

NESTLING PROVISIONING BY HAIRY AND WHITE-HEADED WOODPECKERS IN MANAGED PONDEROSA PINE FORESTS

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ABSTRACT.—Parental roles in nestling provisioning and composition of prey brought to nestlings are not well-studied for North American woodpeckers (Picidae). We studied nestling diets and the role of adult Hairy (*Picoides villosus*) and White-headed woodpeckers (*Picoides albolarvatus*) in provisioning nestlings and nest sanitation during 2009–2011 in managed ponderosa pine (*Pinus ponderosa*) forests, Cascade Range, Washington, USA. Male White-headed Woodpeckers removed fecal material from cavities more frequently than females; a difference we did not observe between sexes in Hairy Woodpeckers. Male and female White-headed Woodpeckers, and female Hairy Woodpeckers, fed significantly more small (beak closed when holding prey) than large prey (beak unable to close when holding prey) to nestlings. We did not find differences in provisioning rates by sex of the parent, by nestling age, or by date of provisioning trip for either species. Morisita's Index (C) of diet overlap showed a large similarity in the nestling diets of Hairy and White-headed woodpeckers ($C = 0.81$), and dietary niche breadth was low for both species. Of the prey we identified, larvae of wood-boring beetles (Coleoptera: Cerambycidae and Buprestidae) were most frequently fed to nestlings by both species. White-headed Woodpeckers fed caterpillars (Lepidoptera) and winged prey to nestlings more often than Hairy Woodpeckers. The diet of Hairy Woodpecker nestlings did not change appreciably over the nesting season, with wood-boring beetle larvae having the highest relative frequency for most of the breeding period. In contrast, relative frequency of wood-boring beetle larvae in the diet of White-headed Woodpecker nestlings declined toward the end of the breeding period as the relative frequency of caterpillars increased. Our results suggest that both sexes of these woodpeckers contribute equally to nestling provisioning. Received 11 December 2012. Accepted 8 March 2013.

Key words: Hairy Woodpecker, nest sanitation, nestling provisioning, *Picoides*, ponderosa pine, White-headed Woodpecker, woodpecker.

Evaluating rates of nestling provisioning by adult birds provides insight into foraging strategies and reproductive effort (Barba et al. 2009). In most biparental avian species, both males and females provision the young, although this task is not always shared equally between sexes (Nordlund and Barber 2005). In woodpeckers (Picidae), biparental care is thought to be necessary to successfully raise offspring (see Wiebe 2005 for an exception in the Northern Flicker [*Colaptes auratus*]), resulting in social monogamy for most woodpecker species (Chazarreta et al. 2011). Unlike other avian groups, such as passerines, where females generally invest more than males in raising offspring (Wiktander et al. 2000), male woodpeckers contribute significantly to raising young by performing nocturnal incubation and brooding (Wiktander et al. 2000, Wiebe 2008), and contribute equally to or greater than females in regard to nest sanitation and feeding of nestlings (Hogstad and Stenberg 1997, Michalek

and Winkler 2001, Rossmann et al. 2009, Chazarreta et al. 2011).

Few studies address nestling provisioning rates and nestling diets for North American woodpeckers. For example, we found provisioning rates for only 8 of the 20 non-cooperatively breeding woodpeckers that nest north of Mexico (American Three-toed Woodpecker [*Picoides dorsalis*; Gibbon 1966], Nuttall's Woodpecker [*P. nuttallii*; Miller and Bock 1972], Yellow-bellied Sapsucker [*Sphyrapicus varius*; Kilham 1977], Pileated Woodpecker [*Dryocopus pileatus*; Bull and Meslow 1988], Gila Woodpecker [*Melanerpes uropygialis*; Martindale and Lamm 1984], Lewis's Woodpecker [*M. lewis*; Tashiro-Vierling 1994], Downy Woodpecker [*P. pubescens*; Hawkins and Ritchison 1996], and Northern Flicker [Wiebe and Elchuk 2003]). In addition to quantifying provisioning rates, identification of important arthropod prey to nestling woodpeckers will increase understanding of breeding season habitat use, because woodpecker prey can be linked to specific habitat features (e.g., Cerambycidae larvae are linked to recently dead wood, bark beetles [Coleoptera] are linked to diseased or stressed trees).

