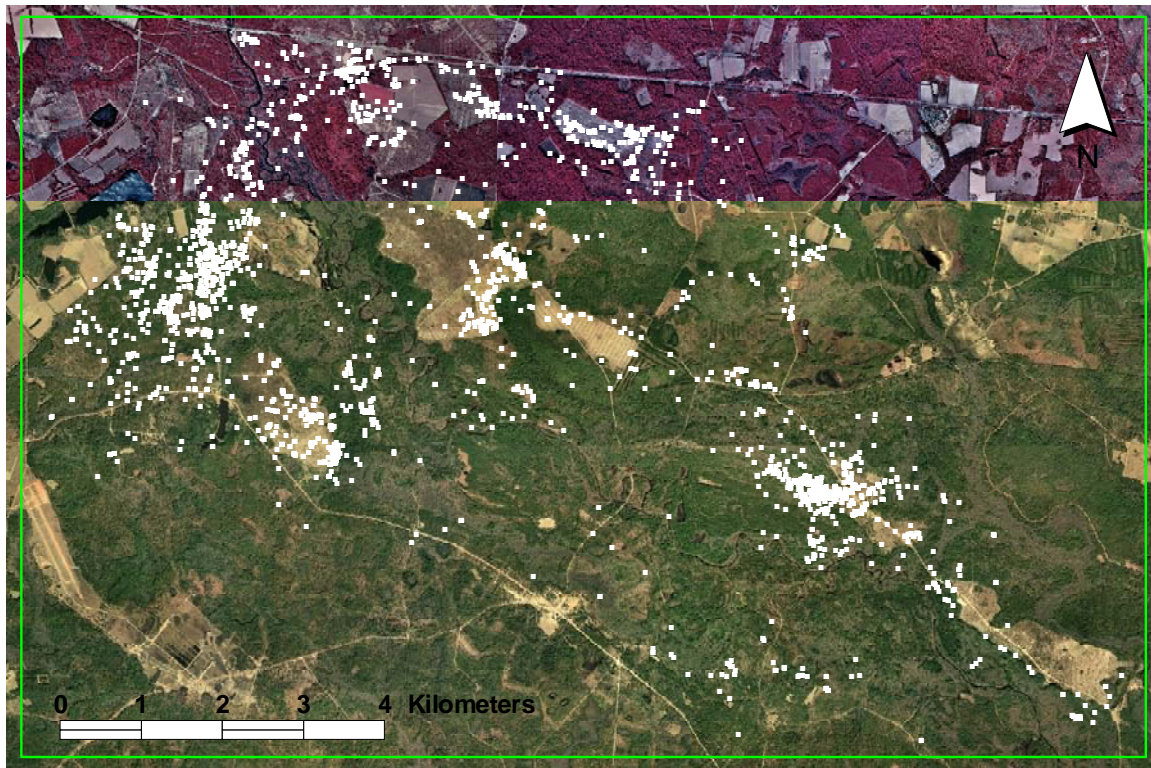
Fig. 1. Spatial distribution of *D. couperi* radiolocations (white dots) collected between January 2003 and December 2004, Liberty and Bryan Counties, Georgia. Red line represents Fort Stewart boundary; green rectangle is approximate boundary of study site (area ~ 167 km^2).
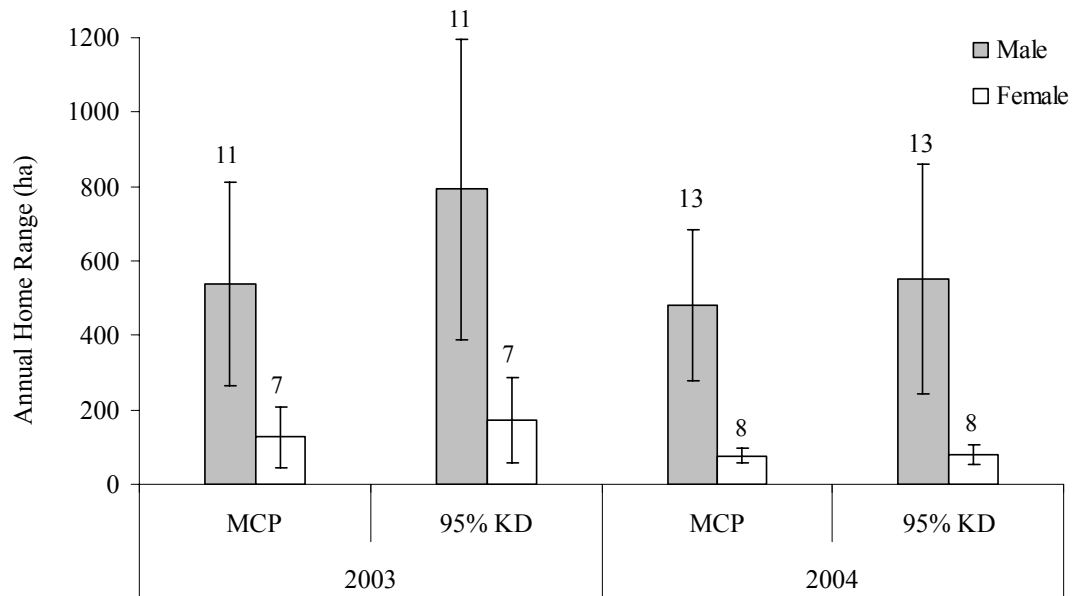
Fig. 2. Mean 100% minimum convex polygons (MCP) and 95% kernel density (KD) annual home ranges (ha; 95% CI) for male and female radiotracked *D. couperi*, 2003-2004, Bryan and Liberty Counties, Georgia. All snakes tracked ≥ 9 months. Sample sizes indicated above bars.
