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# Terrestrial Habitat Use by Aquatic Turtles from a Seasonally Fluctuating Wetland: Implications for Wetland Conservation Boundaries

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ABSTRACT. – **Terrestrial habitat use by eight sympatric species of aquatic turtles was monitored at Dry Bay, a Carolina bay wetland on the Upper Coastal Plain of South Carolina, USA. During a three-year study, a total of 1446 captures and recaptures, averaging 1.2 turtles/d, was made at a drift fence that completely encircled the wetland. Emigrations (defined as movements away from Dry Bay to other water bodies) totaled 152 (10.5%), whereas immigrations (defined as arrivals from other water bodies) totaled 99 (6.8%). Hatchlings arriving at Dry Bay from nests accounted for 409 captures (28.3%). Gravid females exiting the bay on nesting forays accounted for 271 captures (18.7%). Turtles exiting Dry Bay to seek terrestrial refugia within the adjacent upland habitat (and later returning) accounted for 515 captures (35.6%). Five species of turtles used adjacent upland terrestrial habitats for refugia. *Deirochelys reticularia* and *Kinosternon subrubrum* were found commonly in refugia during late summer through winter at distances up to 165 m and 135 m, respectively, from the delineated wetland boundary. Some *Sternotherus odoratus*, *Chelydra serpentina*, and *Kinosternon baurii* also used terrestrial refugia. The average duration in refugia was 185 d for *Deirochelys* and 170 d for *Kinosternon*. A majority of turtles selected a closed-canopy pine-oak forest, but some entered a recently clearcut (4–8 year-old), open-canopy pine plantation. Most turtles in the closed-canopy forest remained inactive until they returned to the water in March, while many in the clearcut changed their location one or more times. Individual turtles demonstrated site fidelity to refugia in successive years. *Trachemys scripta* and *Pseudemys floridana* did not use upland refugia but emigrated directly towards other bodies of permanent water, demonstrating the need for movement corridors. Nests were clustered in specific open-canopy upland areas, whereas terrestrial refugia were dispersed throughout the forest that surrounded the wetland. Adjacent upland terrestrial habitats, as used by turtles, are critical components of the wetland ecosystem. Because upland habitats are used for seasonal refugia, nesting, and as corridors to other water bodies, human alteration of such habitats will affect the survival of individuals and the long-term persistence of turtle populations.**

KEY WORDS. – **Reptilia; Testudines; Emydidae; Kinosternidae; Chelydridae; *Deirochelys reticularia*; *Kinosternon subrubrum*; *Kinosternon baurii*; *Sternotherus odoratus*; *Chelydra serpentina*; *Trachemys scripta*; *Pseudemys floridana*; *Clemmys guttata*; turtle; ecology; conservation; buffers; Carolina bays; critical upland habitats; corridors; landscape management; site fidelity; survivorship; terrestrial refugia; wetlands delineation; South Carolina; USA**

Organisms living in natural, seasonally fluctuating wetlands include those in greatest need of conservation management due to human alteration of the landscape. Within the last 200 years, more than 53% of the wetlands of the United States have been eliminated by human activities (Meffe and Carroll, 1994), and wetland habitats continue to be destroyed, altered, or left isolated in fragmented landscapes (Tiner, 1987). Improved land management and successful design of natural area preserves requires natural history information of target species (Noss, 1987; Burkey, 1989; Hansson 1991; Congdon and Dunham, 1994; Dunning et al., 1995). At present, wetland boundaries for conservation purposes currently are delineated by their soils, hydrology, and vegetation, but without consideration to zoology (Willard et al., 1990). However, empirical evidence suggests that the protection of upland terrestrial habitats surrounding wetlands is critical to maintaining wetland herpetofaunal components (Gibbons, 1970; Wygoda, 1979; Semlitsch, 1981, 1983, 1998; Buhlmann et al., 1993; Dodd, 1993; Burke and Gibbons, 1995; Dodd, 1995, 1996; Graham, 1995; Means et al., 1996; Lewis and Ritzenthaler, 1997; Madison, 1997; Palis, 1997).

Our study was conducted to provide a better understanding of annual terrestrial habitat use by a suite of turtle species that occurred in a seasonally fluctuating wetland, thus providing information that could be used for turtle conservation, management, and improved ecological delineation of wetland systems.

## MATERIALS AND METHODS

*Study Site.* — Studies were conducted between 1993 and 1997 at Dry Bay, a Carolina bay, on the U.S. Department of Energy's (DOE) Savannah River Site (SRS), on the Upper Coastal Plain in Aiken County, South Carolina, USA. Occurring in the southeastern United States, Carolina bays are elliptical wetlands of uncertain geological origin (Sharitz and Gibbons, 1982; Lide, 1997) and collectively they contain a diverse flora and fauna (Benke, 1976; Mahoney et al., 1990; Gibbons et al., 1997; Sharitz and Gresham, 1998; Taylor et al., 1998).

Dry Bay and the surrounding upland area have been designated a DOE Research Set-Aside (Davis and Janecek, 1997). When full, Dry Bay is approximately 4.8 ha, and 0.8–2.1 m deep. Dry Bay has dried only twice since 1967, in 1981 and 1986 (Gibbons and Semlitsch, 1991). The bay did not dry during this study (Fig. 1), although water surface area was reduced by 50% at times. The bay contains areas of open water, as well as patches of water lilies (*Nymphaea* spp. and panic grass (*Panicum hemitomon*). The edge is dominated by buttonbush (*Cephalanthus occidentalis*) and a narrow strip of black gum (*Nyssa sylvatica*), sweet gum (*Liquidambar styraciflua*), and bald cypress (*Taxodium distichum*). The adjacent upland habitats include an open-canopy, loblolly pine (*Pinus taeda*) plantation (PP) on the southern side of Dry Bay that extends 1200 m to a bottomland floodplain forest. Clearcut in 1989, the pine plantation (PP) aged from four to eight years during the study. Closed-canopy, mixed forest (MF) is found on the other three sides and includes several patches of 60-yr-old loblolly pine and laurel oak (*Quercus hemisphaerica*), and stands of 40-yr-old slash pine (*Pinus elliotii*) and other hardwoods. A two-lane paved highway on the west side separates Dry Bay from MF and two other Carolina bays at distances of 440 and 515 m away. A grass-dominated powerline right-of-way (ROW) is 280 m northeast of Dry Bay and an old logging road is located along the south side. Aerial photographs from 1943 indicate that Dry Bay was surrounded at that time by agricultural fields containing the loblolly pine patches that are still present.

Eight species of turtles have been recorded from Dry Bay: eastern chicken turtle (*Deirochelys reticularia*), yellow-bellied slider (*Trachemys scripta*), Florida cooter (*Pseudemys floridana*), eastern mud turtle (*Kinosternon subrubrum*), common musk turtle (*Sternotherus odoratus*), common snapping turtle (*Chelydra serpentina*), striped mud turtle (*Kinosternon baurii*), and spotted turtle (*Clemmys guttata*).

*Methodology.* — Fyke nets and hoop nets (Buhlmann, 1995) were used during 1993 to determine population size and species composition of the aquatic turtle assemblage at Dry Bay. Four *Deirochelys* were monitored with radiotelemetry during 1993 to obtain preliminary data about movements and behavior. During August 1994, a 1006 m drift fence that completely enclosed Dry Bay was constructed of 0.75 m tall aluminum sheeting. Thirty openings were made in the fence approximately every 35 m. A live animal trap (raccoon size, Tomahawk Live Trap Co., Tomahawk, WI) was installed in each opening to capture all turtles exiting the wetland. Trap mesh size allowed unhindered passage of small mammals, snakes, most frogs, and salamanders. Adult and juvenile turtles entering the wetland were recovered by hand on the outside of the fence and pitfall buckets were used to capture hatchlings. The fence was patrolled for turtles at least daily (usually in the afternoon) from 24 August 1994 to 31 December 1997 (1225 days). In addition, the fence was monitored several times daily during nesting seasons and after major rains. Environmental variables recorded each time the fence was checked included date, time, precipitation (cm) since last patrol, air and water temperatures (°C; current, max, min), water depth (cm), estimated cloud cover, and wind speed.

