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MELINDA S. LABRANCHE AND JEFFREY R. WALTERS, *Dept. of Zoology, North Carolina State Univ., Campus Box 7617, Raleigh, North Carolina 27695-7617* (Present address MSL: *Dept. of Biology, SUNY College at Fredonia, Fredonia, New York 14063*); AND KEVIN S. LAVES, *Southeastern Forest Experiment Station, Dept. of Forestry, Clemson Univ., Clemson, South Carolina 29634-1003.* *Received 12 Jan. 1993, accepted 20 Sept. 1993.*

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Direct use of wings by foraging woodpeckers.—Wing use in food-gathering activities has not been observed frequently in birds; the direct use of wings in foraging appears to be quite rare. We define direct wing use as the use of wings in behaviors directly involved in food item "capture" and retention. In contrast, indirect wing use is characterized by the use of wings in behaviors related to, but not directly involved in, food item capture. Here we describe direct use of wings by four species of woodpeckers. These observations, combined with scattered references to similar behavior in other woodpecker species (MacRoberts and MacRoberts 1976, Jackson 1983), bring the total number of woodpecker species in which direct use of wings has been observed thus far to six. We discuss these observations in the context of general patterns of wing use in avian foraging, as well as with respect to speculated evolutionary pathways to avian flight, some of which hypothesize foraging as a function of the avian "proto-wing".

We observed direct wing use in foraging by free-ranging woodpeckers during a series of experiments examining tradeoffs between foraging behavior and vigilance. Experiments were conducted by the senior author in a mature 20-ha deciduous woodlot in western Vigo County, Indiana, from January through March 1993. Woodpeckers had free access to 1-m long sassafras (*Sassafras albidum*) logs. In each log, 1-cm diameter holes were drilled at 5-cm intervals; these holes were filled with purified beef fat before each experimental session. The beef fat provided an essentially non-depleting food resource for the birds (Lima 1992). Logs were aligned 1.5 m apart and were presented in one of four possible pair-wise combinations of diameter (1.5 and 20 cm) and orientation (horizontal and vertical). Approximately 35 h of observations were videotaped from a house through a camouflaged window at a 10-m distance in March 1993. A filming session began at dawn and lasted for approximately 100 min. Behavior was recorded at the equivalent of 30 frames/sec. Woodpecker species foraging on experimental logs were Downy Woodpeckers (*Picoides pubescens*), Hairy Woodpeckers (*P. villosus*), Red-bellied Woodpeckers (*Melanerpes carolinus*), Red-headed Woodpeckers (*M. erythrocephalus*), Pileated Woodpeckers (*Dryocopus pileatus*), and Northern Flickers (*Colaptes auratus*). Other species feeding on the logs were Carolina Chickadees (*Parus carolinensis*), Tufted Titmice (*P. bicolor*), White-breasted Nuthatches (*Sitta carolinensis*), and Carolina Wrens (*Thryothorus ludovicianus*).

"Wing-catching" of food items was observed in Downy, Hairy, Red-bellied, and Pileated woodpeckers. Wing-catching refers to the extension of a wing to prevent a food item (in

this study, a fat fragment) from falling to the ground. Fig. 1 shows a Red-bellied Woodpecker in lateral view on a vertical surface, performing a typical wing-catching sequence. After a series of pecks had dislodged a fat fragment (Fig. 1A), the bird typically probed with its tongue to extract the item. If the item was dropped, or ricocheted from the force of a peck, a wing-catching attempt was made. This consisted of retraction of both metatarsi, pulling the breast into the tree-truck (Fig. 1B), forward extension of the radius-ulna to capture the food item (Fig. 1C), and retrieval of the food item with the bill (Fig. 1D). Only one wing was extended at a time, always on the side of the dropped food item; there was little or no spreading of the primaries. This basic sequence was similar when performed on a horizontal surface, but was observed only once (for the resident female Pileated Woodpecker), although birds dropped or spilled food as often as they did on a vertical surface. This behavior was most prevalent during cold days (<0°C); at low temperatures, the beef fat was brittle, and it often fragmented after the bird delivered a blow with its bill. The frequency of wing-catching behavior was thus a function of the extent to which the beef fat fragmented, but each wing-catching species performed this behavior at least once each session, and often several times per feeding bout. Wing-catching was not observed in either Red-headed Woodpeckers or Northern Flickers, despite repeated opportunities to do so.

The direct use of wings in feeding has been mentioned for Acorn Woodpeckers *M. formicivorous* (MacRoberts and MacRoberts 1976) and for captive juvenile Red-cockaded Woodpeckers *P. borealis* (Jackson 1983). In both species, the wings were extended to catch dropped food; Acorn Woodpeckers apparently use the "pocket" formed by the wing and breast against the branch surface to "capture" dislodged acorns (MacRoberts and MacRoberts 1976). Other species of woodpeckers have been observed to use their breast to manipulate food items. Although wing involvement was not mentioned, both Red-bellied and Crimson-crested (*Campephilus melanoleucos*) woodpeckers have been observed to trap dislodged and falling food items between the breast and the tree-truck (Kilham 1972, 1983). We observed the use of the breast to trap food by most woodpecker species in our study, including Red-headed Woodpeckers, which were not observed to wing-catch. Neither behavior was observed for flickers, suggesting that these types of food manipulation behaviors may be restricted to more arboreal species. For woodpeckers in general (and possibly other species of bark-foragers), it seems likely that capture and retention of food items by either the breast or the wings, or both, would be observed during natural foraging, since dropping prey items (such as wood-boring larvae) during extraction appears to be fairly common (Kilham 1972, 1983).