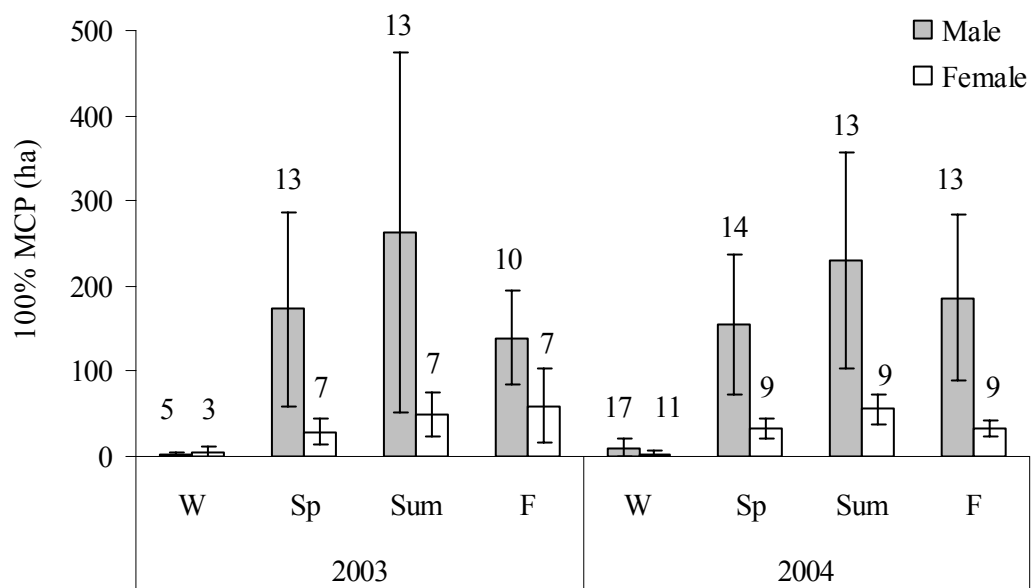
Fig. 3. Mean 100% minimum convex polygon (MCP) seasonal home ranges (95% CI) for male and female *D. couperi* radiotracked for complete seasons, 2003 and 2004, Bryan and Liberty Counties, Georgia.
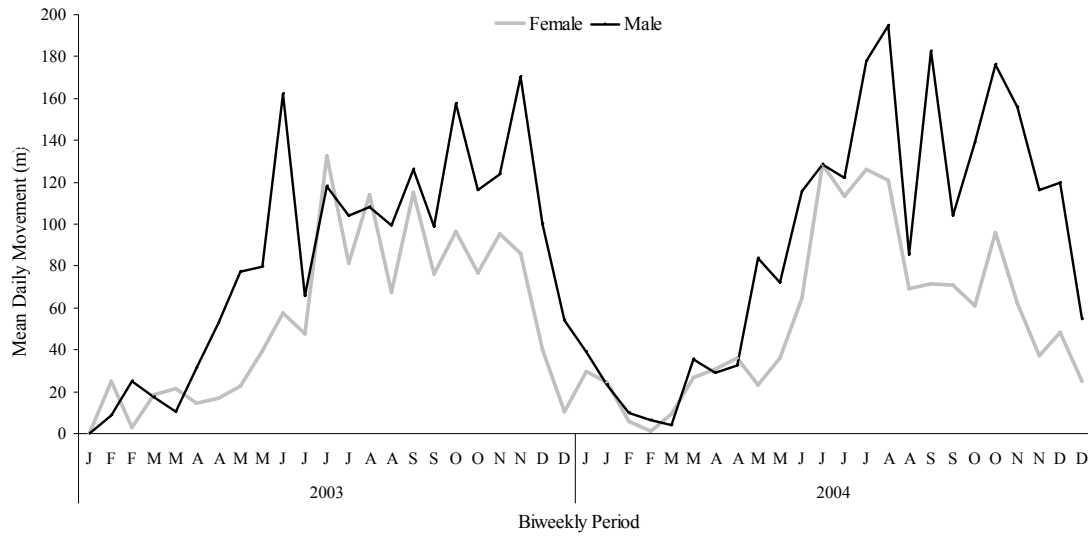
Fig. 4. Mean daily movement distance, averaged over each 2-week period of 2003 and 2004 for male and female *D. couperi* radiotracked in Liberty and Bryan Counties, Georgia. Month abbreviations in each year denote the approximate 2-week period, with 2 periods per month (except for January 2003, with only the second half of the month included).