The boundary of the Dry Bay wetland was delineated using U.S. Army Corps of Engineers methodology (Army

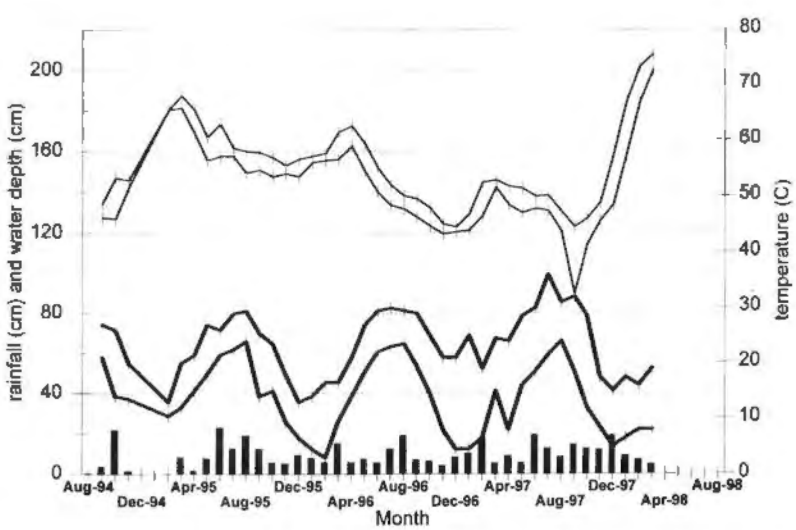


**Figure 1.** Water depth, water temperature, and rainfall at Dry Bay, August 1994 – March 1998. Maximum and minimum monthly water depths (cm, left axis) are represented by the two upper thin lines. Maximum and minimum monthly water temperatures (°C, right axis) are represented by the two lower thick lines. Cumulative monthly precipitation (cm, left axis) is indicated as vertical bars.

**Table 1.** Total numbers of individual turtles captured in the Dry Bay population, 1993–97.

| Species | Males | Females | Juveniles* | Total MFJ | Hatchlings** | Total Individuals |
|---|---|---|---|---|---|---|
| *Chelydra serpentina* | 7 | 5 | 7 | 19 | 27 | 46 |
| *Clemmys guttata* | 2 | 0 | 0 | 2 | 0 | 2 |
| *Deirochelys reticularia* | 95 | 24 | 74 | 193 | 207 | 400 |
| *Kinosternon baurii* | 7 | 0 | 0 | 7 | 0 | 7 |
| *Kinosternon subrubrum* | 34 | 17 | 3 | 54 | 7 | 61 |
| *Pseudemys floridana* | 17 | 22 | 3 | 42 | 38 | 80 |
| *Sternotherus odoratus* | 68 | 101 | 3 | 172 | 25 | 197 |
| *Trachemys scripta* | 51 | 57 | 29 | 137 | 52 | 189 |
| Totals | | | | 626 | 356 | 982 |

* juveniles that had survived at least one growing season
** turtles marked entering the bay as hatchlings, but never recaptured during the study

Corps of Engineers, 1987). The placement of the wetland delineation line was determined by presence and percentage of obligate and facultative plant species (Resource Management Group, Inc., 1992) and soil structure using Munsell Soil Color Charts (Kollmorgen Corp., 1975).

Each captured turtle was taken to the laboratory and given an individual code by marking marginal scutes (Cagle, 1939; Gibbons, 1969). Data collected from each turtle included date of capture, plastron length (PL; mm), weight (g), preanal tail length (mm), and location along the fence. Females were x-rayed (Gibbons and Greene, 1979). Since weather conditions often differed from the time a turtle was captured and when it was returned from the lab (usually within 1–2 days), turtles were always released into the bay nearest their point of exiting or entering. Turtles subsequently exited the bay, usually within 1–30 d after being returned from the lab, and were placed outside the fence. A thread bobbin (32 mm x 11 mm, 175 m of thread, Culver Textile Co., West New York, NJ; or 63 mm x 25 mm, 305 m, The Game Tracker Co., Flushing, MI) was attached to the dried carapace with duct tape. The end of the thread was attached to a stake flag and the turtle released. Each thread trail was followed within several days to determine direction of emigration or to locate nest sites or terrestrial refugia. Not every turtle could be successfully thread-tracked to its destination. Some thread trails were broken; duct tape would not stick to turtles with profuse algal accumulations on the carapace (notably *Sternotherus*, and some *Deirochelys*); some *Chelydra* would return to the wetland after human disturbance.

Locations of terrestrial refugia were plotted with measuring tape and compass and entered into an XY coordinate layout (QuatroPro 6.0, Corel Corp. Ltd.). Global Positioning System (GPS) technology was unable to obtain readings and locate most refugia under forest canopy. However, 13 GPS northing and easting points (UTMs) were collected (GPS: Trimble ProXR, Trimble Navigation Ltd, Sunnyvale, CA) from identifiable locations on the landscape. GPS points were used to convert XY-coordinates into UTM positions and thus plot turtle refugia onto aerial photographs. Distances of refugia from the delineated wetland boundary were calculated using GIS software (ArcView 3.0a, Environmental Systems Research Institute Inc., Redlands, CA). Miniature data loggers (Onset Computer Corp, Pocasset, MA) were used to monitor temperatures in selected refugia from September 1995 to May 1996.

## RESULTS

*Turtle Population and Movements.* — Between August 1994 and December 1997, 982 individuals of eight turtle species were captured at Dry Bay (Table 1). *Deirochelys reticularia* was the most abundant resident at Dry Bay, followed in decreasing abundance by: *S. odoratus*, *T. scripta*, *K. subrubrum*, *P. floridana*, and *C. serpentina*. Males of both *K. baurii* and *C. guttata* were visitors from other sites. A total of 1446 captures and recaptures was made at the drift fence, averaging 1.2 turtles/d. Emigrations (defined as movements away from Dry Bay to other water bodies) totaled 152 (10.5%), whereas immigrations (defined as arrivals from other water bodies) totaled 99 (6.8%; includes adults and juveniles). Hatchlings arriving at Dry Bay from nests accounted for 409 captures (28.3%). Gravid females exiting the bay on nesting forays accounted for 271 captures (18.7%). Turtles exiting Dry Bay to seek terrestrial refugia within the adjacent upland habitat (and later returning) accounted for 515 captures (35.6%).

*Description of Refugia.* — Thread-tracked turtles traveled away from the bay into surrounding terrestrial habitat and excavated subsurface refugia. Well-drained sites were selected. Turtles dug head first through the duff and humus layer, and into the sandy soil below (Wagram Series soils, well-drained, moderately permeable; Rogers, 1990). Refugium depths varied among turtles; the top of the carapace was usually 2–6 cm below the sandy soil surface. Litter depth above buried turtles ranged from 6–12 cm in MF and 3–6 cm in PP. Refugia soils were moist and soft; dry sand and hard-packed soils were avoided or soon abandoned. Initially, a refugium entrance could be identified in the leaf litter, but it was obscured with the next rain or leaf fall. Turtles in refugia were inactive but alert (i.e., individuals would hiss or shift their body in response to stimuli, such as probing fingers).

