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Factors affecting the survival of Ovenbirds wintering in the Northeast.—The northern limit of the usual winter range of the Ovenbird (*Seiurus aurocapillus*) is coastal North Carolina (ca 36°N latitude; Root 1988a), with casual winter occurrences as far north as the Great Lakes region and New England (AOU. 1983). In general, the Ovenbird does not winter in areas where the average minimum January temperature is less than about 0°C and it is most abundant where this temperature is about 10°C (i.e., southern Florida; Root 1988a). Among the wood warblers, only the Yellow-rumped Warbler (*Dendroica coronata*) routinely winters where average minimum January temperatures are below freezing (Root 1988a). This is probably because the generalized foraging behavior (Morse 1989) and specialized gastrointestinal traits of the Yellow-rumped Warbler (Place and Stiles 1992) enable it to exploit alternative, energy-rich food resources, such as bayberry (*Myrica* spp.) available in these areas (Wilz and Giampa 1978).

In addition to labile feeding habits and specialized digestive physiology, other behavioral and physiological adaptations, such as huddling, roosting in protected sites, facultative migration, and nocturnal hypothermy may enhance the ability of largely insectivorous birds to survive winter in cold climates (Frazier and Nolan 1959, Kendeigh et al. 1977, Blem and Pagels 1984, Walsberg 1985, Terrill and Ohmart 1984). Without such adaptations, species such as the Ovenbird are not expected to survive the winter at more northerly latitudes due to energetic constraints (Seibert 1949; Root 1988b, 1989). Observations of birds attempting to winter beyond the normal range of their species can provide empirical evidence to test this prediction and may help clarify environmental and other factors that influence winter distributions.

Study area and methods.—On 4 Jan. 1983 an Ovenbird appeared outside the bird banding laboratory at Powdermill Nature Reserve, Carnegie Museum of Natural History's field research station, three miles south of Rector, Westmoreland County, Pennsylvania (40°10′N, 79°16′W). In the mountain valley in which Powdermill is situated, minimum January temperatures average < -5°C and regularly drop below -17°C (J. F. Merritt, unpubl. data). This sighting provided just the second winter occurrence of the species in western Pennsylvania and the first January record; subsequently, an Ovenbird was seen at Warren in northwestern Pennsylvania as late as 27 Jan. 1988 (Hall 1988). The species has never been observed in western Pennsylvania in February or March (Leberman 1988), suggesting that it may be incapable of maintaining a positive energy balance for the duration of the winter at this latitude. What makes the Powdermill record noteworthy is that the bird was captured, banded, and rehandled twice in the space of two weeks (body mass and subcutaneous fat levels were recorded each time), in addition to being observed almost daily during the same period.

We used our observations of foraging behavior and body mass variation in this bird, correlated to local weather data, to assess possible factors affecting the survival of individuals that attempt to winter north of the usual winter range of this species. Because little can be confidently concluded from our data for a single Ovenbird, we also reviewed extralimital winter records of the species (i.e., birds seen between December and March at sites north of 38°N latitude) published in *Audubon Field Notes* and *American Birds* from 1970–1995.

Results and discussion.—We captured the Ovenbird at 11:45 h (EST) on 8 Jan. in a mist net erected near a thicket and bird feeding area adjacent to our banding lab. We identified it as a bird hatched in the previous calendar year ("SY" in banding terminology), based on retained juvenal wing feathers (see Mulvihill 1993); its skull was completely pneumatized. Its unflattened wing chord measured 74.0 mm, and we judged it to have moderate subcutaneous, furcular fat deposits, rating a "2" on a scale of 0–3 (none to fat mounded; Leber-