Fig. 5. Mean movement frequency for each 2-week period of 2003 and 2004 for male and female *D. couperi* radiotracked in Liberty and Bryan Counties, Georgia. Month abbreviations in each year denote the approximate 2-week period, with 2 periods per month.
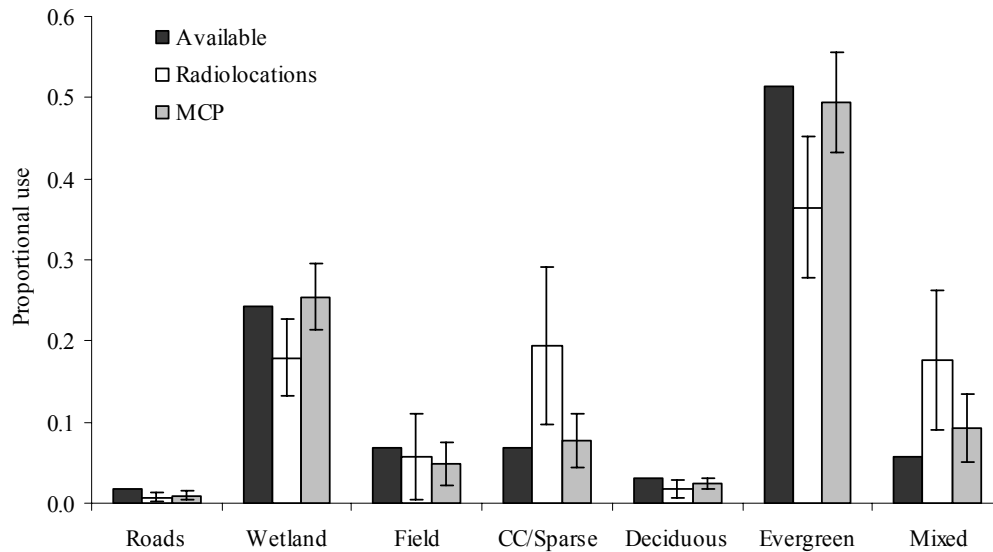
Fig. 6. Proportion of habitats available at the study site, mean proportion at radiolocations (± 95% CI), and mean proportion within 100% minimum convex polygon cumulative home ranges (± 95% CI) for radiotracked *D. couperi*, 2003 and 2004, Liberty and Bryan Counties, Georgia. Habitat types were derived from GAP classifications and included: roads and urban areas (roads); open water, forested, and non-forested wetlands (wetlands); agricultural and other fields (field); clear-cuts and other sparsely vegetated habitats (CC/sparse); forests with at least 75% deciduous trees (deciduous); forests with at least 75% evergreen trees, including managed pine plantations (evergreen); and pine-hardwood mixed forest, including shrub/scrub habitats (mixed).
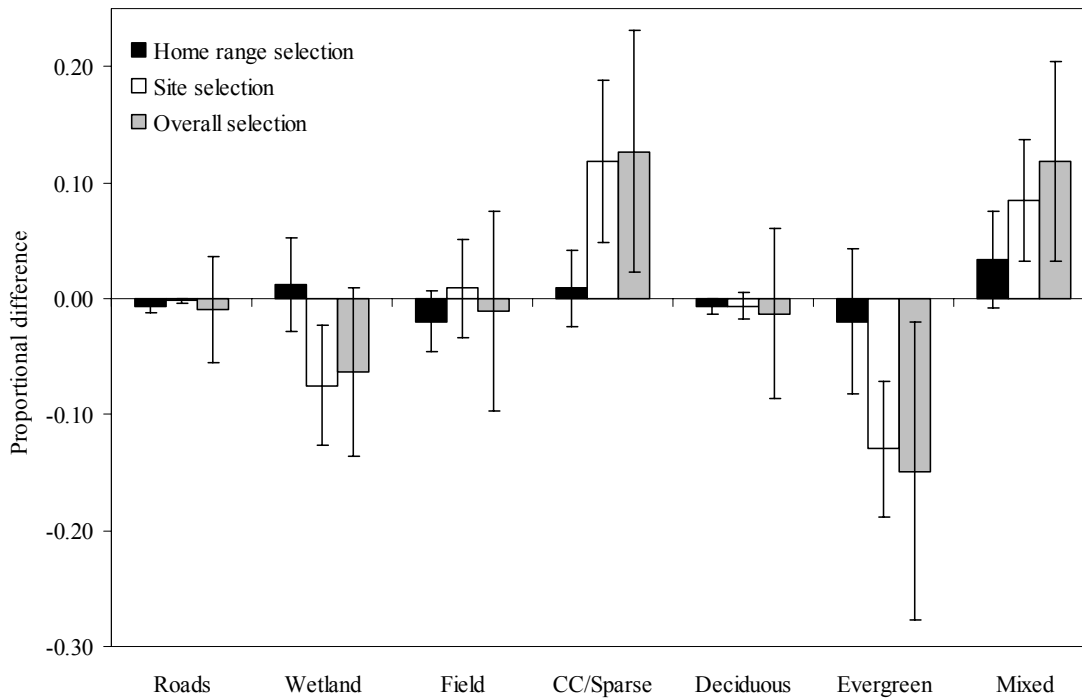