The White-headed Woodpecker (*P. albolarvatus*) is primarily associated with pine (*Pinus* spp.)

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forests resulting in a narrow and fragmented distribution throughout the western United States and southern British Columbia (Garrett et al. 1996). In the Pacific Northwest, the White-headed Woodpecker primarily inhabits interior, ponderosa pine (*Pinus ponderosa*) dominated forests along the eastern slope of the Cascade Range and in the Blue Mountains. Although once labeled as one of the most poorly studied woodpeckers in North America (Garrett et al. 1996), recent studies have focused on foraging (Kozma 2010), nesting habitat (Buchanan et al. 2003; Kozma 2011, 2012), phylogeography (Alexander and Burns 2006), and reproductive success (Wightman et al. 2010, Hollenbeck et al. 2011, Kozma and Kroll 2012). Despite these studies, information on sex-specific roles in provisioning nestlings and nest sanitation, as well as detailed information on the diet of nestlings, is lacking.

The Hairy Woodpecker (*P. villosus*) occurs in a wide variety of forest types in North America (Jackson et al. 2002) and occurs throughout the range of the White-headed Woodpecker. In contrast to the White-headed Woodpecker, the reproductive biology of the Hairy Woodpecker has received greater attention. However, the diet of Hairy Woodpecker nestlings has not been studied in detail and considerable variation exists in parental care demonstrated by this species (Jackson et al. 2002). For example, Kilham (1968) found that female Hairy Woodpeckers fed nestlings up to four times more frequently than males, whereas de Kiriline Lawrence (1967) found that both sexes fed nestlings at nearly equal rates. These studies were conducted in the central or eastern United States and Canada; the results of which may differ from areas in the western portion of the species' range.

We evaluated the diets of both Hairy and White-headed woodpecker nestlings and sex-specific roles of adults when provisioning nestlings in ponderosa pine-dominated forests of the eastern Cascade Range, Washington, USA. Specifically, our objectives were to: (1) determine if differences exist between the sexes in their rate of nestling provisioning and nest sanitation, and the size of prey delivered to nestlings for both species, (2) describe to the finest taxonomic level the diversity and frequency of prey fed to nestlings, and (3) compare nestling diet overlap between the two species.

METHODS

Study Area.—We conducted this study along the eastern slope of the Cascade Range in

southern Kittitas and Yakima counties, Washington (46° 46' N, 120° 59' W), from 2009–2011. The climate in this region is characterized by hot, dry summers, with over 80% of the annual precipitation occurring in winter, primarily as snow (Wright and Agee 2004). The eastern slope of the Cascades is characterized by complex topography (Everett et al. 2000). Our study area contained 24 sites located on lands managed by Okanogan-Wenatchee National Forest (10 sites), Washington Department of Natural Resources (10 sites), and three private landowners (four sites). Through yearly censusing of known breeding territories of White-headed Woodpeckers, we determined that each site contained only one White-headed Woodpecker breeding pair. Each site consisted of the forested stand the pair was known to occupy where the mean breeding season home range from 95% fixed kernel estimates is 105 ha (SD = 36 ha, $n = 13$; T. Lorenz, unpubl. data) and all sites are part of a long-term study on the reproductive biology of White-headed Woodpeckers (Kozma and Kroll 2012). We selected these sites opportunistically based on recent sightings from regional biologists and foresters, historical records of sightings of White-headed Woodpeckers (Buchanan et al. 2003), and by finding breeding pairs opportunistically in the study area as we conducted field work. We easily located nesting areas of Hairy Woodpeckers, because Hairy Woodpeckers are common in our study area and occurred in all breeding territories of White-headed Woodpeckers.

