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ABSTRACT.—Food-value theory states that territorial animals space themselves such that each territory contains adequate food for rearing young. The ovenbird (*Seiurus aurocapilla*) is often cited as a species for which this hypothesis is supported because ovenbird territory size is inversely related to ground-invertebrate abundance within territories. However, little is known about juvenile ovenbird diet and whether food availability is accurately assessed using ground-sampling methods. We examined the relationship between ground-litter food availability and juvenile ovenbird diet in mixed northern hardwood-coniferous forests of north-central Minnesota. We sampled food availability with pitfall traps and litter samples, and concurrently sampled diet of juvenile ovenbirds from stomach samples. We found that juvenile ovenbirds were fed selectively from available food resources. In addition, we found that both ground-sampling methods greatly under-sampled forest caterpillars and snails, which together comprised 63% of juvenile ovenbird diet by mass. Combined with recent radio-telemetry findings that spot-mapping methods can poorly estimate territory size for forest songbirds, our results suggest that comparisons of spot-mapped ovenbird territories with ground-sampled invertebrate availability may not be reliable tests of food-value theory.

Food abundance is hypothesized to be one of the proximate cues used by songbirds when they select nesting territories (Smith and Shugart, 1987), and food availability can have important implications for incubating females, nestlings, and fledglings (Martin, 1987). For example, greater abundance of food items may result in increased growth rate in nestlings (Naef-Daenzer and Keller, 1999) and earlier fledging (Stodola *et al.*, 2010), thereby reducing exposure to nest predation. Greater mass of juveniles at fledging also increases the likelihood of survival in some species (Tinbergen and Boerlijst, 1990; Ringsby *et al.*, 1998; Yackel Adams *et al.*, 2006), particularly when prey item abundance decreases during the post-fledging period (Naef-Daezner *et al.*, 2001). Anthropogenic alterations such as forest fragmentation may affect arthropod (a key component of the diet of many songbirds) abundance and composition (Burke and Nol, 1998; Van Wilgenburg *et al.*, 2001). Thus, studies that effectively quantify the availability of relevant food items are necessary to assess the suitability of habitat and management for breeding birds (Robinson, 1998) as well as predict specific life-history strategies.

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Food-value theory posits that animals space themselves within an area such that there is adequate food within each territory to successfully raise young (Nice, 1941). That hypothesis implies that territory size is inversely related to food availability within each territory. It is logical that relatively high food density would allow an animal to feed in a smaller area, thereby reducing energy costs and possibly reducing competition with neighboring conspecifics. This food-value theory was once so accepted that many behavioral social organization models were based on its premise (Ebersole, 1980), and it was commonly discussed in behavioral and ecological textbooks (Ricklefs, 1973; Brown, 1975). However, experimental studies indicated that food availability has less effect on territory size than other factors such as conspecific intrusion rate (*e.g.*, Eberhard and Ewald, 1994). Indeed, a growing literature suggests that territory size is largely insensitive to food availability (Adams, 2001). However, recent studies testing the effects of food availability on territory or home-range size commonly cite studies of a few species, including ovenbirds (*Seiurus aurocapilla*; Stenger, 1958; Smith and Shugart, 1987) for which a strong relationship between the two has been reported (Zabel *et al.*, 1995; Burke and Nol, 1998).

The ovenbird is considered a convenient species for assessing food availability with respect to territory size. Ovenbirds often forage on the ground and their diet consists nearly exclusively of invertebrates (Holmes and Robinson, 1988; Van Horn and Donovan, 1994); therefore, ovenbird territories are often treated as two-dimensional areas (*i.e.*, forest floor only) with respect to food availability (Stenger, 1958; Smith and Shugart, 1987; Burke and Nol, 1998). Moreover, ovenbird territory size is negatively correlated with ground-litter invertebrate availability (Stenger, 1958; Smith and Shugart, 1987), which supports the food-value theory. However, the food-value theory specifically states that territories include adequate food for rearing young. Therefore, tests of that hypothesis require knowledge of adult and juvenile diet in addition to accurate estimates of food availability. Contents of adult ovenbird stomachs indicate that they forage non-selectively from invertebrates available in ground litter, except that lepidopteran larvae are about twice as common in their diet as in ground litter (Stenger, 1958). Stomach samples from five nestlings (Stenger, 1958) and observations of food items brought by adults to monitored nests (Van Horn and Donovan, 1994) suggested that a large portion of juvenile ovenbird diet is comprised by lepidopteran larvae, similar to many forest-nesting songbirds (Poole, 2005). Because larvae of most forest-dwelling lepidopterans occupy and feed nearly exclusively on leaves of herbaceous and woody plants (Summerville and Crist, 2003), these observations suggest that ground-litter invertebrate sampling methods may not adequately sample availability of a main component of juvenile ovenbird diet. If so, ground invertebrate availability does not reflect availability of juvenile ovenbird food and may not be sufficient for assessing food-value theory.

