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Dietary Overlap in Three Sympatric Congeneric Freshwater Turtles (*Pseudemys*) in Florida

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Florida has one of the highest species diversities of freshwater emydid turtles in the western hemisphere (Jackson, 1988), and many of these species, particularly in the genus *Pseudemys*, are known to be primarily

Table 1. Percent volume (mean and standard deviation) of diet categories in stomach contents of three species of turtles from one area of the Withlacoochee River, Citrus County, Florida, in August 1973. "Unidentified" refers to plant material, amounts too small to measure (< 0.2 ml) are listed as "trace." p is probability from Kruskal-Wallis tests.

	P. concinna (n = 5)		*P. floridana* (n = 8)		*P. nelsoni* (n = 4)		
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	p
Egeria	11 ± 24	0–54	36 ± 33	1–83	54 ± 45	13–100	0.035
Hydrilla	30 ± 32	0–78	23 ± 26	0–66	20 ± 17	0–41	0.944
Vallisneria	23 ± 8	14–32	26 ± 23	0–68	26 ± 30	0–56	0.993
Algal mat	28 ± 38	0–70	6 ± 7	0–19	0.1 ± 0.2	0–0.4	0.399
Ceratophyllum	5 ± 9	0–21	0	—	0	—	0.017
Najas	4 ± 7	0–15	0.2 ± 0.6	0–2	0	—	0.226
Lemna	0	—	trace	—	0	—	—
Leptodictyum	trace	—	trace	—	trace	—	—
Unidentified	0	—	9 ± 17	0–51	0.4 ± 0.8	0–2	0.007

herbivorous as adults (Ernst et al., 1994). However, few quantitative studies have been conducted on the feeding habits of these species, and the extent of dietary overlap in sympatric populations of *Pseudemys* has not been studied. In this paper we evaluate stomach contents from three species — *Pseudemys concinna*, *P. floridana*, and *P. nelsoni* — that were captured in a limited area of the Withlacoochee River, Citrus County, Florida, during a one-month period. We evaluate the degree of dietary overlap among these species and assess the extent to which these turtles feed on introduced plant species.

Five *P. concinna suwanniensis* (1 female, 4 males, plastron length [PL] 200–340 mm), 8 *P. floridana peninsularis* (6 females, 2 males, PL 150–320 mm), and 4 *P. nelsoni* (1 female, 3 males, PL 220–280 mm) were captured in the Withlacoochee River, Florida (28°58'N, 82°22'W) in August 1973 and sacrificed as part of a larger study on the reproductive biology of this group (Jackson, 1988). The slow-moving waters of the Withlacoochee River support substantial populations of all three turtle species, whereas normally *P. concinna* predominates in riverine habitats and *P. floridana* and *P. nelsoni* predominate in lentic waters (Jackson, pers. obs.). Taxonomy follows Jackson (1995).

Stomach contents, preserved in 10% formalin or AFA (an aqueous solution of acetic acid, formalin, and ethanol), were sorted to species except for masses of filamentous organisms — "algal mats." These algal mat communities comprise various filamentous algae (e.g., *Compsopogon coeruleus*, *Oedogonium* sp., *Spirogyra* sp.), diatoms (e.g., *Mastogloia* sp., *Tabelleria* sp.), and cyanobacteria (e.g., *Lyngbya* sp., *Microcoleus* sp.) and were considered as a unit because these species live intertwined in mats, are nearly impossible to separate, and are fed upon by turtles as a unit.

Diet categories were evaluated by percent frequency of occurrence, percent volume, and index of relative importance. Because stomach contents had been preserved in formalin, percent mass was not evaluated. Percent volume was determined by displacement of water in graduated cylinders; items of less than 0.2 ml volume were identified as "trace." Percent volumes of diet plants were compared among turtle species by Kruskal-Wallis tests with $\alpha = 0.05$ (Ryan et al., 1985).

We developed an index of relative importance (IRI), which is modified from Hyslop (1980) to be appropriate for herbivores, and calculated for each diet category i by the equation

$$\mathrm{IRI} = \frac{100(F_i V_i)}{\sum_{i=1}^{n}(F_i V_i)}$$

where **F** is percent frequency of occurrence, **V** is percent volume, and n is number of diet categories. As has been noted (Hyslop, 1980; Bjorndal, 1997), either percent frequency of occurrence or percent volume (or mass) analyzed alone can yield misleading interpretations on the relative importance of diet categories. Foods with a 100% frequency of occurrence may be present in only trace amounts in each stomach. Large percent volume or mass values may result from only a few individuals consuming large quantities of that food, particularly when only small numbers of stomachs are examined. The IRI provides a more reliable measure for ranking the relative importance of diet categories because frequency of occurrence and volume (or mass) are integrated.