Fig. 7. Mean differences in proportional use and availability of habitats ($\pm$ 95% CI; n = 27) for radiotracked *D. couperi*, 2003 and 2004, Liberty and Bryan Counties, Georgia. See Fig. 6 for GAP habitat type descriptions. Home range selection contrasts landscape-level habitat composition of 100 % minimum convex polygon home ranges of individuals to habitat composition of the study area. Site selection was evaluated by comparing habitat at radiolocations to the 100% MCP home ranges. Overall selection compared habitat at individual radiolocations with the proportion of habitats available at the study site.
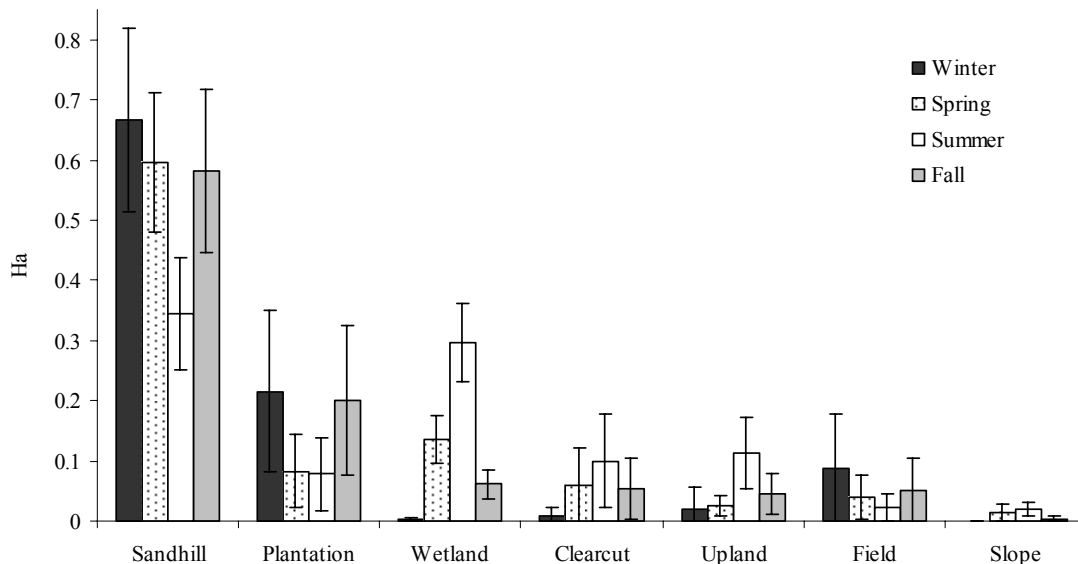
Fig. 8. Mean proportional (± 95% CI) *D. couperi* seasonal landscape-level habitat use, 2003 and 2004, Bryan and Liberty Counties, Georgia. Habitat categories were recorded during radiotracking and include: sandhill (xeric uplands with longleaf pine overstory and gopher tortoise burrows), clear-cut, field (includes old-field, low maintenance hay fields, and food plots), plantation, slope forest (transitional habitat between xeric uplands and wetlands), miscellaneous uplands (xeric uplands with mixed overstory composition), and wetlands.
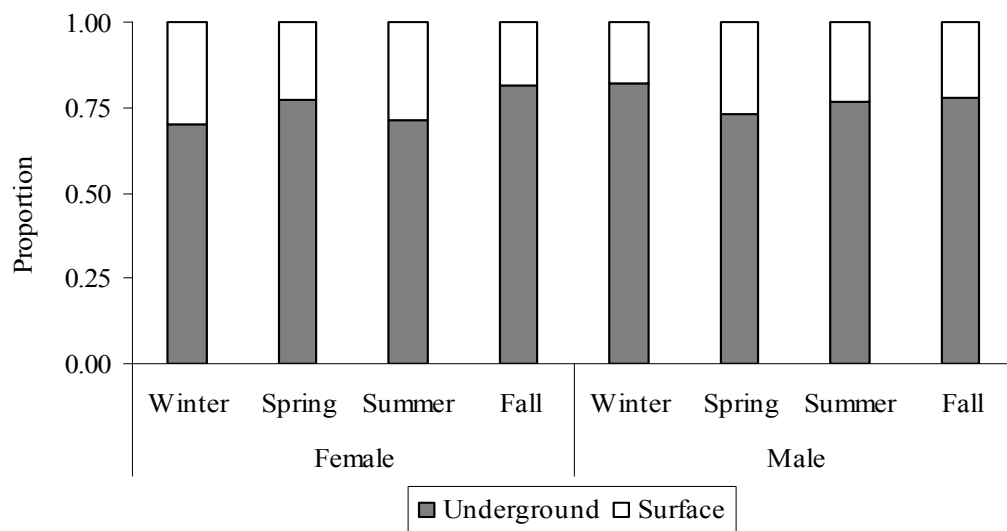
Fig. 9. Mean proportion of surface and underground radiolocations for males (M) and