We investigated juvenile ovenbird diet and ground-litter invertebrate availability in a mixed northern hardwood-coniferous forest. Our objectives were to (1) determine whether adult ovenbirds feed juveniles various invertebrate groups based on the relative availability of those invertebrates in ground litter, and (2) assess whether ground-litter invertebrate sampling techniques are adequate for estimating availability of food for juvenile ovenbirds. We expected that juvenile ovenbird diet would consist primarily of lepidopteran larvae but that ground-invertebrate samples would include very few lepidopteran larvae. We also expected the remaining non-lepidopteran larvae portion of juvenile ovenbird diet to reflect relative availability of other invertebrate groups in ground-litter samples.

<center>Methods</center>

*Diet sampling.*—During the 2008 breeding season, we used radio telemetry and monitored survival of juvenile ovenbirds in mixed northern hardwood-coniferous forests in north-

central Minnesota. The birds fledged between 12 Jun. and 1 Jul. from nests we monitored in 16 10-ha plots within mature forest at two study sites in the Chippewa National Forest (CNF), Cass County, Minnesota, USA. The study sites were separated by 25 km and were located in the Cutfoot Sioux (47°29′37″N, 93°59′50″W) and Suomi Hills (47°26′19″N, 93°40′07″W) areas of the CNF. Mature forest stands at our study sites ranged from 60 to 120 y old (after timber harvest), and ranged from entirely deciduous to nearly entirely coniferous dominant trees. We randomly selected the 16 plots within mature forest at our study sites, searched each plot once every 4 d, and monitored discovered nests on the same 4-d cycle. For a thorough description of our study sites and nest monitoring methods, *see* Streby and Andersen (2011). During a previous radio-telemetry study, we observed that many juvenile ovenbird mortalities occurred without total loss of the bird; some birds were cached in ground litter or predator burrows, some were only partially depredated, and some mortalities were associated with blow fly infection (Streby *et al.*, 2009), allowing for diet analysis on intact stomachs of recovered birds. Therefore, in 2008, when a nestling or fledgling ovenbird was discovered dead but at least partially intact, we dissected the bird, removed the stomach, and stored it in 50% ethanol solution. We later examined stomach contents and identified (to order) invertebrates and invertebrate parts therein. We recorded the number of invertebrates of each order represented in a sample. Because many invertebrates within each stomach sample were broken into several parts, we estimated the number of those invertebrates based on the number of body parts that could be attributed to unique individuals (*i.e.*, those body parts that could be identified as being from different species or individuals of different size).

*Ground invertebrate sampling.*—We sampled ground invertebrates with two common ground-sampling techniques at 120 points concurrent with tracking fledglings. Half (60) of the invertebrate sampling points were ≤2 m from specific locations to which we tracked fledgling ovenbirds ≤5 d after fledging. The other 60 points were each 25 m in a random direction from those 60 fledgling locations. Each point was sampled immediately after tracking a fledgling. At each point we collected a 0.25-m$^2$ sample of litter down to the humus layer and sifted through the sample by hand in a shallow box. We collected all macro invertebrates and stored them in 50% ethanol solution. In addition, we set a pitfall trap at each invertebrate sampling point. For each pitfall trap, we used a 473-ml plastic cup containing ~50 ml of 50% ethanol solution. We buried the cup such that the top was flush with the ground surface, and we replaced surrounding litter to contact the edge of the cup. We collected pitfall trap contents after 24 h and stored them in 50% ethanol solution. We counted and identified (to order) invertebrates from each litter and pitfall sample. We then dried samples for 24 h in a drying oven and measured dry mass to within 0.0001 g.