The study area contained a mix of tree species dominated by ponderosa pine, with lower abundances of Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), grand fir (*Abies grandis*), and quaking aspen (*Populus tremuloides*; Kozma 2011). Antelope bitterbrush (*Purshia tridentata*), wax currant (*Ribes cereum*), snowbrush ceanothus (*Ceanothus velutinus*), common snowberry (*Symphoricarpos albus*), and shinyleaf spiraea (*Spiraea betulifolia* var. *lucida*) were dominant understory plants. In general, “hot-dry shrub/herb” (ponderosa pine/bitterbrush/bluebunch wheatgrass [*Pseudoroegneria spicata*]) and “warm-dry shrub/herb” (Douglas-fir/bitterbrush/bluebunch wheatgrass) vegetation types dominated the study area (Harrod et al. 1999). Seventeen of 24 sites occurred in unburned stands where timber had been harvested within the past 25 years. Seven sites occurred in stands that had burned at least once in the previous 12 years

and, salvage logging occurred in five of the burned stands.

Nest Searching and Monitoring.—We searched for nests from April to early-July. We systematically searched a subset of the 24 sites each year because of time constraints and because new sites were added each year as we discovered new breeding pairs. We broadcasted playback calls and drumming of Hairy and White-headed woodpeckers at random locations as we moved through known breeding territories to locate woodpeckers (Melletti and Penteriani 2003, Nappi and Drapeau 2009). We followed either sex during the nesting season to find cavities, because both sexes of these woodpeckers take part in cavity excavation, incubation, brooding, and nestling feeding. If this failed to result in locating a cavity, we followed adult distress calls or sounds of begging chicks to reveal the cavity's location. To determine the number and age of nestlings, we viewed contents of cavities up to 11 m above ground with a Tree Top Peeper IV nest-inspection system (Kozma and Kroll 2012). We estimated nestling age from the incubation start date or hatch date if known, or from feather development of young (Kozma and Kroll 2012). We calculated the nest-initiation date (day the first egg was laid) by backdating from the day of hatching or fledging, or from the estimated age of young, assuming that incubation began on the day the last egg was laid and that one egg was laid each day during the laying period (Pechacek 2006).

Nestling Provisioning.—We used a 65ED spotting scope with a XW 10 eyepiece positioned 30–50 m from the nest cavity to record feeding observations during 2-hr time periods (Schaefer et al. 2004, Rossmanith et al. 2007). Because some previous studies have shown little evidence of diurnal variation in provisioning rates for a variety of bird species (Goodbred and Holmes 1996, Sethi and Bhatt 2007, Barba et al. 2009, Maccarone et al. 2012), we made all observations from 0800–1230 hrs (Connor et al. 1999, Schaefer et al. 2004), May to July in each year. We attempted to observe each nest once when nestlings were 1–13 days old (early) and once when nestlings were 14–25 days old (late), totaling two observation periods (4 hrs) for most nesting pairs. However, in some cases, we found nests when young were older than 13 days and some nests failed before young were 14 days old, and therefore we obtained only one observation period for those nesting pairs. We dressed in

camouflage clothing and positioned ourselves near shrubs or downed wood to blend into the environment and reduce stress on the parent birds, because they can become agitated with humans near their nest cavity, especially when nestlings are greater than 10 days old (JMK, pers. obs.). Although we took steps to reduce the bias of our presence affecting woodpecker provisioning behavior, adults provisioning young probably became habituated to our presence thereby modifying their behavior patterns in order to keep the observer under surveillance (Morrison et al. 2006). We feel that this did not greatly influence the rate at which they provisioned young. We began recording feeding observations after adults had resumed normal activity and no longer gave alarm calls, which usually took from 15–30 mins. If adult woodpeckers failed to resume normal activity, we abandoned the observation attempt and returned the next day.

During each observation period, we determined the age and number of nestlings using the nest inspection system, the sex of the parent delivering prey to the cavity nest, if fecal material was removed, the size and type of prey delivered, and the time elapsed between feeding visits. We considered each trip to the nest with prey as a single visit regardless of the number of prey delivered (Pinkowski 1978). We calculated provisioning rates (number of feeding trips/nestling/hour) during the early and late nestling periods for males and females of each woodpecker species (Nordlund and Barber 2005, Reed et al. 2007). When calculating provisioning rates, we used only those nests where we could determine the number of young (cavities ≤ 11 m in height). We were unable to view the contents of only two Hairy Woodpecker nests and this likely did not affect our results. We classified all prey items as either small, where prey is held with the beak completely closed, or large where the beak is unable to close. We further identified prey items to order or family (e.g., adult beetle [Coleoptera], ant [Formicidae]) whenever possible. We calculated the relative frequency of occurrence for each prey type, because we were unable to identify all prey items (Rossmanith et al. 2007). When calculating the contribution of each sex to nestling care, we only used nests where we verified both parents were alive during observation periods (Nour et al. 1998, Wiktander et al. 2000).