*Deirochelys* accounted for 267 instances of refugium use (122 males, 110 un-sexed juveniles, 35 juvenile females); 169 were successfully thread-tracked (Fig. 2). All males and juveniles (including those having completed their first growing season) captured in aquatic traps in Dry Bay also were captured at the drift fence; those that failed to exit in a given autumn were never recaptured and are believed dead. No non-gravid adult female *Deirochelys* exited the bay, but gravid females used terrestrial refugia (28 instances) in association with nesting (see Nesting Forays).

All adult male and female *K. subrubrum* in Dry Bay used terrestrial refugia during the study and accounted for 80 instances of fall-winter use (48 males, 30 females, 2 juveniles) and 30 instances of summer use (10 females, 20 males); 52 were successfully thread-tracked (Fig. 2). Two male *K. baurii* wintered in terrestrial refugia (Fig. 2).

For female *Sternotherus*, 74 instances of exiting to presumably use refugia were recorded; 24 turtles were successfully thread-tracked to refugia (Fig. 2). However, turtles that had lost their threads returned to Dry Bay during the same time period as turtles from known refugia locations. Ten male *Sternotherus* exited, but none buried in refugia, and all returned to the wetland within one day.

*Chelydra* accounted for 24 (10 males, 7 females, 7 juveniles) exits to presumed refugia; two were successfully thread-tracked to upland terrestrial refugia (Fig. 2). Two other *Chelydra* wintered in the moist mud of a dry drainage ditch they encountered in MF (Fig. 2). Other refugia were not located, but all turtles returned to Dry Bay near their exiting point in the spring and thus were suspected of wintering in upland refugia.

*Trachemys* and *Pseudemys* did not use upland habitat for refugia, but instead as movement corridors between other permanent water habitat (see Emigration).

*Seasonality of Refugium Use.* — Most movements to terrestrial refugia occurred during August through November (Fig. 3), but earliest dates of exiting the bay varied among years. *Deirochelys* first exited in August (1994 and 1995), July (1996), and May (1997). *Kinosternon subrubrum* first exited in August (1994-96) and May (1997). *Sternotherus* exited in September (1994) and August (1995-97) and always during rain. *Deirochelys* and *K. subrubrum* exited on sunny or rainy days. A trend of decreasing water depth and warmer water temperatures in August with earlier exiting of turtles was noted each subsequent year.

*Refugium Habitat and Distance.* — All 24 successfully thread-tracked *Sternotherus* sought refugia in MF habitats. Of 169 successfully tracked *Deirochelys*, more selected MF ($n = 96$, 57%) than PP ($n = 73$, 43%) (G- test, Gadj. = 6.25, $p < 0.05$) over the course of the study. In 1994, when PP was most open, 42 of 52 (81%) *Deirochelys* used MF rather than PP ($n = 10$, 20%). Of 52 *K. subrubrum*, more selected MF ($n = 35$, 67%) than PP (17 turtles, 33%) (G-test, Gadj = 12.54, $p < 0.05$). Of the 24 instances of refugia use by 12 *Chelydra* (6 males, 2 females, 4 juveniles), 20 sought refugia in MF and 4 in PP.

Distances to refugia from the delineated wetland boundary differed among species (F = 14.65, df = 2, 244, $p < 0.0001$), with *Sternotherus* remaining closer to the wetland than *Deirochelys* and *K. subrubrum* (Table 2; Fig. 2). Maximum distances of refugia from the delineated wetland boundary were 164.6 m (*Deirochelys*), 134.5 m (*K. subrubrum*), and 48.7 m (*Sternotherus*), but do not include post-

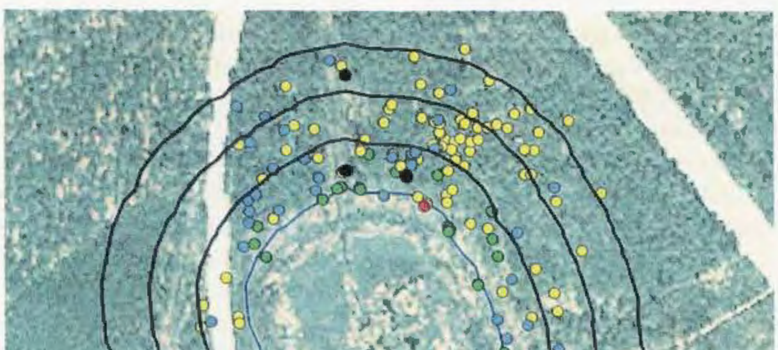

**Figure 2.** Dry Bay, a Carolina bay wetland, and the surrounding upland environment. Colored circles indicate the locations of terrestrial refugia for *Deirochelys reticularia* (yellow), *Kinosternon subrubrum* (blue), *Sternotherus odoratus* (green), *Chelydra serpentina* (black), and *Kinosternon baurii* (red) during 1994–97. The inner blue line represents the delineated wetland boundary. The three black lines represent 50, 100, and 150 m boundaries from the delineated wetland boundary. A two-lane state highway borders Dry Bay on the west (left) and a powerline right-of-way is located to the northeast (right).

**Table 2.** Distances (m) from the delineated wetland boundary of Dry Bay that turtles of three species were found in terrestrial refugia, 1993–96. A negative value indicates a refugium inside the delineated wetland boundary.

| Species | Year | *n* | Mean | ± 1 S.D. | Minimum | Maximum |
|---|---|---|---|---|---|---|
| *Deirochelys reticularia* | 1993 | 4 | 120.1 | 29.1 | 95.5 | 162.3 |
| | 1994 | 44 | 57.8 | 40.2 | -3.7 | 143.4 |
| | 1995 | 85 | 51.8 | 40.7 | -1.6 | 164.6 |
| | 1996 | 36 | 51.2 | 37.2 | -2.4 | 128.3 |
| | Total | 169 | 54.9 | 40.7 | -3.7 | 164.6 |
| *Kinosternon subrubrum* | | 52 | 44.6 | 32.8 | -4.0 | 134.5 |
| *Sternotherus odoratus* | | 24 | 12.8 | 16.7 | -8.4 | 48.7 |

nesting *Deirochelys* (see Nesting Forays). Refugium distances from the wetland for *Deirochelys* did not differ among years ($F = 0.39$, df = 2, 162, $p = 0.6776$, Table 2). Mean distance of *Deirochelys* refugia from the wetland was greater in MF ($\bar{x} = 63.8$ m ± 43.2) than PP ($\bar{x} = 43.2$ m ± 34.1) ($F = 11.28$, df = 1, 167, $p < 0.001$). Mean distances of *K. subrubrum* refugia did not differ between MF ($\bar{x} = 47.4$ m ± 38.1) and PP ($\bar{x} = 38.7$ m ± 16.8) ($F = 0.80$, df = 1, 50, $p = 0.3751$).

Only adults of *K. subrubrum* (63–88 mm PL) and *Sternotherus* (63–73 mm PL) sought refugia, but first year juveniles, mature males, and large juvenile females of *Deirochelys* (54–141 mm PL) used refugia. Smaller *Deirochelys* sought refugia slightly closer to the wetland than larger individuals (ANOVA, $F = 5.16$, df = 4, 164, $r^2 = 0.097$, $p < 0.001$). Mean refugium distance for *Deirochelys* in the smallest size category (54–69 mm PL) was 44.1 m ± 34.5, whereas turtles in the 103–119 mm PL category averaged 92.7 m ± 40.1.