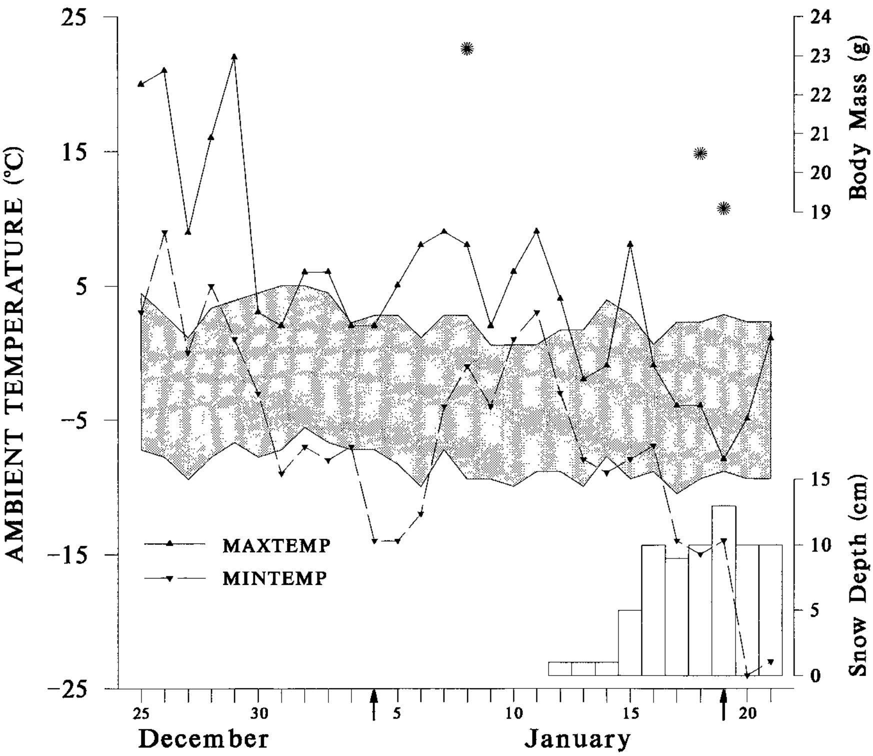

FIG. 1. Ambient temperatures and snow cover in relation to body mass measurements of an Ovenbird banded and recaptured at Powdermill Nature Reserve in southwestern Pennsylvania. The shaded area shows average daily minimum and maximum temperatures recorded at Powdermill Nature Reserve from 1972–1995. First and last seen dates for the bird are shown by arrows on the x-axis.

man 1967). It weighed 23.2 g and appeared healthy with no aberrations or indications of earlier injury. Its body mass at first handling exceeded all mean monthly values for the species at Powdermill from April–October (Clench and Leberman 1978). Local weather prior to the Ovenbird's capture was unseasonably mild, with daytime temperatures well above freezing and no snowcover (Fig. 1). Nonetheless, the Ovenbird had survived several nights with below freezing temperatures, apparently in good condition. It may have been the very cold overnight minimum temperature on 3–4 Jan. (Fig. 1), however, that caused the Ovenbird to seek out the bird feeding area beside our banding lab in the first place.

During the period of comparatively mild weather from 5–12 Jan., when daytime high temperatures were well above freezing and there was no snowcover (Fig. 1), the Ovenbird often fed on the lawn immediately adjacent to the banding lab, usually within a few feet of our windows. The Ovenbird's foraging behavior suggested that it was searching for and finding small invertebrate prey; on several occasions we observed it feeding on earthworms. Sprunt (1957) reported the Ovenbirds' food habits as "Largely insectivorous but also ground life, such as snails, slugs and earthworms. A few seeds and fruits taken at times."

After 12 Jan., the weather worsened with colder temperatures and light snowcover (Fig. 1). During this time we kept some grassy areas free of snow and turned sod in a few places to expose buried invertebrate prey. We observed the Ovenbird using these areas, as well as a narrow strip of grass sheltered from the snow by an overhanging roof. Following heavier snowfalls on 15–16 Jan., it was no longer able to forage for invertebrates and joined many other birds feeding at scattered seed piles on top of the snow. The Ovenbird ate mostly white millet and interacted with several species at the seed piles, especially Dark-eyed Juncos (*Junco hyemalis*), White-throated Sparrows (*Zonotrichia albicollis*), Song Sparrows (*Melospiza melodia*), American Tree Sparrow (*Spizella arborea*), and Tufted Titmice (*Parus bicolor*). It was rarely displaced by any of these birds and was seen to initiate and win aggressive encounters with several of them, at times monopolizing a seed pile for several minutes.