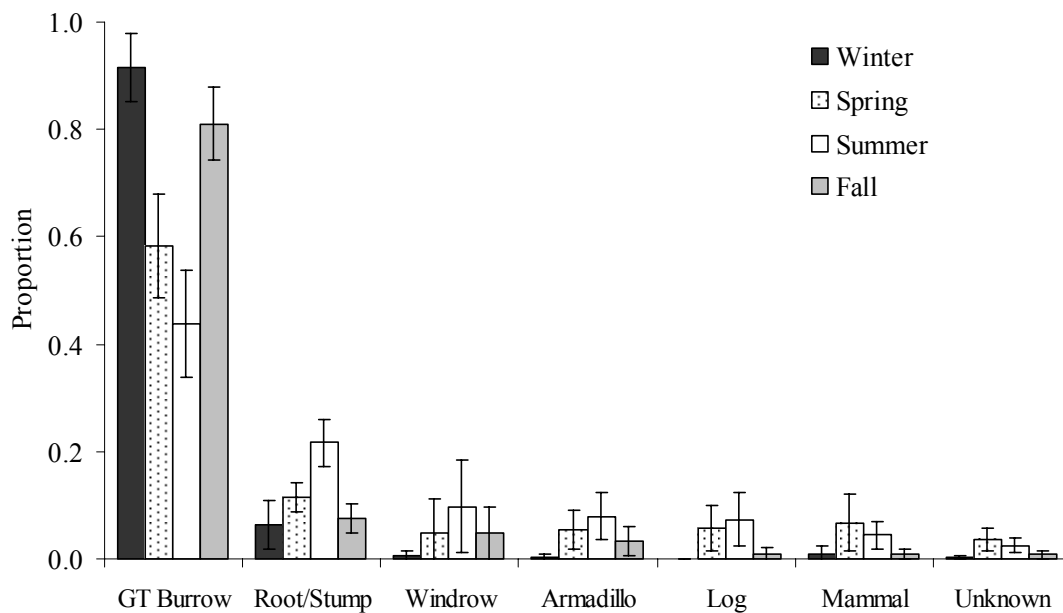females (F) *D. couperi*, 2003-2004, Bryan and Liberty Counties, Georgia.