*Direction of Travel to Refugia.* — Most movements of turtles to terrestrial refugia occurred to the north, east, and south (Fig. 2). No turtles crossed the highway on the west side of Dry Bay during autumn 1994; two crossed in 1995 and did not return. In 1995, one *Deirochelys* and two *K. subrubrum* traveled to the edge of the pavement, but turned around and retreated back towards the bay and selected refugia. One of these *K. subrubrum* attempted to cross the road three times before selecting a refugium on the grassy edge of the road. In 1996, four *Deirochelys* and one *K. subrubrum* crossed the highway and found refugia in the forest (Fig. 2); one *Deirochelys* and the *K. subrubrum* did not return. Upon emerging from a refugium, one *Deirochelys* attempted to cross the road to return to the bay four times, but each time retreated back from the pavement edge and into the forest. It was located and returned to the bay by hand.

*Duration in Refugia.* — The number of days turtles remained in terrestrial refugia differed among species ($F = 95.57$, df = 2, 209, $p < 0.0001$). *Deirochelys* ($n = 150$, $\bar{x} = 184.8$ d ± 24.6, range = 121–285 d) and *K. subrubrum* ($n = 47$, $\bar{x} = 169.9$ d ± 60.5, range = 19–323 d) were not different from each other, but *Sternotherus* ($n = 15$, $\bar{x} = 50.5$ d ± 44.3, range = 1–128 d) remained in refugia for shorter periods of time. Most *Sternotherus* returned to the water by early February of each year, whereas *K. subrubrum* returned mid-February to mid-March and *Deirochelys* returned from late February to mid-April. The greatest number of consecutive days in a refugium for *Deirochelys* was 285 d (1 August 1996 – 13 May 1997) for a juvenile female and 271 d (2 August 1996 – 30 April 1997) for an adult male. One male *K. subrubrum* remained in a refugium for 323 d (7 July 1996 – 26 May 1997). For *Deirochelys* and *K. subrubrum* combined, the number of days spent on land among PP ($\bar{x} = 182.9$ d ± 15.3) and MF ($\bar{x} = 183.2$ d ± 20.0) were not different ($p = 0.473$). Some *K. subrubrum* used refugia during the summer months for shorter periods of time (June–September; 11–65 d), although some did not return until the following spring (e.g., the *K. subrubrum* that remained in a refugium from July to May). *Chelydra* exited the bay from mid-September to late October and returned by late March to early April. Four *Chelydra* (not thread-tracked) were presumably in refugia as long as 157, 167, 183, and 223 d. Two *K. baurii* used refugia from early September to late February.

*Behavior in Refugia.* — *Deirochelys* and *K. subrubrum* that searched for terrestrial refugia in MF moved directly away from the bay, whereas those in the thick underbrush of PP made many turns, even circling back on their previous

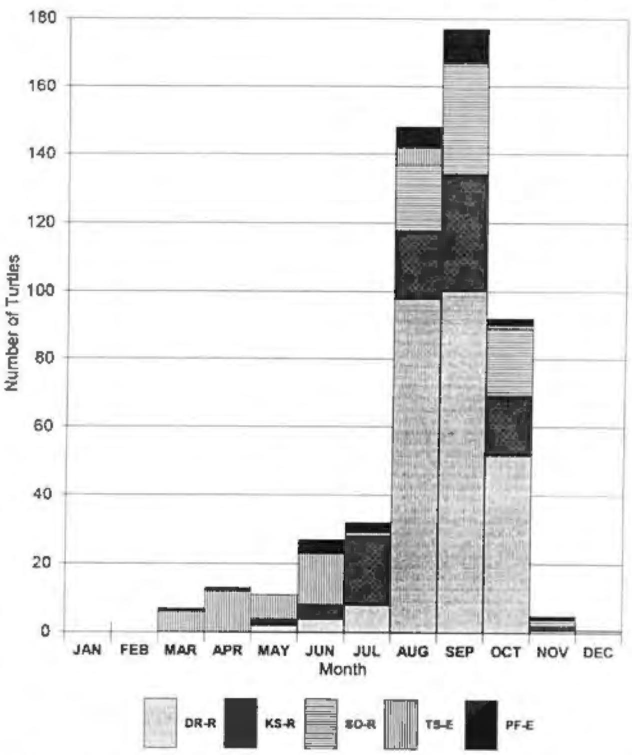


**Figure 3.** Number of turtles by species exiting from the bay to use terrestrial refugia or emigrate to other sources of water, by month for all years 1994–97. DR-R = *D. reticularia* to refugia, KS-R = *K. subrubrum* to refugia, SO-R = *S. odoratus* to refugia, TS-E = *T. scripta* emigrating, and PF-E = *P. floridana* emigrating.

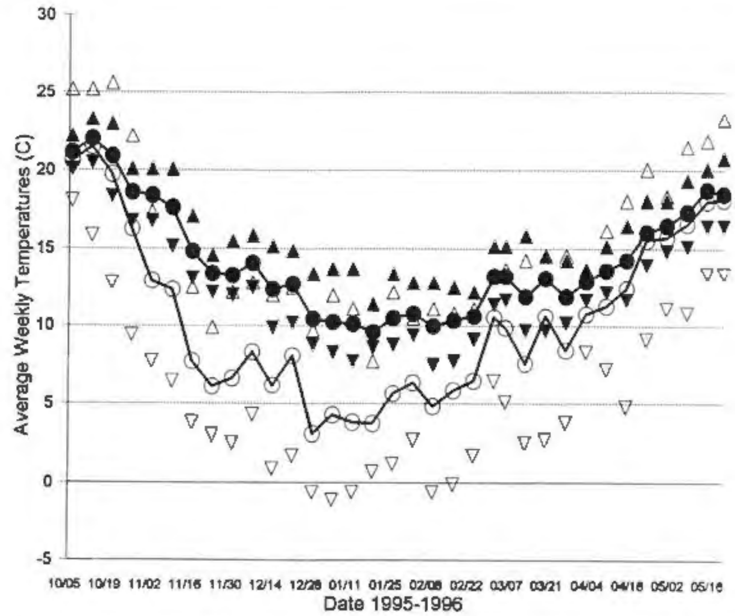


**Figure 4.** Average weekly temperatures of terrestrial turtle refugia in the closed-canopy, mixed forest (MF) and recently clearcut, open-canopy, pine plantation (PP) surrounding Dry Bay for the period 5 October 1995 – 16 May 1996. Solid triangles and circles indicate maximum and minimum plus mean weekly temperatures for MF. Open triangles and circles indicate maximum and minimum plus mean weekly temperatures for PP.

path. Turtles in PP often abandoned their initial refugia during autumn and found replacements when substrate temperatures apparently became too hot. In both 1994 and 1995, 90.3% ($n = 31$) and 90.6% ($n = 32$) of *Deirochelys* in MF stayed in the first refugium they selected, whereas in PP only 38.5% ($n = 13$) and 43.8% ($n = 48$) remained at the first refugium they selected. In PP, six *Deirochelys* each dug 5–8 different refugia during autumn, and four others returned to the wetland after apparently failing to find a suitable refugium. In 1994 and 1995, 100% and 89% of all *K. subrubrum* remained in the first MF refugium selected, whereas in 1994 only 28% that selected PP refugia remained in their first refugium. However, 100% remained in their first PP refugium in 1995. No *Sternotherus* sought refugia in PP.

*Refugium Temperatures and Mass Loss.* — Data collected at four representative refugia in both MF and PP (one reading every 2.4 hrs, 27 September 1995 – 9 May 1996) detected significant differences in soil temperature (Fig. 4). Turtles in MF refugia ($\bar{x}$ = 14.22°C ± 3.6) experienced less temperature fluctuation than turtles in PP refugia ($\bar{x}$ = 10.45°C ± 5.4; t-test, $p < 0.001$). Mean temperature in PP was hotter than in MF during both initial and final stages of the terrestrial period. During the coldest period, temperatures in PP were as low as -1.1°C, contrasting with 7.5°C in MF (Fig. 4).