*Statistical analysis.*—It is possible that stomach contents may be affected by cause of death (*e.g.*, birds with blow-fly infections may starve due to parental neglect in response to fledgling condition). If so, our samples would not accurately reflect diet for juvenile ovenbirds in our population because nine (50%) of our samples came from birds with blow-fly infections, but only 21% of nests we monitored were infested with blowflies. Therefore, we tested for differences in stomach sample mass between birds with blow-fly infections and those without using a Student's *t*-test. Because stomach samples were small, for diet analysis we combined all stomach samples into one diet sample, and compared that sample to each ground invertebrate sample. We compared counts of invertebrates from each order between the litter sample and the pitfall sample and between each of those samples and the diet sample with $\chi^2$ tests-of-independence. We considered tests statistically significant at the α = 0.05 level. A similar test on dry mass would be inappropriate because the sample size in a $\chi^2$

TABLE 1.—Counts and dry mass (g) of invertebrate groups collected in pitfall traps (n = 120), litter samples (n = 120), and in the stomachs[a] of 18 juvenile ovenbirds (*Seiurus aurocapilla*) during 2008 in the Chippewa National Forest, Minnesota, USA. Proportions of invertebrates were significantly different between ground sampling methods and between each ground sampling method and juvenile diet

| Invertebrate group[b] | No. pitfall (%) | No. litter (%) | No. diet (%) | Mass pitfall (%) | Mass litter (%) | Mass diet (%) |
|---|---|---|---|---|---|---|
| Araneida | 252 (26) | 37 (20) | 20 (11) | 0.504 (10) | 0.074 (9) | 0.040 (2) |
| Coleoptera | 358 (38) | 33 (18) | 52 (28) | 3.222 (65) | 0.297 (36) | 0.468 (29) |
| Hymenoptera | 336 (35) | 106 (58) | 32 (17) | 1.008 (21) | 0.318 (39) | 0.096 (6) |
| Lepidoptera | 12 (1) | 7 (4) | 47 (25) | 0.204 (4) | 0.119 (15) | 0.799 (50) |
| Pulmonata | 0 (0) | 1 (0) | 35 (19) | 0.000 (0) | 0.006 (1) | 0.210 (13) |

[a] Other items in juvenile ovenbird stomachs included seeds (n = 2), small rocks (n = 2), hollow synthetic fiber fill (n = 2), and a reduviid bug (n = 1)

[b] Includes only invertebrate groups present in stomach samples and ground-litter samples

tests-of-independence on mass would depend on our unit of measurement. However, we report proportions of invertebrate groups by dry mass in each sample (Table 1).

## RESULTS

We collected stomachs from 18 juvenile ovenbirds that died in the first 4 d after fledging (8–12 d after hatching) with mortalities attributable to predation (n = 9), blow-fly infection (n = 8), and predation of a blow fly-infected bird (n = 1). Stomach samples contained 0–25 ($\bar{x}$ = 11) identifiable whole or unique parts of invertebrates representing six orders. One sample included one reduviid bug (Hemiptera), and all other invertebrates were of five orders (Table 1). Each stomach sample contained a small amount of unidentifiable invertebrate remains (<5% of total sample mass). Some stomach samples also contained small stones (n = 2) and seeds (n = 2), and two samples included small pieces of hollow synthetic tubing that appeared to be synthetic fiber fill. Stomach-sample dry mass ranged from 0.0110 to 0.2364 g ($\bar{x}$ = 0.1028 g) and mass did not differ between samples from birds with and without blow-fly infections ($t_{16}$ = 2.12, P = 0.55).

Proportions of ground samples comprised by each invertebrate group were different between the litter sample and the pitfall sample ($\chi^2$ = 48.3, df = 4, P < 0.01; Table 1). Proportions of juvenile diet comprised by each invertebrate order differed from those in litter samples ($\chi^2$ = 423.5, df = 4, P < 0.01) and in pitfall samples ($\chi^2$ = 423.5, df = 4, P < 0.01). The largest difference between the diet sample and both ground-invertebrate samples was in lepidopteran larvae (caterpillars). After we removed caterpillars from analysis, assuming ground-sampling methods may not have accurately estimated their abundance, proportions of the remaining four invertebrate orders still differed between juvenile ovenbird diet and both ground-sampling methods (both P's < 0.01). The differences in proportions of invertebrate groups between ground-sampling methods and juvenile ovenbird diet were even larger when measured by dry mass (Table 1).