At 10:45 h (EST) on 18 Jan., we recaptured the Ovenbird in a four-cell, Potter-type wire trap placed on the ground and baited with seed. Compared to its initial capture, the Ovenbird had lost 2.7 g and had no visible fat deposits. We recaptured it a second time, again in a wire ground trap, at 11:40 h (EST) on 19 Jan. At this handling it had lost an additional 1.4 g and again had no visible fat deposits. Following its release, the Ovenbird resumed feeding on bird seed. Overnight temperatures (early morning 20 Jan.) dropped to −24°C (Fig. 1), and we did not see the bird the following day. Temperatures the next night fell to −23°C, and although the daytime high temperature on 21 Jan. was above freezing, we did not observe the Ovenbird.

Since it had been seen daily for over two weeks, we assume that the Ovenbird starved during the long, bitterly cold night of 19–20 Jan. Its last recorded body mass, 19.1 g on 19 Jan., was similar to lean body mass values of Ovenbirds caught in Jamaica from October to February (Diamond et al. 1977) and to the average body mass of the species from June through August at Powdermill (Clench and Leberman 1978). The similarity of the Ovenbird's mass to that of breeding birds at Powdermill suggests that it had depleted most, if not all, of its usable lipid reserves (Blem 1990). The observed mass loss, 18% overall 7% between the last two handlings, showed that it was not maintaining a positive energy balance immediately prior to the night of 19–20 Jan.

Root (1988c) observed that the northern winter distribution limits of many species coincide with average minimum January temperature isotherms, and later sought a physiological basis for this observation (Root 1988b). She concluded, based on estimates of the resting metabolic rate of several of these species at the northern edge of their winter range, that passerines showing this distributional pattern are restricted to areas where they do not need to raise their "northern boundary metabolic rate" (NBMR) more than 2.45 times their basal metabolic rate (BMR) in order to counteract the effects of low ambient temperature. She suggested that the consistency of this relationship across many species " demonstrates a physiological limit imposed by ambient temperature regardless of body size, diet, or general habitat" (but see Castro 1989).

Using Root's (1988b) equations (2), (8), and (9), we estimated the 19 g Ovenbird's BMR as 24.2 $kJ \cdot d^{-1}$, thermal conductance (COND) as 1.45 $kJ \cdot (d \cdot bird \cdot °C)^{-1}$, and lower critical temperature (TCRIT) as 24°C. Using these values, and the average minimum January temperature (0°C) at the species' northern distribution limit (TDIST), we estimated its NBMR, according to Castro's (1989) corrected form of Root's (1988b) Eq. 1:

$$NBMR = COND \times (TCRIT - TDIST) + BMR \quad (1)$$

We calculated the Ovenbird's NBMR as 59.0 $kJ \cdot d^{-1}$ or 2.44 times BMR, in close agreement with Root's (1988b) proposed "physiological limit" of 2.45 times BMR; substituting the average minimum January temperature at Powdermill (−5°C) for TDIST raised NBMR to 2.8 times BMR.

Using the same equation, we estimated the Ovenbird's metabolic rate during the 24-h period between its last two captures (average temperature −10°C) as 73.5 $kJ{\cdot}d^{-1}$, which would give a mass loss of 1.9 g if the bird were metabolizing fat (caloric density of fat = 37.7 $kJ{\cdot}g^{-1}$). The bird actually lost 1.4 g during the period, suggesting that it had some remaining fat reserves (probably intraperitoneal fat, since it had no visible subcutaneous fat at the beginning of the period) and may even have gained some metabolizable mass while feeding during the daylight hours of 18 Jan. It clearly was experiencing a negative energy balance at this time, however, and by the end of the day on 19 Jan. likely had depleted all of its fat reserves.

Finally, we estimated the Ovenbird's metabolic rate on the night of 19–20 Jan. (assuming an average overnight temperature of −16°C) would have been 82.2 $kJ{\cdot}d^{-1}$ or 3.4 times BMR. In the absence of any energy-conserving physiological or behavioral adjustments, a minimum fat deposit of 1.3 g would have been needed to fuel the Ovenbird's metabolism for an inactive period of 14 h on the night of 19–20 Jan. (overnight metabolic demand = 48 kJ; caloric density of fat = 37.7 $kJ{\cdot}g^{-1}$). The body mass of the Ovenbird reported on here varied by 2.7–4.1 g between a lean (fat score "0") and moderately fattened (fat score "2") condition. On average, Ovenbirds add 1.5 g to their body mass for each increase in fat score, giving an average gain 4.5 g between a visibly lean and a maximally fattened condition (Mulvihilll, unpubl. data). Although these data suggest that the Ovenbird was physiologically capable of accumulating more than enough fat to meet increased metabolic demands associated with extremely cold temperatures, it clearly was unable to locate food resources of sufficient quantity or quality to do so immediately prior to the night of 19–20 Jan.