Body mass lost (g) by *Deirochelys* in refugia did not differ between PP ($n = 41$, $\bar{x}$ = -6.1 g ± 4.1) and MF ($n = 32$, -7.4 g ± 4.0; $p = 0.077$). Percent body mass lost was not different (PP = -7.3% ± 5.6; MF = -7.7% ± 4.9, $p = 0.395$). However, in both habitats some smaller *Deirochelys* lost a greater proportion of their body weight than larger ones (Fig. 5).

*Site Fidelity to Refugia.* — Of 54 *Deirochelys* that exited Dry Bay in 1994, 35 also sought refugia in 1995, and 27 (77.0%) were captured exiting the bay either in the same trap (ST) or within the same quadrant (SQ; within ±45°) of the drift fence. In 1996, 10 of those 35 turtles again exited the bay and 8 (80%) were captured in ST or SQ.

Of 22 *K. subrubrum* that sought refugia in 1994, 9 again sought refugia in 1995 and 8 (88.9%) were captured either in ST or SQ. In 1996, 8 of those 9 exited the bay and 7 (87.5%) were captured in ST or SQ. Of 5 *K. subrubrum* that exited the bay for the first time in 1995, 3 again sought refugia in 1996 and all (100%) were captured either in ST or SQ. The maximum separation distance between the refugia of one male *K. subrubrum* for four consecutive years (1994–97) was 29.8 m.

Eleven female *Sternotherus* exited the bay in 1994; of those, 7 sought refugia in 1995 and 6 (85.7%) were captured either in ST or SQ. In 1996, all 7 turtles (100%) were

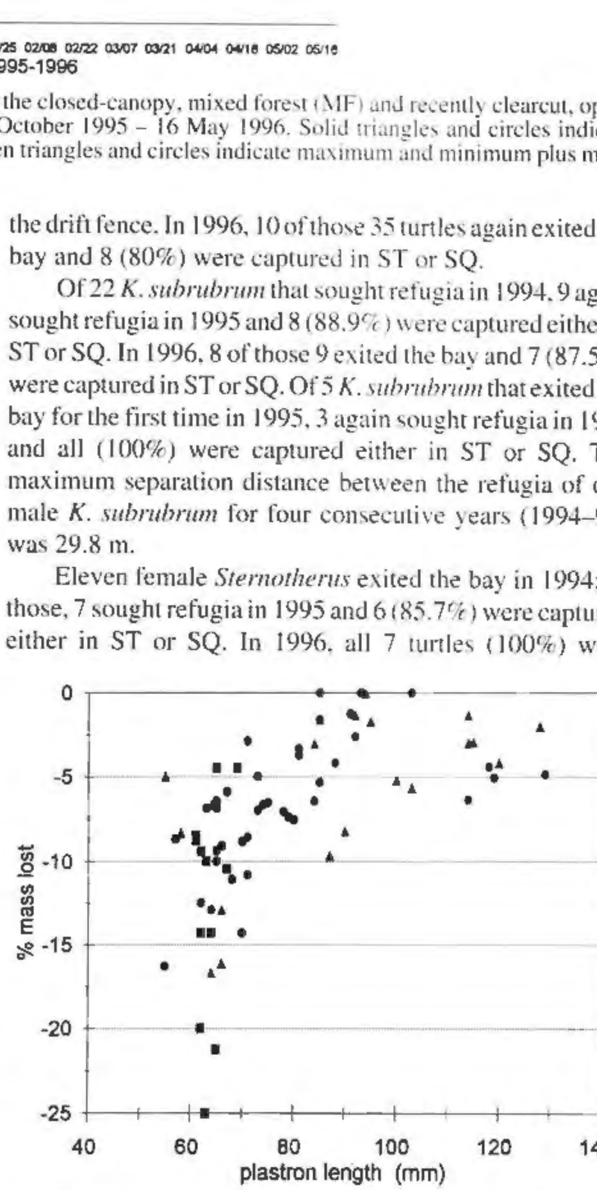


**Figure 5.** Percent mass lost in *Deirochelys reticularia* plotted against plastron length. Turtles sampled were in terrestrial refugia during fall 1995 through spring 1996; circle = male, triangle = juvenile female, square = un-sexed juvenile.

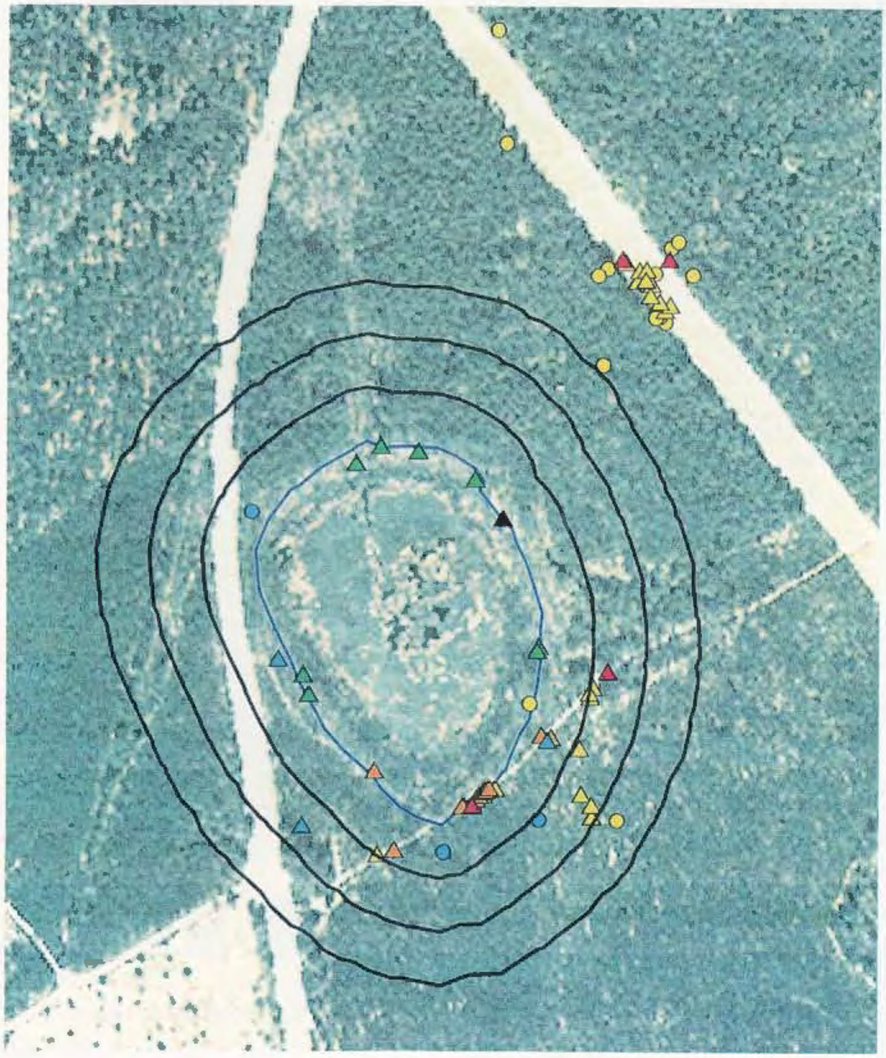

**Figure 6.** Turtle nest sites at Dry Bay. Nests are indicated by colored triangles: *Deirochelys* = yellow, *Pseudemys* = red, *Trachemys* = orange, *Kinosternon* = blue, *Sternotherus* = green, *Chelydra* = black. Upland refugia of pre- and post-gravid female turtles are indicated with colored circles: *Deirochelys* = yellow, *Kinosternon* = blue.

captured in ST or SQ. One male *Chelydra* exited from ST for 4 consecutive years (1994–97), and another male and one female exited from ST for 2 consecutive years. One female *Chelydra* exited from SQ for 4 consecutive years (1994–97).

