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Dead-leaf-searching by the Orange-crowned Warbler in Louisiana in winter.—Searching for arthropods in dead leaves caught in vegetation above ground is a foraging behavior used heavily by many Neotropical and some North American bird species, the latter mainly on their Neotropical wintering grounds (Remsen and Parker 1984 and references therein; Greenberg 1987; Rosenberg, in press). Such dead-leaf-searching has been reported for four species in the wood-warbler (Parulinae) genus *Vermivora* (Golden-winged Warbler, *V. chrysoptera*; Blue-winged Warbler, *V. pinus*; Bachman's Warbler, *V. bachmanii*, and Orange-crowned Warbler, *V. celata*; Ficken and Ficken 1968 and references therein; other references in Remsen and Parker 1984; Greenberg 1987). Although the degree to which these species of *Vermivora* specialize on this foraging behavior is generally unknown, Greenberg (1987) found that in winter the Blue-winged Warbler searched dead leaves in 40% of 75 foraging maneuvers, and K. V. Rosenberg (in litt.) found that in winter in Costa Rica the Golden-winged Warbler searched dead leaves in 82% of 22 foraging maneuvers. In general, the *Vermivora* warblers frequently use probing and gaping motions to investigate curled green leaves, leaf clusters, leaf buds, flowers, bark crevices, moss, and sap wells made by *Sphyrapicus* sapsuckers (Root 1967, Ficken and Ficken 1968, Ehrlich and Daily 1988); the more acute, icterid-like bill of most *Vermivora* species relative to most other wood-warblers presumably reflects adaptation for such probing and gaping movements.

Remsen's initial observations of Orange-crowned Warblers wintering in south-central Louisiana indicated that this species searches dead leaves more frequently than any other

TABLE 1
SUBSTRATE USE BY THREE SMALL INSECTIVOROUS BIRDS WINTERING IN LOUISIANA

Species	Number of observations (% total)					N
	Dead leaf	Green leaf	Branch	Moss	Other	
Orange-crowned Warbler	145 (37)	29 (15)	18 (9)	3 (2)	5 (3)	200
Yellow-rumped Warbler	2 (3)	35 (43)	44 (54)	—	—	81
Ruby-crowned Kinglet	6 (5)	45 (40)	63 (55)	—	—	114

substrate. In fact, wintering Orange-crowned Warblers could be located consistently by searching areas in second-growth woodland and forest edge where dense undergrowth and vine tangles trapped many dead leaves above ground. The purpose of this study was to quantify the degree of specialization on dead-leaf-searching by Orange-crowned Warblers in winter.

Methods.—We studied the foraging behavior of Orange-crowned Warblers in second-growth deciduous forest and forest edge in southern Louisiana, with 95% of all data recorded from two sites: (1) Burbank Drive, 1–3 km south of the campus of Louisiana State University, Baton Rouge, East Baton Rouge Parish, and (2) Bonnet-Carré Spillway, near Norco, St. Charles Parish, Louisiana. Observations were recorded from late December to early March in 1984 and 1986–89. Individual birds were followed for as long as possible. Each foraging maneuver (=bird unambiguously picked or probed substrate) was scored as to type of substrate used, i.e., dead leaf, green leaf, branch, moss, etc. Data were gathered from at least 17 individual birds. Similar data were gathered simultaneously on two other small, wintering insectivores, the Ruby-crowned Kinglet (*Regulus calendula*) and Yellow-rumped Warbler (*Dendroica coronata*), for comparison.

Results.—Of 200 records of substrates searched by Orange-crowned Warblers, 145 (73%) were dead leaves; this contrasts strongly with data for the Ruby-crowned Kinglets and Yellow-rumped Warblers at the same study sites, neither of which searched dead leaves in more than 5% of our foraging observations (Table 1). However, our qualitative observations of three other passerine species that are permanent residents (Carolina Wren, *Thryothorus ludovicianus*; Carolina Chickadee, *Parus carolinensis*; Tufted Titmouse, *P. bicolor*) indicated that these three species regularly search dead leaves; quantification of their frequency of use of dead leaves is in progress (as is arthropod availability in dead leaves in winter).

Discussion.—Although Orange-crowned Warblers at our study sites searched dead leaves more frequently than any other substrate, the degree of specialization on dead-leaf-searching does not approach the 90%-level shown by some species of tropical forest passerines (Remsen and Parker 1984; Rosenberg, in press).

Greenberg (1987) found that another species of parulid, the Worm-eating Warbler (*Helminthos vermivorus*), searched dead leaves in 75% of its foraging maneuvers on its tropical wintering grounds. Thus, the data for Orange-crowned and Worm-eating warblers in winter are remarkably similar. Greenberg found that during the breeding season, the Worm-eating Warbler shifted its substrate preference to green foliage, where 78% of all foraging maneuvers were directed. Unfortunately, comparable data for the Orange-crowned Warbler in the breeding season do not exist. Further, although Root (1967) studied the foraging behavior of the Orange-crowned Warbler during the breeding season, he studied a different subspecies (*V. c. lutescens*) from the one that winters in Louisiana (*V. c. celata*). Although Root found

that the California birds searched foliage almost exclusively (97% of all observations), he did not distinguish live from dead foliage; we suspect, however, that in view of the careful detail of Root's observations, he would have noted this specifically if the California Orange-crowned Warblers searched dead leaves frequently. Nonetheless, a comparison of summer and winter foraging behavior to determine whether Orange-crowned Warblers, like Worm-eating Warblers, undergo pronounced seasonal shifts in substrate preference will require additional data from the breeding season.