Diet Composition. — Percent volume of dietary components (Table 1), percent frequency of occurrence, and IRI (Table 2) confirm that these three turtle species are herbivores. The aquatic plants found in measurable quantities were egeria (*Egeria densa*), hydrilla (*Hydrilla*

Table 2. Percent volume (%V), frequency of occurrence (%F), and index of relative importance (IRI) for diet categories in stomach contents of three species of turtles from one area of the Withlacoochee River, Citrus County, Florida, in August 1973. "Unidentified" refers to plant material, "tr" is trace. IRI values cannot be recalculated from the summary values presented below because turtles with trace amounts of a diet item were not included in %V but were included in %F.

	P. concinna (n = 5)			*P. floridana* (n = 8)			*P. nelsoni* (n = 4)		
	%V	%F	IRI	%V	%F	IRI	%V	%F	IRI
Egeria	11	40	6.5	36	100	34.0	54	100	58.0
Hydrilla	30	80	36.0	23	88	19.5	20	100	21.8
Vallisneria	23	100	34.7	26	100	24.4	26	50	13.8
Algal mat	28	40	16.6	6	75	13.4	0.1	50	6.0
Ceratophyllum	5	60	4.0	0	13	0	0	25	0
Najas	4	40	2.1	0.2	13	0.02	0	0	0
Lemna	0	0	0	tr	13	0	0	0	0
Leptodictyum	tr	20	0	tr	63	0	tr	50	0
Unidentified	0	0	0	9	100	8.6	0.4	75	0.3

verticillata), eelgrass (*Vallisneria americana*), algal mat (see above), coontail (*Ceratophyllum demersum*), and southern naiad (*Najas guadalupensis*). The aquatic moss *Leptodictyum riparium* was found in trace amounts in turtles of all three species, and five leaflets of duckweed (*Lemna minor*), were found in one *P. floridana* (Table 2). These last two plant species were considered to have zero volume in calculations of IRI and dietary overlap.

Animal matter was found in only trace amounts in a few turtles. Snail fragments were found in one individual of each turtle species, a fish scale in one *P. concinna*, and a beetle elytron in one *P. floridana*.

The value of calculating IRI can be seen in a comparison of relative rankings of diet categories by the three measures presented in the study: percent volume, percent frequency of occurrence, and IRI (Table 2). For example, in *P. concinna*, algal mat is ranked second and *Vallisneria* a close third by percent volume. However, when percent frequency of occurrence of these two plants is also considered, the IRI values reverse the rankings with *Vallisneria* second and algal mat a distant third.

Diet components recorded for these turtle species in other areas are similar to those reported here. Plant species in the diet vary, undoubtedly because of differences in availability, but the types and growth forms of the plants are similar.

Of the three turtle species, the greatest number of quantitative diet studies have been conducted with *P. concinna*. Ten *P. concinna* (identified as *P. floridana suwanniensis*) from Hart Springs, Gilchrist County, Florida, had ingested *Najas* (82%), *Lemna* (7%), *Ceratophyllum* (5%), *Sagittaria* (3%), and filamentous algae (3%) (Marchand, 1942). For *P. concinna* (identified as *Chrysemys floridana*) in Lafourche Parish, Louisiana, the major diet plants were duckweeds (*Spirodela* and *Lemna*), submersed plants (*Egeria* sp., *Najas* sp., *Potamogeton* sp., *Ceratophyllum* sp.), and the larger floating plants *Eichhornia* sp. and *Limnobium* sp. (Hart, 1979). In the Tallapoosa River, Alabama, *P. concinna* fed primarily on *Podostemon ceratophyllum* and filamentous algae *Spirogyra* sp. (Fahey, 1987). Adult *P. concinna* in the New River, West Virginia, consumed *Vallisneria americana*, *Elodea canadensis*, and filamentous algae (Buhlmann and Vaughan, 1991). In Wakulla Springs, Florida, the major plant species in the diet of *P. concinna* were the green alga *Cladophora* sp., *Egeria densa*, *Sagittaria kurziana*, *Vallisneria americana*, and *Ceratophyllum demersum* (Lagueux et al., 1995).

Marchand (1942) reported that the stomach contents from two *P. floridana* from Rainbow Run, Florida, contained 95% *Najas* sp., 5% *Sagittaria lorata*, and trace amounts of *Lemna* sp. A series of *P. floridana* and *P. nelsoni* from lentic waters in Alachua County, Florida, had been feeding on aquatic vegetation, including *Lemna minor* and *Wolffiella floridana* (Jackson, unpubl. data).

Exotic Species. — The introduced aquatic plants *Egeria densa* and *Hydrilla verticillata* have overwhelmed many aquatic habitats throughout Florida and have substantially modified the ecosystems they have invaded (Myers and Ewel, 1990). Both of these exotic species are major diet components in the three turtle species. Based on IRI values, these plants, respectively, rank 4 and 1 in importance for *P. concinna*, 1 and 3 for *P. floridana*, and 1 and 2 for *P. nelsoni*. A similarly high degree of reliance on *Egeria densa* was reported for *P. concinna suwanniensis* in Wakulla Springs, Florida (Lagueux et al., 1995), where *E. densa* was the second most important diet species. Extensive control and eradication programs for these introduced aquatic plants are conducted throughout the southeastern USA. Effects on turtle populations should be considered in the design of such programs because they can affect significantly the food supply of turtles, at least until the introduced species regenerate or the natural vegetation re-establishes itself. The latter process can be a relatively slow one.