Statistical Analysis.—To determine if sexes removed fecal material from cavities equally and

if males brought more large prey to nestlings than females, we used a Wilcoxon signed-rank test (data did not meet the assumptions of a normal distribution; Steel and Torrie 1980, Conrad and Robertson 1993). We used 95% CI to determine if each sex brought small and large prey items equally, for both Hairy and White-headed woodpeckers. We used 95% CI to compare mean provisioning rates between broods of two, three, and four nestlings, where non-overlapping CI suggested a statistically significant difference. We used mixed models (REML) to evaluate differences in parental provisioning rates for both woodpecker species (Reed et al. 2007). Our response variable was provisioning rate and we treated sex of parent, age of nestlings, and date of provisioning trip (i.e., did seasonal variation exist in provisioning rate?) as fixed effects in our models. Given that individual nests are subsamples, we treated both year and location as random effects in our model. We fit mixed models with PROC MIXED in SAS Version 9.2 (SAS Institute 2012).

We used Morisita's index (C ; Morisita 1959), which is considered by Smith and Zaret (1982) to be the least biased estimator of diet overlap, to compare the similarity of nestling diet between the two species (Hanula et al. 2000b). To determine the degree of dietary specialization for each woodpecker species, we calculated a standardized dietary niche breadth value (B_{st} ; Lewis et al. 2006) for each nest where $B_{st} = (B - 1)/(n - 1)$, and where $B = 1/\sum p_j^2$, p_j is the proportion of individuals in prey category j , and n is the number of prey categories. We used a standardized value of B because there were unequal prey categories among nests (Lewis et al. 2006). Results are presented as mean \pm 1 SE unless otherwise noted.

RESULTS

We recorded 641 prey deliveries to nestlings during 32 observation periods at 22 nest cavities of Hairy Woodpeckers and 728 prey deliveries to nestlings during 45 observation periods at 28 nest cavities of White-headed Woodpeckers. Male and female White-headed Woodpeckers delivered more small prey items to nestlings than large prey items, as did female Hairy Woodpeckers (Fig. 1). No difference existed in proportion of nest visits made by male Hairy Woodpeckers with large versus small prey (Fig. 1). Male White-headed Woodpeckers brought large prey and

removed fecal material during a greater proportion of nestling feedings than did females ($df = 23$; $z = 2.4$, $P = 0.016$ and $z = 2.2$, $P = 0.032$; respectively), whereas no difference existed between male and female Hairy Woodpeckers in the proportion of nestling feeding visits containing large prey or the removal of fecal material ($df = 21$, $z = 1.50$, $P = 0.13$ and $z = 1.56$, $P = 0.12$; respectively; Table 1). For both species, mean provisioning rate did not differ between broods of two, three, or four nestlings, and it declined as brood size increased (Fig. 2). Provisioning rates did not differ between female and male Hairy Woodpeckers ($n = 62$, $F_{1,42} = 2.78$, $P = 0.100$). We found no evidence of variation in Hairy Woodpecker provisioning rate by age of nestlings ($n = 62$, $F_{1,42} = 0.11$, $P = 0.74$) or date of provisioning trip ($n = 62$, $F_{1,42} = 0.09$, $P = 0.76$). Similarly, provisioning rates did not differ between male and female White-headed Woodpeckers ($n = 83$, $F_{1,59} = 0.01$, $P = 0.95$). We found no evidence of variation in White-headed Woodpecker provisioning rate by age of nestlings ($n = 83$, $F_{1,59} = 0.04$, $P = 0.53$) or date of provisioning trip ($n = 83$, $F_{1,59} = 3.36$, $P = 0.070$).