## DISCUSSION

Juvenile ovenbird diet reflected selective feeding by adults from available food, and ground-sampling methods (litter sampling and pitfall traps) were inadequate for sampling the main component of juvenile ovenbird diet, lepidopteran larvae (caterpillars). Importantly, estimates of relative availability of invertebrate groups differed between the

litter sample and the pitfall sample. Unfortunately, it was not the case that at least one method adequately sampled each of the invertebrate groups so that somehow combining the methods would improve those estimates. Although the ground-sampling methods produced different estimates from each other, they both undersampled caterpillars and snails. Even when caterpillars were excluded from analyses, juvenile ovenbird diet (as determined from stomach contents) was still significantly different from available food in both ground samples: stomach samples then included more beetles and snails and fewer spiders and ants than were available based on litter samples and pitfall traps. Those differences may reflect a propensity for adults to consume smaller prey (spiders and ants) while foraging and carry mostly larger prey (beetles) to young, although that is only speculation.

Caterpillars and snails were rare in ground litter samples but constituted 63% of juvenile ovenbird diet by mass. There are at least three potential explanations for this discrepancy: (1) ovenbirds selectively search ground litter for larger (and relatively rare) food types to feed to their young; (2) our sampling methods grossly underestimated the availability of these food types in ground litter; or (3) ovenbirds foraged for these items somewhere other than on the ground. The terrestrial snails we found in ovenbird stomachs occur nearly exclusively in ground litter and under decaying wood (Baker, 1935). Terrestrial snail abundance has been effectively sampled using pitfall traps (Poulin and Lefebvre, 1997) and ground-litter sampling (Stenger, 1958), though ground-litter sampling may undersample larger snails (Hotopp, 2002). Snails are included in the diets of many passerines for their shells, because the calcium in forest arthropods is not sufficient for songbird egg shell deposition or juvenile skeletal development (Graveland and Van Gijzen, 1994). However, we found only one snail and no shells in 120 litter samples, suggesting that ovenbirds may actively search for them. It is possible that adult ovenbirds searched specifically for snails, focusing foraging efforts within decaying woody debris rather than in leaf litter. It is also possible that ovenbirds gather shells of dead snails, which would not be detectable using pitfall traps. Caterpillars, on the other hand, were very rarely seen on the ground in our study sites but were ubiquitous on leaves of shrubs and understory trees, as is typical of lepidopteran larvae. It is clear that ground-sampling methods inadequately sample availability of forest caterpillars, which constituted roughly half of juvenile ovenbird diet and as much as one-third of adult ovenbird diet (Stenger, 1958). Indeed, Holmes and Robinson (1988) reported that 35% of ovenbird prey attacks occur above ground, despite the common perception that ovenbirds forage exclusively on the ground. Transect-based methods that more effectively quantify lepidopteran larvae (Stodola et al., 2010) and snails (McDade and Maguire, 2005) are probably necessary in addition to ground-sampling methods to meaningfully sample food availability for ovenbirds.

It is surprising that the reported negative correlation between ovenbird territory size and ground-invertebrate availability is so strong ($r^2 = 0.82$; Stenger, 1958), considering how poorly ground-sampling methods sample >50% of ovenbird diet, and how spot-mapping methods can poorly estimate territory size in forest songbirds (Anich et al., 2009; Streby et al., 2012). One possible explanation is that litter-invertebrate abundance and/or biomass relates strongly to above-ground lepidopteran larvae abundance and/or biomass. However, the authors of Stodola et al. (2010) found that litter depth, a common index of litter-invertebrate biomass, had no relationship with abundance of above-ground lepidopteran larvae at any spatial scale (K. Stodola, pers. comm.). Together, these findings suggest that relating spot-mapped ovenbird territory size and ground-litter invertebrate abundance probably is not a reliable test of food value theory. We suggest that at least sampling above-ground

lepidopteran larvae abundance within territories, and probably delineating territories with a more intensive method such as telemetry, would be necessary for a reliable comparison.

Finally, we found hollow synthetic fibers in the stomachs of two juvenile ovenbirds we recovered >1 km apart. The fibers we found appeared to be insulating fill that is common in coats, vests, blankets, and sleeping bags. During fall and winter, our study area is used by hunters, hikers, and snowmobile riders, all of whom use insulated products. It is possible that we were the source of these fibers, but we used few insulated products during the summer study period. It is difficult to infer from two stomach samples whether our observations are evidence of the seeming ubiquity of terrestrial and marine plastic pollution (Barnes *et al.*, 2009). However, regardless of the source, it is disconcerting that plastic fibers were consumed by songbirds, and we recommend close inspection for these products in future studies of songbird diet.

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