Dietary Overlap. — Diets of the three species overlap considerably (Tables 1, 2). Proportions of *Hydrilla*, *Vallisneria*, algal mat, and *Najas* in the diet do not vary significantly among the three species (Kruskal-Wallis tests, p values in Table 1). Proportions of *Egeria* and *Ceratophyllum* do vary significantly (Kruskal-Wallis tests, p values in Table 1).

To evaluate the extent of dietary overlap between turtle species, we calculated the overlap measure described by Horn (1966):

$$\hat{C}\lambda = \frac{2\sum_{i=1}^{n} \mathbf{x}_i \mathbf{y}_i}{\sum_{i=1}^{n} \mathbf{x}_i^2 + \sum_{i=1}^{n} \mathbf{y}_i^2}$$

where $\boldsymbol{n}$ is the number of diet categories, $\mathbf{x}_i$ is the proportion of the diet of turtle species $\mathbf{x}$ composed of diet category $\boldsymbol{i}$, and $\mathbf{y}_i$ is the same value for turtle species $\mathbf{y}$. A value of 0 represents no overlap; a value of 1 indicates total dietary overlap. $\hat{C}\lambda$ is equivalent to the index of interspecific competition (α) described by MacArthur and Levins (1967) when averaged for the two species under comparison. Both of these measures have been widely used in ecological studies.

The overlap indices are 0.75 for *P. concinna* and *P. floridana*, 0.56 for *P. concinna* and *P. nelsoni*, and 0.94 for *P. floridana* and *P. nelsoni*. Therefore, there is a near total overlap between the diets of *P. floridana* and *P. nelsoni* with less, but still substantial, overlap between *P. concinna* and *P. floridana*, and between *P. concinna* and *P. nelsoni*.

The extent of dietary overlap probably reflects the constant and abundant food resources available to these turtles in aquatic habitats in Florida. With unlimited food resources, partitioning would not be necessary. The extent to which the introduced species, *Hydrilla* and *Egeria*, have affected dietary overlap cannot be determined from this study. However, if the Withlacoochee River had lower total plant biomass and greater plant diversity before the introduction of these exotic plants, the diets of the three turtle species may have had less overlap.

These results must be interpreted with caution because of the small sample sizes and short duration of the study. To evaluate dietary overlap among these species more thoroughly, studies with larger sample sizes are needed that incorporate seasonal variation and that relate availability of plant species with diet selection. Studies in habitats that have not been invaded by exotic aquatic plants would be of great value.

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Predation by the Imported Fire Ant (*Solenopsis invicta*) on Loggerhead Sea Turtle (*Caretta caretta*) Nests on Wassaw National Wildlife Refuge, Georgia

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Little information concerning predation by ants on eggs or hatchlings of turtles is available. McAllister et al. (1965) and Hughes (1970, 1971, 1972, 1974) referred to ants (*Dorylus* sp.) preying upon the eggs of loggerhead turtles (*Caretta caretta*) in southeastern Africa. Hughes (1975) indicated that a hatchery containing 10 *Caretta* and 2 leatherback (*Dermochelys coriacea*) nests, unprotected by ant poison, suffered 100% mortality during one nesting season. Congdon et al. (1983) reported that an unidentified ant caused destruction of the eggs of a Blanding's turtle (*Emydoidea blandingii*) in Michigan. Dodd (1988) listed ants as a predator on *Caretta* eggs but did not identify species or mention to what degree this predation occurred.

Imported fire ants (*Solenopsis invicta*) have been implicated by some researchers as potential or actual predators upon turtle and other reptile eggs in the USA. Mount et al. (1981) showed through field experiments that *S. invicta* will attack and consume eggs of the lizard *Cnemidophorus sexlineatus*. In addition Mount (1981) reported an observation of fire ants invading the nest of a chicken turtle (*Deirochelys reticularia*). Upon excavation, this nest contained several dead hatchlings. Landers et al. (1980) reported fire ants destroying 10 hatchlings from three separate nests of the gopher tortoise (*Gopherus polyphemus*). Mapes (1985) listed fire ants as a predator upon loggerhead eggs from Sarasota County, Florida. LeBuff (1990) provided slightly more information when he remarked that the native Florida fire ant (*Solenopsis geminata*) was a frequent invader of *Caretta* nests on Sanibel Island, Lee County, Florida. He noted that these ants caused insignificant losses to eggs, but hatchlings ascending the nest chamber were vulnerable to ant attack. LeBuff also stated that nests deposited in partially shaded or vegetated areas where ants foraged were seriously threatened. Although nests located in unshaded areas were not necessarily excluded from this threat, predation there was much less. He concluded that once ants reached the nest cavity, hatchlings quickly fell victim to the formic acid injected by the sting of the insects. Although no evidence exists on the susceptibility of hatchling turtles to the sting of fire ants, Mount (1981) indicated that a hatchling box turtle (*Terrapene