We identified prey items to major taxonomic group during 57% of Hairy Woodpecker ($n = 365$ observations) and 51% of White-headed Woodpecker ($n = 372$ observations) prey deliveries (Table 2). From these observations, we calculated a Morisita's index of $C = 0.81$. The dietary niche-breadth for the Hairy Woodpecker was low ($B_{st} = 0.14 \pm 0.01$, range = 0.10–0.20) and nearly identical to that of the White-headed Woodpecker ($B_{st} = 0.15 \pm 0.01$, range 0.07–0.29). Larvae of wood-boring beetles (Cerambycidae and Buprestidae), adult ants and their larvae, insect larvae, and adult beetles comprised 39, 20, 15, and 14%, respectively, of prey brought to nestlings by Hairy Woodpeckers (Table 2). Wood-boring beetle larvae, caterpillars (Lepidoptera), adult ants and their larvae, and insect larvae comprised 25, 23, 18 and 6%, respectively, of prey brought to nestlings by White-headed Woodpeckers (Table 2). Excluding adult beetles, winged prey (adult antlion [Myrmeleontidae], bumblebee [Apidae], cicada [Cicadidae], crane fly [Tipulidae], adult fly [Diptera], mayfly [Ephemeroptera], moth [Lepidoptera], grasshopper [Acrididae], and all other winged insects) accounted for 12% of prey brought to White-headed Woodpecker nestlings compared to only 3% of prey brought to Hairy Woodpecker nestlings.

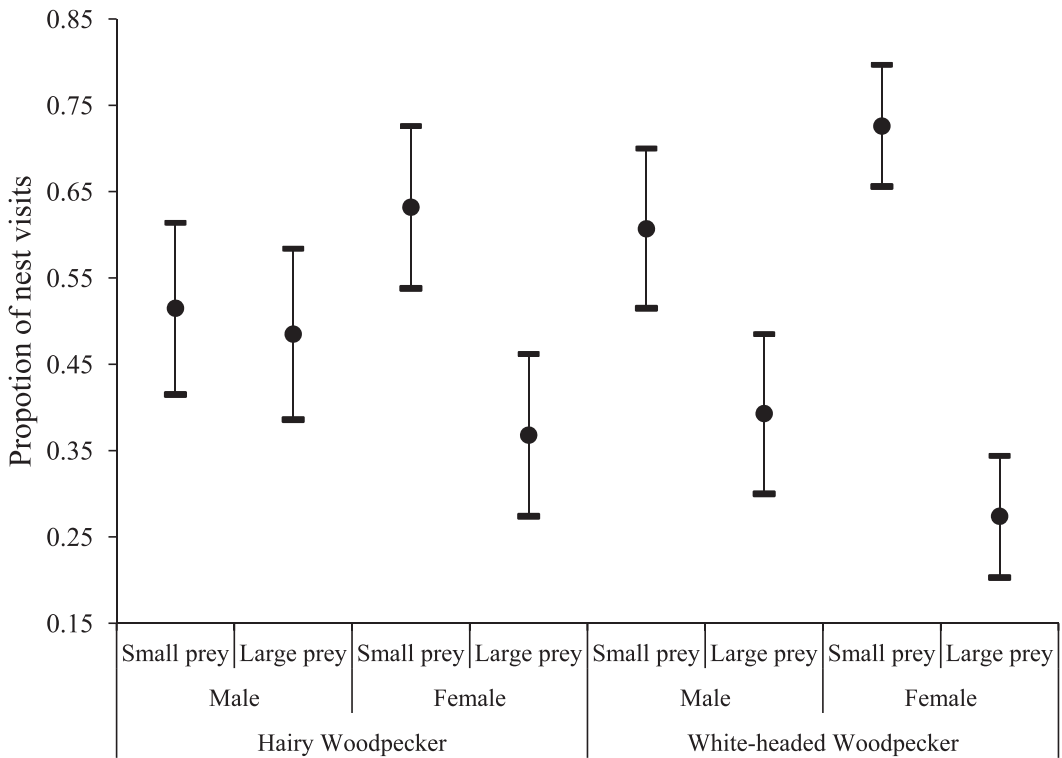


FIG. 1. Proportion of small and large prey (mean ± 95% CI) brought to nestlings by male and female Hairy Woodpeckers and White-headed Woodpeckers in managed ponderosa pine forests of the east Cascade Range, Washington, 2009–2011.