We suspect that the Orange-crowned Warbler may extensively search substrates other than dead leaves in other habitats in winter. For example, substantial numbers winter in acacia (*Acacia smallii*) thickets in coastal southwestern Louisiana, where dead leaves are not common and where all of our foraging observations so far (N = 18) are of probing moss or bark and of searching green foliage. Also, in suburban Baton Rouge, one individual Orange-crowned Warbler visited a hummingbird feeder for sugar water daily from 26 January to 14 February 1988 (Remsen and C. L. Cummins pers. obs.); feeding at hummingbird feeders is noted occasionally in southern Louisiana (N. L. Newfield pers. comm.) and the lower Colorado River Valley (Rosenberg et al., in press). At the latter locality, Rosenberg et al. (in press) also found that Orange-crowned Warblers that winter there feed frequently in flowering trees and shrubs (40% of 336 observations). Also, P. E. Scott (pers. comm.) has found that in San Diego County, California, the Orange-crowned Warbler feeds extensively on the nectar of *Beloperone californica* by piercing the bases of its flowers. Therefore, the species as a whole is flexible in its preference of foraging substrates, even within the same season and geographic region. Such flexibility is, so far, unknown in the many tropical species that heavily use the dead-leaf-searching foraging behavior, regardless of habitat, season, or geographic region (T. A. Parker, K. V. Rosenberg, and J. V. Remsen unpubl. data).

Year-round availability of dead leaves has been proposed as a resource that contributes to species richness in tropical bird communities (Remsen and Parker 1984, Remsen 1985). With the untested assumption that removal of a substrate used by a bird in over 70% of its foraging maneuvers would also remove the bird species from the local avifauna, our data suggest that winter availability of dead leaves adds at least one species, Orange-crowned Warbler, to certain bird communities in the southeastern United States.

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The significance of mate loss in Florida Sandhill Cranes.—Monogamy, in which “one male and one female join to rear at least a single brood” (Wilson 1975), is the most common mating system among birds. In perennial monogamy the pairbond is persistent, even during the non-breeding season (Brown 1975) and is common in species with prolonged parent/offspring involvement. Established adult pairs of Sandhill Cranes (*Grus canadensis*) i.e., those with a history of fledging young, are perennially monogamous (Walkinshaw 1973, Nesbitt and Wenner 1987). Re-pairing of adults following separation or the death of a mate has been reported (Littlefield 1981; Nesbitt and Wenner 1987; Bishop 1988; Bennett and Bennett, in press) although the circumstances preceding and following these cases of mate loss were not usually known.

Florida Sandhill Cranes (*G. c. pratensis*) captured as part of a long-term study were individually color banded beginning in 1977 (Nesbitt 1981). Each bird was aged at banding as adult (> 3 years), subadult (1–3 years), or juvenile (< 1 year), based on plumage characters (Lewis 1979, Nesbitt 1987). Sex of pair members was determined, in the field, during episodes of unison calling. The territories of these pairs were in Paynes Prairie and Kanapaha Prairie (Fig. 1), areas of freshwater marsh and improved pasture in southern Alachua County in north central Florida. Twenty-one nesting pairs were monitored for a total of 122 crane-pair years between 1977 and 1988 (Table 1). Seven pairs (33%) remained together while 14 (67%) changed mates (1 four times) for a total of 17 re-pairings. Nine of 17 (53%) re-pairings followed the known death of a pair member, three (18%) resulted from “divorce” (separation of a pair that had nested previously), in five (29%) the fate of the missing pair member was unknown.

Minton (1968) observed a 14% divorce rate among breeding pairs of Mute Swans (*Cygnus olor*). In the Black-legged Kittiwake (*Rissa tridactyla*), Coulson and Thomas (1983) found a higher divorce rate among younger breeding pairs that was “correlated with the failure of the pair to rear young.” Prior to the three recorded divorces in Florida Sandhill Cranes, although the pair nested and the female laid fertile eggs, they never fledged young. Pair #113, for example, hatched two young in 1986, failed to fledge either, then separated briefly during summer 1986. In 1987, after one nesting attempt with his first mate (a 4-year-old female), the male (a 3-year-old) paired with a new (3-year-old) female and made two additional nesting attempts with her in 1987. His former mate remained within the vicinity of the territory and associated with a mixed flock of adult and subadult cranes before leaving the area.

Unproductive pairs did not necessarily always divorce. The KSE pair remained together between 1984 and 1988 without fledging young, though they nested several times and hatched young three times. It is possible they produced young prior to 1984. Pairs with a reproductive history have remained together for several years without producing young. The first YEL