Indirect use of wings in foraging has been documented much more frequently than direct wing use. Such behavior has been suggested for the Northern Mockingbird (*Mimus polyglottos*) and for several species of herons (Ardeidae). Evidence suggests that wing-flashing in mockingbirds is a behavior which startles prey and thus increases prey accessibility (Hailman 1960). Herons show a much greater diversity in wing use during feeding. Like wing-flashing, "wing-flicking" by herons may serve to startle prey. Presumably, the "canopy" posture and "tenting" behaviors, exhibited by egrets and the Black Heron (*Egretta ardesiaca*) respectively, increase prey visibility in the highly reflective aquatic environment (Meyerriecks 1962, Hancock and Kushlan 1984, Welty and Baptista 1988). However, because prey items are not directly retained or manipulated by the wings in these species, these behaviors are clearly in a different category from those performed by foraging woodpeckers.

The observations reported here for woodpeckers will be useful for evaluating the role of wings in early avian species such as *Archaeopteryx*. Although purely conjectural, the so-called "insect-net" behavior of *Archaeopteryx* is probably the most famous example of direct wing involvement in foraging. Ostrom (1974) suggested that the *Archaeopteryx* "pro-

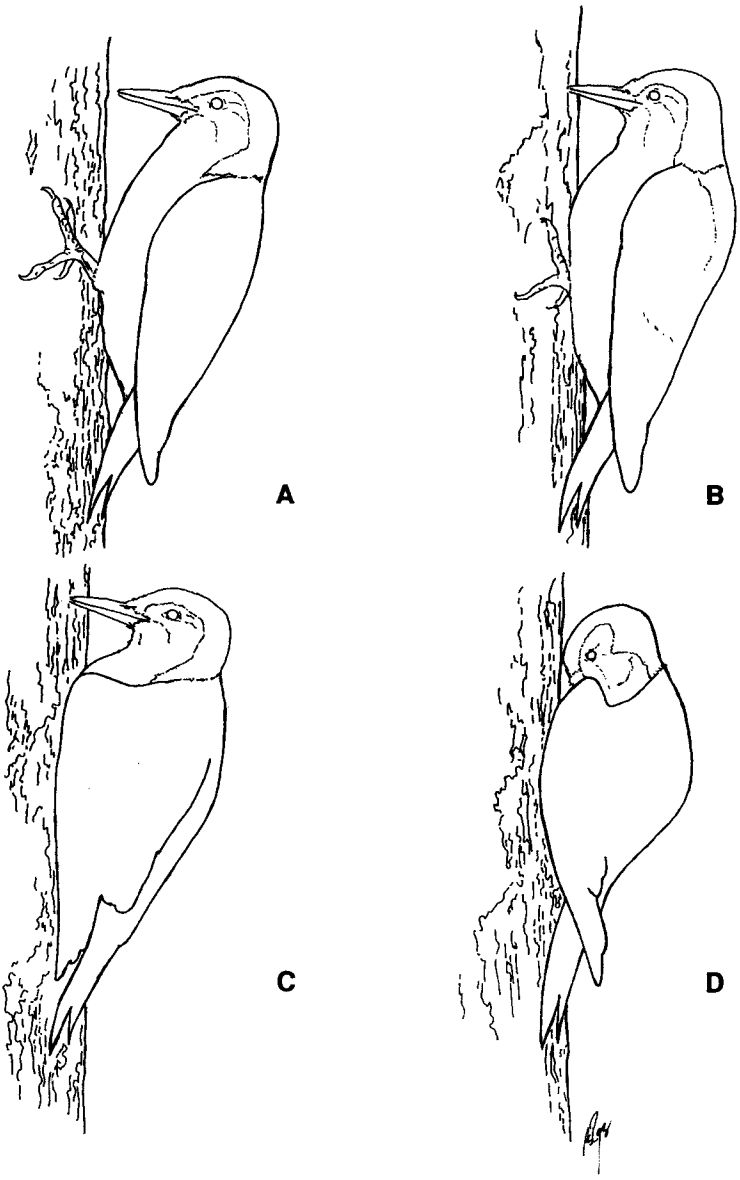

FIG. 1. Typical wing-catching sequence in a Red-bellied Woodpecker. Sequential postures at 0.2-sec intervals. See text for details.

to-wing'' was used as a snare to surround or corral small prey, such as insects and small reptiles. However there are two main objections to this theory. First, although wing use in agonistic or aggressive encounters or for balance is cited as support, there has been no direct analogue to insect-net behavior reported for living bird species. Second, the ''net'' analogy itself has been considered inadequate; presumably feather structure, while adequate for retaining prey items, would not allow sufficient air passage as would be observed in an actual net (Bock 1986). However, woodpecker behavioral analogues suggest that the feathered wings of *Archaeopteryx* would be appropriate for a less-active ''cupping'' behavior or a pounce onto active small prey, especially if the concept of *Archaeopteryx* as an arboreal climber and percher is correct (Feduccia 1993).

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PENNY S. REYNOLDS AND STEVEN L. LIMA, *Dept. Life Sciences, Indiana State Univ., Terre Haute, Indiana 47809.* (Present address PSR: *Div. of Biological Sciences, Univ. of Montana, Missoula, Montana 59812*). *Received 22 July 1993, accepted 10 Oct. 1993.*