The diet composition of Hairy Woodpecker nestlings did not change appreciably over the nesting season (Fig. 3). Wood-boring beetle larvae had the highest relative frequency in the nestlings’ diet for most of the breeding period, with the greatest frequency occurring during the early part of the nesting season. Similarly, wood-

boring beetle larvae had the highest relative frequency in the diet of White-headed Woodpecker nestlings during the first half of the breeding period, but declined steadily toward the end of the breeding period as the relative frequency of caterpillars increased nearly six-fold (Fig. 3).

TABLE 1. Nestling provisioning and nest sanitation, mean (SE), by male and female Hairy Woodpeckers ($n = 22$ nests) and White-headed Woodpeckers ($n = 24$ nests) in managed ponderosa pine forests of the eastern Cascade Range, Washington, 2009–2011.

	Hairy Woodpecker		White-headed Woodpecker	
	Male	Female	Male	Female
Proportion of visits with large prey	0.49 (0.05)	0.37 (0.05)	0.39 (0.04)	0.27 (0.03)
Proportion of visits with fecal removals	0.16 (0.03)	0.12 (0.05)	0.21 (0.04)	0.08 (0.02)
Early ^a feeding rate (deliveries/nestling/hour) ^b	1.7 (0.2)	1.7 (0.3)	1.6 (0.1)	1.6 (0.1)
Late ^c feeding rate (deliveries/nestling/hour) ^d	1.4 (0.2)	2.1 (0.3)	1.6 (0.2)	1.7 (0.3)

^a Nestling age of 1–13 days.

^b $n = 14$ Hairy Woodpecker nests and $n = 21$ White-headed Woodpecker nests.

^c Nestling age of 14–25 days.

^d $n = 15$ Hairy Woodpecker nests and $n = 17$ White-headed Woodpecker nests.

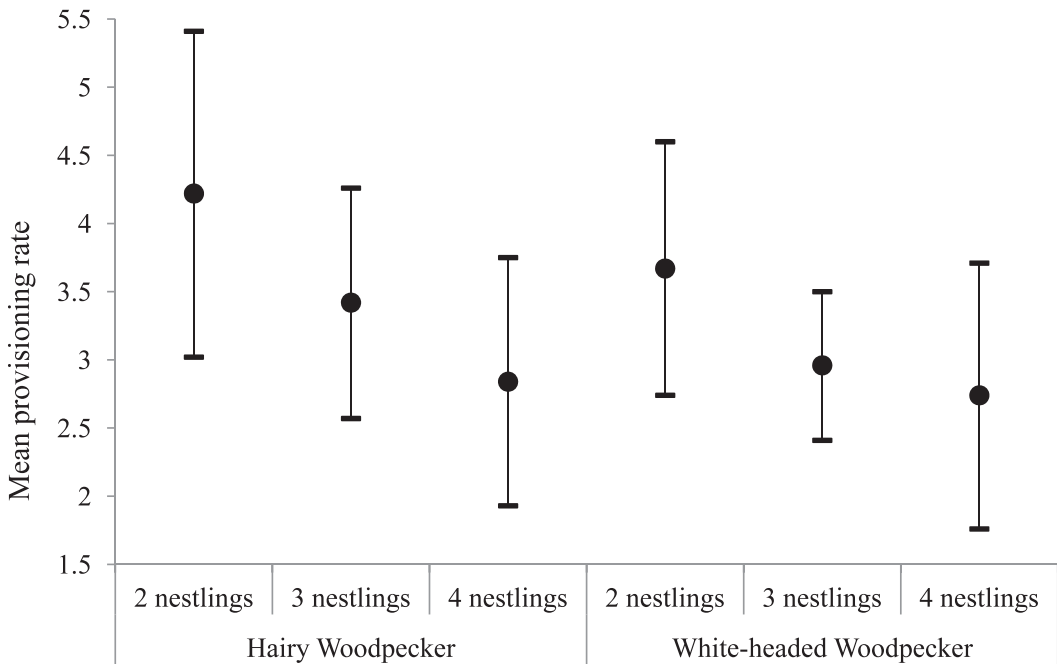


FIG. 2. Mean nestling provisioning rates (feedings/nestling/hour, 95% CI) for Hairy Woodpeckers and White-headed Woodpeckers (sexes combined) in relation to brood size in managed ponderosa pine forests of the east Cascade Range, Washington 2009–2011.