Of 38 hatchling *Deirochelys* that emerged from their nests, traveled through the terrestrial habitat, arrived at the wetland, survived their first growing season, and later exited the bay to seek terrestrial refugia, 27 (71.1%) exited the bay at the same ST or SQ they had entered.

*Survivorship in Refugia.* — Survivorship of male and juvenile *Deirochelys* in terrestrial refugia was higher in 1994 (96.3%) and 1995 (95.8%) than in 1996 (62.5%). Survivorship of turtles was greater in refugia than during the following aquatic period (1995, 67.3%; 1996, 45.7%; 1997, 40.0%) for each year. A pair of otter (*Lutra canadensis*) immigrated to Dry Bay and killed many turtles in late 1996–97. Adult male and juvenile *Deirochelys* that failed to seek refugia the next autumn were never observed again. Nine *Deirochelys* were killed by predators while using terrestrial refugia, one by fire ants (*Solenopsis invicta*) in a PP refugium; raccoons (*Procyon lotor*) are suspected to have been responsible for the other eight. Of the nine mortalities, six occurred in PP, two occurred within the wetland boundary (only four *Deirochelys* used this habitat during the entire study), and one occurred in MF.

Terrestrial survivorship of *K. subrubrum* was 100% for all years. *Sternotherus* survivorship was 100% in 1994 and 1995, but 66.7% in 1996. Those turtles were eaten by mammalian predators. Survivorship estimates during the intervening aquatic period could not be made since some individuals of both species skip years of autumn emergence.

*Nesting Forays.* — All 271 nesting forays made by resident female turtles at Dry Bay during 1994–97 involved travel into surrounding open, upland habitats, except for a few *Sternotherus* that nested inside the delineated wetland boundary in closed-canopy forest (Fig. 6). *Pseudemys* and *Deirochelys* females exiting from the north end of Dry Bay traveled 280 m through MF and nested on a powerline ROW. *Pseudemys*, *Deirochelys*, and *Trachemys* that emerged on

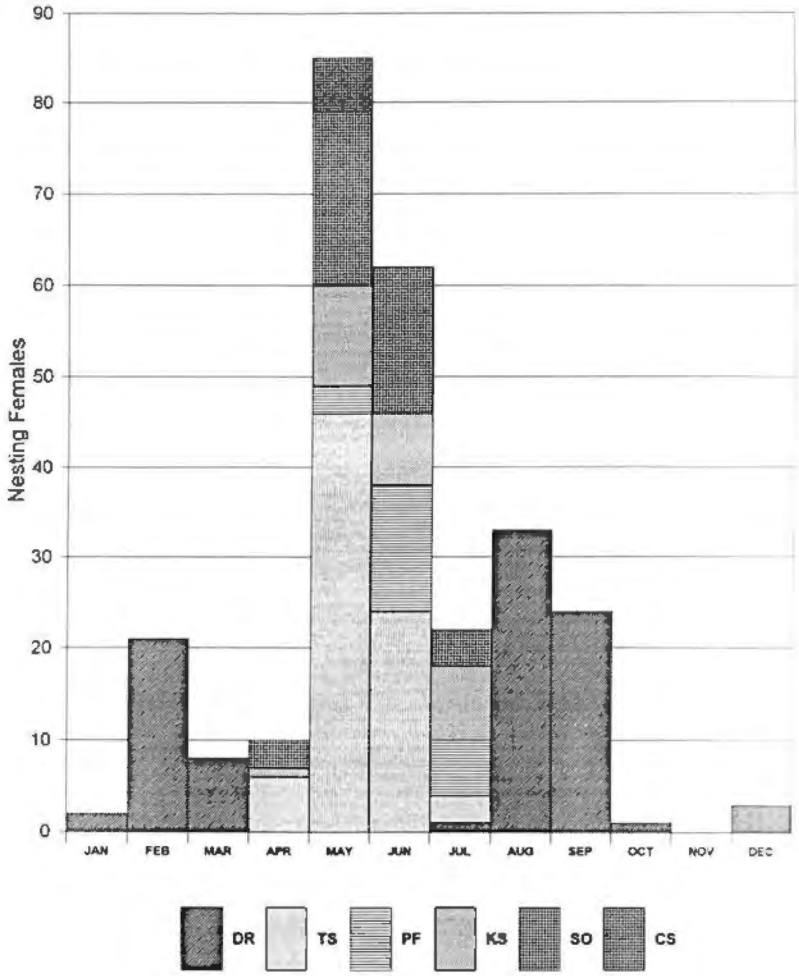


**Figure 7.** Seasonality of nesting among six species of turtles at Dry Bay, 1995–97. DR = *D. reticularia*, TS = *T. scripta*, PF = *P. floridana*, KS = *K. subrubrum*, SO = *S. odoratus*, and CS = *C. serpentina*.

the south end traveled less than 10 m and nested on an old logging road. Nests of *K. subrubrum* and *Chelydra* were located in open-canopy areas, such as the logging road and PP (Fig. 6).

Gravid *Deirochelys* ($n$ = 24 turtles) were captured leaving Dry Bay a total of 93 times during the nesting seasons. Twenty-eight of the nesting forays (30.1%) included use of terrestrial refugia for 1–12 d ($\bar{x}$ = 3.3 d) before or after nesting, or both (Fig. 6). One female retained eggs while buried in a refugium for 153 days (30 September 1994 – 2 March 1995) before nesting. Three females remained buried for 166, 180, and 190 days (September–March) after nesting. Open areas selected for nesting were not used for terrestrial refugia; females buried in nearby forested habitat.

Female *K. subrubrum* often buried in refugia for 1–16 d ($\bar{x}$ = 7.1 d) prior to or after nesting (Fig. 6). Two females emigrated from the Dry Bay area after nest construction. *Trachemys* and *Pseudemys* females on nesting forays occasionally concealed themselves in leaf litter but never burrowed into the soil; they remained concealed for short periods of time (< 24 hrs) before returning to the wetland.

*Deirochelys* nested throughout August and September, and again in February and March. *Chelydra* nested during the latter part of May. The remaining species nested from late April through July (Fig. 7).

*Emigration.* — Emigration to other aquatic habitats was recorded 152 times during the study. *Trachemys* accounted for the greatest number of emigrations; females ($n$ = 7) moved in May and June, whereas males ($n$ = 40) moved March to October with activity peaks in April and June. More *Trachemys* of both sexes left the bay in 1996 (21) and 1997 (16) than in 1995 (10); none left during the portion of 1994 that the study was in operation. *Pseudemys* ($n$ = 31; 16 females, 12 males, 5 juveniles) emigrated from Dry Bay between March and November (Fig. 3). More *Pseudemys* left the bay in 1996 (12) and 1997 (15) than in 1995 (1); none left in 1994. An overall trend of declining water levels was noted throughout the study (Fig. 1). Thread trails of *Trachemys* and *Pseudemys* indicated that turtles never buried in refugia but instead took direct paths toward permanent water (Fig. 8).