Fig. 10. Mean (± 95% CI) underground shelter use for *D. couperi* radiotracked in winter

(n = 30), spring (n = 32), summer (n = 28), and fall (n = 26) in Liberty and Bryan

Counties, Georgia, 2003-2004. Underground shelter types include: gopher tortoise

burrows (GT burrow), root and stump openings (root/stump), debris piles created during

timber harvest and site preparation (windrow), armadillo burrows, shelters associated

with fallen woody debris (log), burrows created by mammals other than armadillos

(mammal), and unknown underground shelters. Values on the y-axis represent the mean

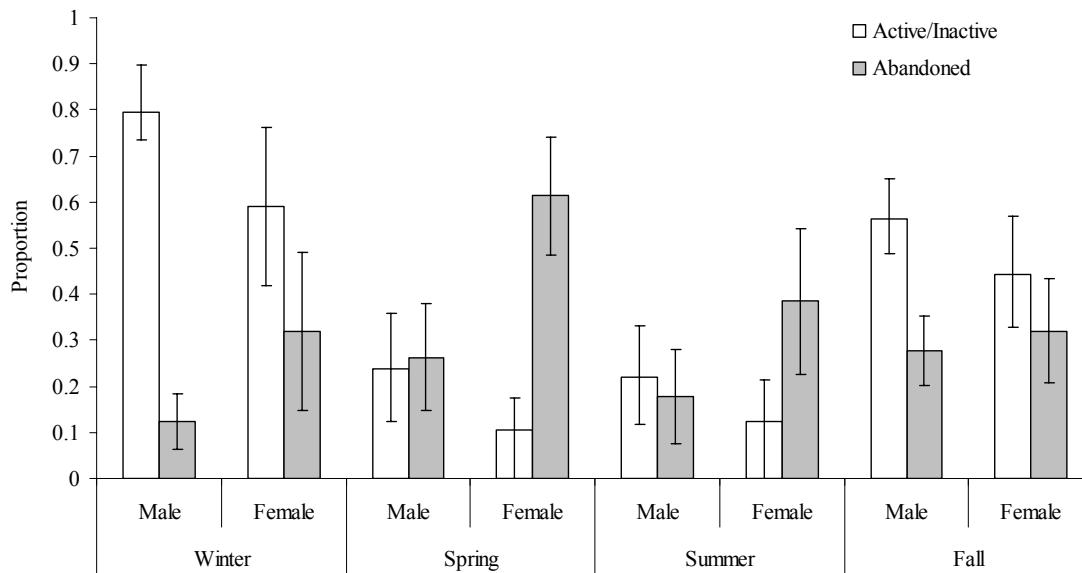proportion of underground locations, with the individual as the sampling unit.

Fig. 11. Mean seasonal (± 95% CI) *D. couperi* gopher tortoise burrow use for male and female radiotracked snakes at active/inactive and abandoned burrows in Liberty and Bryan Counties, Georgia, 2003-2004. Values on the y-axis represent the mean proportion of underground locations, with the individual retained as the sampling unit.