DISCUSSION

Woodpeckers are keystone species that serve critical roles in ecosystem dynamics (Virkkala 2006). Information on foraging ecology of woodpeckers can inform management guidelines and promote sustainable woodpecker populations at the landscape scale (Hanula et al. 2000b, Raley and Aubry 2006, Edworthy et al. 2011). For example, knowledge of nestling diets can guide requirements for retention/creation of habitat components that attract prey species used by woodpeckers during the breeding season. Comparing woodpecker provisioning rates and nestling diets across geographic areas can inform species- and region-specific management practices (e.g., moist coastal forests versus dry interior forests, old growth versus young stands; Hanula and Engstrom 2000, Hanula et al. 2000b).

We did not find differences between male and female provisioning rates for either Hairy or White-headed woodpeckers. Similar results have been found for Lesser Spotted (*Dendrocopos minor*; Wiktander et al. 2000), Nuttall's (Miller and Bock 1972), and Magellanic (*Campephilus magellanicus*; Chazarreta et al. 2011) woodpeckers. Although

the sexes fed nestlings at similar rates in both species, provisioning rates may also be influenced by quantity of food brought by each sex (Wiebe and Elchuk 2003). However, we did not measure food quantity in this study. Furthermore, we did not evaluate the influence of time of day on provisioning rates because our observations occurred only in the morning. Temperature fluctuations associated with time of day may influence provisioning rate of White-headed Woodpeckers, especially later in the nesting period when surface-dwelling and aerial prey make up a greater proportion of the nestling diet (Miller and Bock 1972). Both Hairy and White-headed woodpeckers fed nestlings at similar rates regardless of nestling age or date, suggesting that older nestlings were not fed more frequently than younger nestlings, which contrasts with previous studies (Hogstad and Stenberg 1997, Wiktander et al. 2000). Although provisioning rates did not differ based on brood size for either species, provisioning tended to decline as brood size increased; a pattern also observed in the Northern Flicker (Gow et al. 2013). Our results suggest that both species may be unable to meet the food demands of larger brood sizes, because prey

TABLE 2. Percentage of nestling feeding visits made by adult Hairy Woodpeckers ($n = 365$ visits) and White-headed Woodpeckers ($n = 372$ visits) with each food type in managed ponderosa pine forests of the eastern Cascade Range, Washington, 2009–2011.

	Hairy Woodpecker	White-headed Woodpecker
Wood-boring beetle larvae ^a (Cerambycidae and Buprestidae)	38.9	24.7
Ant larvae and/or adults (Formicidae)	20.0	18.2
Caterpillars (Lepidoptera)	2.7	23.1
Insect larvae	15.3	6.5
Beetle adult (Coleoptera)	13.7	5.4
Insects ^b	2.7	5.9
All other winged insects ^c	0.8	5.6
Moth (Lepidoptera)	1.6	3.8
Spider (Araneae)	3.3	1.1
Cricket (Gryllidae)	0.3	1.6
Cicada (Cicadidae)	0.3	1.1
Termites (Termitoidae)	0	0.8
Fly adult (Diptera)	0	0.5
Antlion adult (Myrmeleontidae)	0	0.3
Bumblebee (Apidae)	0	0.3
Crane Fly (Tipulidae)	0	0.3
Earwig (Dermaptera)	0	0.3
Grasshopper (Acrididae)	0	0.3
Mayfly (Ephemeroptera)	0	0.3
Snail (Mesogastropoda)	0.3	0

^a All large larvae resembled wood-boring beetle larvae; however, some Siricidae larvae may have been present but were unidentifiable.

^b Bolus of unidentified insects.