Few *K. subrubrum* emigrated. Two females emigrated after nesting and six males left after using summer ($n$ = 3) or autumn–winter ($n$ = 3) refugia. Seven female *Sternotherus*

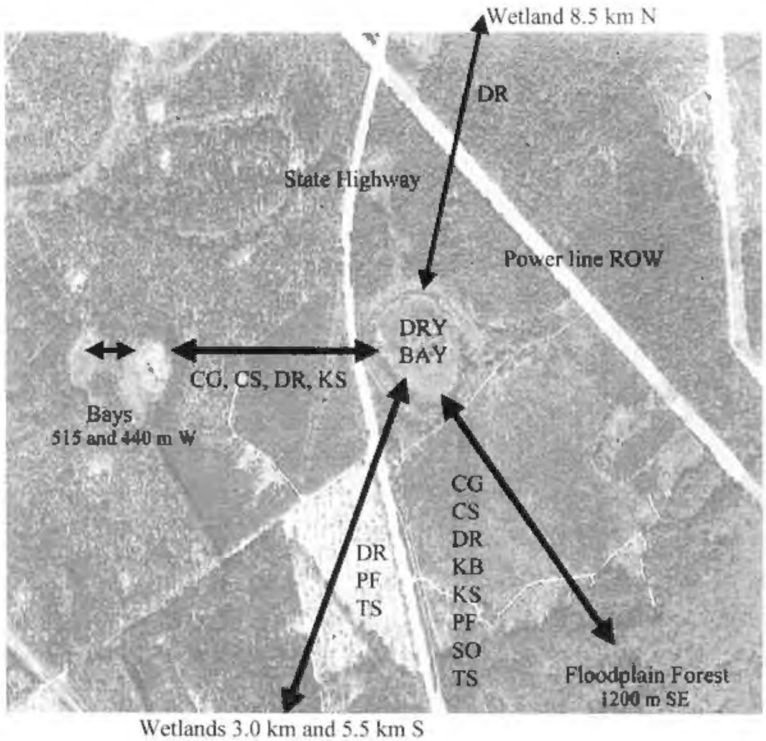


**Figure 8.** Emigration and immigration routes of aquatic turtles at Dry Bay. DR = *D. reticularia*, TS = *T. scripta*, PF = *P. floridana*, KS = *K. subrubrum*, KB = *K. baurii*, SO = *S. odoratus*, CS = *C. serpentina*, and CG = *C. guttata*. Floodplain forest is 1200 m south of Dry Bay, two seasonal Carolina bays are 440 and 515 m west, Ellenton Bay (3.0 km) and another wetland (5.5 km) are southwest, one wetland is 8.5 km northeast.

emigrated during July, August, and January. Male *Sternotherus* ($n$ = 34) exited from May to October, but only one male left the Dry Bay vicinity, in July 1996. Five juveniles exited the bay between June and August and one emigrated. Most male and juvenile *Sternotherus* exits from the bay appear to have been brief terrestrial forays, not movements to other wetlands. Two *Chelydra* emigrated (1 male, November 1997; 1 juvenile, June 1996). One male *Clemmys* left the bay (October 1994) and moved towards another seasonal wetland (515 m distant) known to harbor a population, but was killed by an automobile on the highway that bisects the natural movement corridor (Fig. 8). Five male *K. baurii* and one *Clemmys* emigrated in the spring in the direction of a bottomland swamp forest known to contain populations of both species (Fig. 8). Only 11 *Deirochelys* (7 males, 4 juvenile females) emigrated; all continued away from Dry Bay in spring following emergence from terrestrial refugia. Most *Deirochelys* moved towards seasonal wetlands (east) and bottomland swamp forest (south). However, two males headed north towards a Carolina bay 8.5 km distant, from which another male immigrated to Dry Bay.

*Immigration.* — Excluding hatchlings, 99 individual turtles arrived at Dry Bay from other wetlands during the study: *T. scripta* (42), *S. odoratus* (16), *K. subrubrum* (13), *P. floridana* (12), *D. reticularia* (10), *C. serpentina* (3), *K. baurii* (2), and *C. guttata* (1). Of these, 27 had been previously marked at other wetlands. *Trachemys* males ($n$ = 22), females ($n$ = 9), and juveniles (44–66 mm PL, $n$ = 11) arrived during all months from March to October. Eight males and six females had originally been captured elsewhere, including Ellenton Bay (3.0 km south) and another wetland (5.5 km south). *Trachemys* entered Dry Bay from all directions. *Pseudemys* males ($n$ = 7) and females ($n$ = 5) arrived during all months from March to October. One male had originally been captured in Ellenton Bay in 1968, 29 years earlier. Four females were previously captured in Ellenton Bay. *Pseudemys* entered Dry Bay from the south where a permanent stream and floodplain swamp is located (Fig. 8). Female *Sternotherus* ($n$ = 9) arrived during April–November, and males ($n$ = 7) from June–December; all arrived from the south. One male was severely dehydrated upon arrival and died. *Kinosternon subrubrum* males ($n$ = 7) arrived February–August, females ($n$ = 5) arrived April–July, and 1 juvenile (35 mm PL) arrived in April. All *K. subrubrum* entered from the two other Carolina bays to the west or from the south. One female was marked previously at one of those bays. Between 1976 to the beginning of this study, 10 *K. subrubrum* (7 males, 3 females) were captured crossing the highway that separates Dry Bay and the other bays (J.L. Greene and J.W. Gibbons, unpubl.data). Ten male *Deirochelys* arrived May–August; 4 were originally captured in other bays (2 from 3.0 km south; 1 from 8.5 km north; 1 from 515 m west). Three males captured in Dry Bay at the beginning of the study were previously marked in Ellenton Bay. No adult female *Deirochelys* immigrated to Dry Bay. Three juvenile *Chelydra* (PL = 51, 63, and

80 mm) arrived at Dry Bay from the south during April, June, and August. Two male *K. baurii* arrived from the south in April and August. One male *Clemmys* arrived in March from the south (Fig. 8).

## DISCUSSION

*Terrestrial Movements.* — Movements to and from aquatic habitats occur in a variety of amphibians and reptiles (Gibbons, 1969; Gibbons and Coker, 1977; Dodd, 1992) and are summarized for turtles by Gibbons (1986). Generalized categories of movements include nesting forays (Cagle, 1950; Moll and Legler, 1971; Congdon et al., 1983), mate-seeking (Morreale et al., 1984; Parker, 1984), escape from adverse environmental conditions (Gibbons, 1986; Kennett and Christian, 1994), and movements to hibernacula (Gibbons, 1983; Iverson, 1991). Although nesting is understood as a seasonal behavior, emigration often is viewed as a response to unusual or unexpected conditions resulting in temporary or permanent loss of an individual from a population. Wygoda (1979) suggested that *K. baurii* moved to avoid desiccation, predation, and high water temperatures. Ward et al. (1976) suggested that *C. guttata* left to avoid hot water. Bennett et al. (1970) speculated that turtles leave drying ponds to avoid concentrated searches by predators, unfavorable temperatures, and desiccation. Wygoda (1979) also observed predation of cooters (*Pseudemys* sp.), red-bellied turtles (*P. nelsoni*), and *Sternotherus* that did not move from a drying pond. Kennett et al. (1992) reported that Australian chelids most commonly found in permanent waters are more likely to migrate to another water body, whereas those species favoring seasonal wetland habitats will seek nearby terrestrial refugia. The significance of movements from aquatic to terrestrial habitats on a seasonal basis has perhaps been overlooked. At Dry Bay, more turtle exits from the bay were to access adjacent terrestrial refugia ($n = 515$) than nesting and emigration combined ($n = 423$).

*Use of Upland Refugia.* — Five of eight turtle species at Dry Bay used upland terrestrial refugia. All male and juvenile *Deirochelys* exited from the bay on a seasonal basis during each of four years of study. Adult female *Deirochelys* only used terrestrial refugia in association with nesting forays. However, in other studies where the habitat dried completely, females left the wetland basin and buried themselves in adjacent forests (Buhlmann, 1995).