We cannot pinpoint when the Ovenbird first began to deplete its fat reserves, but we think that this probably occurred after deep snowcover made it impossible for this ground-foraging species to find invertebrate prey. Extending the Ovenbird's rate of mass loss for the 24-h period from 18–19 Jan. (0.11 $g{\cdot}h^{-1}$) backward to 16 Jan., the day when deep snowcover forced it to feed exclusively on bird seed, we reach a body mass similar to that recorded during the bird's initial handling on 8 Jan. (Fig. 1). The largely insectivorous Ovenbird presumably lacks of the morphological and physiological specializations that enable granivorous birds to digest seeds efficiently (Ziswiler and Farner 1972), and reduced metabolizable energy intake on a seed diet (Kendeigh et al. 1977) would explain its inability to maintain fat reserves after 15 Jan. The possibility that the Ovenbird may have maintained a favorable energy balance for more than a week before and after its initial capture, despite minimum temperatures that were mostly well below freezing during this time, suggests that the species could successfully winter in areas that are colder on average, were it not for the likelihood of deep and persistent snowcover in these same areas.

In our review of the literature, we found a total of 80 extralimital winter records of the Ovenbird, including at least one record in each of the 25 seasons that we surveyed. The distribution of these records by month (last seen dates) was December, 61%; January, 25%; February, 9%; March, 5%. In general, multiple records of Ovenbirds (up to eight in 1983–1984; seven in 1990–1991) occurred during winters or portions of winter seasons that were characterized as unusually mild with little or no snowcover. In several cases where an Ovenbird was observed daily at a site for a week or more, the date when it was either last seen or found dead corresponded closely with the onset of a period characterized by *both* cold temperatures and significant snow accumulation. In two cases, Ovenbirds disappeared following severe winter storms that were described as "blizzards;" one of these Ovenbirds, however, apparently had earlier survived a prolonged period of very cold temperatures and deep snowcover by feeding on table scraps and hamburger at a feeder in Plainfield, New Jersey (Paxton et al. 1978). Of four Ovenbirds believed to have survived the winter at northerly latitudes, individuals at feeders in eastern Pennsylvania from 15 Jan.–4 Mar. 1975 (eating suet and peanut butter; M. and J. Dye, pers. comm.) and southeastern New York from 7 Jan.–3 Mar. 1979 (eating mostly small seeds; Richards et al. 1980), as well as a bird observed in northeastern New York on 30 Mar. 1975 (Buckley and Kane 1975), all experienced winters that were unusually mild and pratically devoid of snow cover (Buckley and Kane 1975, Scott and Cutler 1975, Richards et al. 1980). One Ovenbird, however, apparently survived away from feeders at Brunswick, Maine, during the winter of 1983–1984, where the weather was described as mild in December and February but frigid and snowy during most of January (Heil 1984).

In general, the Ovenbird's northern winter range boundary and associated NBMR fit Root's (1988b) model of a generalized energy constraint on the distributions of many bird species. Notwithstanding this, our data on body mass and fat reserves for an extralimital Ovenbird, along with published records documenting the overwinter survival of Ovenbirds at northerly latitudes, demonstrate that this species is capable of meeting energetic demands associated with average mid-winter temperatures that would theoretically require it to raise its metabolic rate much more than 2.45 times its BMR. The factors that limit an Ovenbird's survival at northern latitudes apparently are those affecting its ability to accumulate and maintain energy reserves sufficient to accomodate simultaneously sharply increased metabolic demand and decreased metabolic energy intake associated with extreme climatic conditions (see Blem 1990). The likelihood that complex, species-specific interactions among several environmental, behavioral, morphological, and physiological variables underlie the simple isothermal associations of avian distribution limits (Root 1988b, cf. Seibert 1949) should serve as a caution in interpreting the among-species patterns produced by those associations (see also King 1974).

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