With few exceptions, notably *Sternotherus*, most turtle refugia were located outside of the delineated wetland area and at distances of up to 165 m. The number of movements to refugia ($n = 515$) indicates significant use of both wetland and adjacent upland habitats by turtles and challenges the validity of drawing arbitrary conservation boundaries between these habitats.

*Seasonality of Terrestrial Habitat Use.* — Most *Deirochelys*, *K. subrubrum*, and *Sternotherus* exited to terrestrial refugia during the late summer through early autumn and returned in early spring, although some *K. subrubrum* used refugia during the summer months. No turtles exited to refugia during the spring. However, *Deirochelys* and *K. subrubrum* routinely exited to refugia each autumn even in years when water levels were not dropping. From an evolutionary perspective, it may be advantageous for turtles indigenous to seasonally fluctuating habitats to leave the wetland when it most frequently dries. A concentration of turtles in the remaining areas of decreased water or in the mud may be discovered by mammalian predators (Bennett et al., 1970; Wygoda, 1979). Conversely, individual turtles distributed singly in refugia at varying distances in the surrounding forest might be difficult to detect.

The historical frequency and seasonality of fire may be a selective force on seasonal movements to terrestrial refugia. Turtles remaining in the drying peat of a pond bottom during a dry period might be vulnerable to fire whereas turtles in forest refugia within dry or moist sandy soils would be safe, even as the duff and pine needle layer burned.

*Potential Effects of Timber Harvest.* — Closed-canopy, mixed forests (MF) were preferred by all species in refugia. Although *K. subrubrum* and *Deirochelys* used recently harvested, open-canopy habitats (PP), greater temperature fluctuation (Fig. 4) and the propensity for turtles to abandon refugia suggest that PP was less suitable. Bennett et al. (1970) observed that *K. subrubrum* in open fields experienced temperatures as low as -1.5°C and moved repeatedly to new refugia and Wygoda (1979) suggested that *K. baurii* actively avoided open habitat. Presumably, turtles forced to seek replacement refugia would incur a higher risk of predation and loss of needed energy reserves. Thus, clearing of forest cover adjacent to wetlands may subject turtles to dehydration, freezing, or an increase in predation. Timber plans that call for the removal of all canopy cover around the entirety of a wetland should be re-considered. Also, the use of heavy machinery might crush turtles if timber harvesting occurs when the turtles are using refugia.

*Conflicts Between Land Use and Turtle Site Fidelity.* — Some turtles hesitated or refused to cross a highway that was adjacent to Dry Bay. Overall, fewer turtles exited on the highway side of the wetland. A turtle may succeed in crossing, but the likelihood of mortality is much higher than when exiting to other sides. Turtles in this study demonstrated site fidelity to terrestrial refugia among years, thus survivorship of turtles using refugia across the highway would be expected to decrease through attrition and account for the higher numbers of turtles observed using forests on the north and east sides of Dry Bay.

For *Deirochelys*, a relatively short-lived species (Buhlmann, 1998), survivorship in terrestrial refugia was higher than in the aquatic habitat during a comparable time period. From a management perspective, alterations to terrestrial habitat around wetlands by clearcutting and highway construction may decrease survivorship due to the propensity of turtles to exhibit site fidelity. Hence, human disturbance in adjacent upland habitats may have consequences for long-term persistence of aquatic turtle populations. Most *Deirochelys* found refugia in the oldest section of forest (> 60 yrs) that had deep layers of litter and humus. Perhaps previous human land use patterns and practices still influence turtle survivorship through selection of former refugia sites.

*Emigration and Immigration.* — Many emigrations from the study area by *Trachemys* and *Pseudemys* are likely attributable to unsuitable conditions because they (Fig. 3) correlated with the lowest water levels (Fig. 1). However, some emigrations (and immigrations) of adult *Trachemys* also occurred during the spring months when water levels were increasing, suggesting that movements may have been in response to mate-searching (Morreale et al., 1984; Parker, 1984). Immigrations of male *Clemmys* and *K. baurii* occurred during spring months. Females did not reside in Dry Bay, and the males usually exited again within a few months suggesting that their movements were attributable to mate-searching (Tuberville et al., 1996).

Gibbons et al. (1983) reported that during a drought, most Ellenton Bay *Trachemys* were found in a nearby body of water. *Trachemys*, *Pseudemys*, and *Sternotherus* will frequent seasonal habitats, but are primarily denizens of permanent water. For them, a permanent water habitat probably contains the source population (e.g., Pulliam and Danielson, 1991). Seasonal ponds periodically become sinks from which turtles must evacuate.

The limited emigrations observed for *K. subrubrum* indicate that they are less likely to move long distances overland. Seasonal wetlands are their source aquatic habitats from which they retreat to nearby terrestrial refugia during drying periods. Likewise, Iverson (1991) suggested that use of refugia are more important than immigration and emigration for *K. flavescens* living in Nebraska sandhill ponds.

The capture of *Trachemys* and *Pseudemys* previously marked in other habitats, notably Ellenton Bay, confirms the orientation and movement capabilities (Gibbons and Smith, 1968; Yeomans, 1995) of these two species and supports the metapopulation hypothesis of Burke et al. (1995) for turtles of this region. Some *Deirochelys* are capable of long-range movements as several males captured in Dry Bay were originally marked in Ellenton Bay. The overland movement of these turtles indicates that maintaining connectivity of the landscape with natural habitats, or at least with habitat suitable for movements, should be prioritized.

## Implications for Wetland Conservation Boundaries

Some aquatic turtles may spend a greater proportion of each year in adjacent terrestrial habitat than in the wetland itself. At Dry Bay, an area of upland habitat extending 165 m from the delineated wetland boundary would include all terrestrial refugia used by *Deirochelys* in 1994–97 (Fig. 2). Interestingly, inclusion of upland habitat extending 165 m from the delineated wetland has also been suggested to protect some pond-breeding amphibians, notably ambystomatid salamanders (Semlitsch, 1998). Protecting upland habitat up to 135 m from the wetland would include all refugia of *K. subrubrum*, and is similar to results reported for Ellenton Bay by Burke and Gibbons (1995) and lends additional strength to their findings.

An important distinction between this study and previous ones concerns the definition of buffers. For example, Burke and Gibbons (1995) considered both terrestrial estivation sites and nesting locations together in the design of their "buffer" around Ellenton Bay, but results from the Dry Bay study suggest that nesting and refugium locations should be considered separately. Open-canopy nesting sites are required in the wetland vicinity, but can be located as isolated patches away from the wetland. For example, *Trachemys* have been reported to nest 10 m (this study), 400 m (Moll and Legler, 1971), and 1.6 km (Cagle, 1950) from the aquatic habitat. However, locations of terrestrial refugia are in closed-canopy forests, and turtles are dispersed throughout the uplands that surround a wetland from the delineated boundary out to approximately 165 m. Therefore, lumping nesting and terrestrial refugia together in a recommended "buffer" zone may lead to the erroneous interpretation that clearing forest canopy cover that encircles wetlands might enhance turtle habitat. Nesting habitat may be enhanced by providing small clearings in the forest; however, it is important that the critical upland habitat surrounding the wetland be primarily forested for turtle refugia, and perhaps as movement corridors to other water bodies.

Current wetlands regulations do little to protect wetlands comprehensively because they fail to consider zoological components, focusing only on vegetation and soils. Protecting the adjacent upland habitats that surround wetlands is integral to protecting the wetland community. These upland areas, as used by the turtles in this study, should not be considered simply as "buffers." Rather, they should instead be considered critical associated upland habitats as they are undeniably required to protect the wetland fauna and are thus part of the overall wetland ecosystem. Additional true buffer zones can be designed beyond the critical aquatic and adjacent terrestrial habitat in order to more fully protect the wetland ecosystem from human-induced perturbations.

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