^c Prey was noted to have wings, but further identification was not possible.

availability ultimately influences nestling provisioning rate (Smith et al. 1988, Naef-Daenzer et al. 2000) and/or adults raising larger broods may be working at their maximum capacity (Moreno 1987), especially in managed forests where foraging substrates such as snags are more limited. This conclusion is further supported by the fact that 40% of nests of White-headed Woodpeckers and 23% of nests of Hairy Woodpeckers experienced brood reduction when nestlings were <10 days old (JMK, unpubl. data). We think most brood reductions were because of causes other than predation, because many of the nestlings that died were smaller than their siblings (Stoleson and Beissinger 1997). Brood reduction occurs in other woodpeckers (LaBranche and Walters 1994, Koenig et al. 2001, Chazarreta et al. 2011) but is not well-studied.

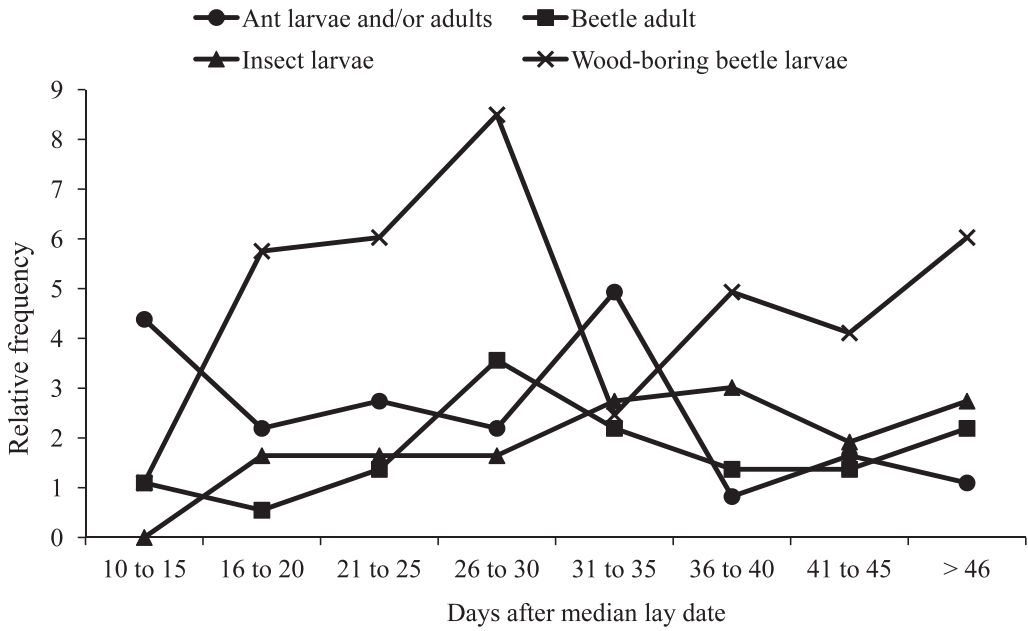
We observed male White-headed Woodpeckers conducting the majority of nest sanitation, similar

to other woodpeckers (Miller and Bock 1972, Rossmann et al. 2009, Chazarreta et al. 2011). In addition, male White-headed Woodpeckers incubate eggs and brood the young at night, and share these duties with females during the day (Garrett et al. 1996). Male White-headed Woodpeckers may invest more effort in raising offspring than females, because females need to restore fat reserves after egg-laying. To do this, females may be consuming more large prey items rather than feeding them to nestlings, which could explain why females brought large prey to nestlings during a smaller proportion of nest visits in both species. We did not observe different fecal removal rates between male and female Hairy Woodpeckers. This differs from de Kiriline Lawrence (1967) and Kilham (1968), both of whom observed male Hairy Woodpeckers conducting most fecal removals from cavities suggesting that the role of nest sanitation is variable in this species.

The low dietary niche breadth we observed for the Hairy Woodpecker suggests prey specialization and a less diverse nestling diet (Lewis et al. 2006). Larvae of wood-boring beetles, ants and their larvae, and adult beetles comprised 73% of the identifiable prey items brought to nestlings. The Hairy Woodpecker is well-known for preying on wood-boring beetle larvae (Villard and Beninger 1993, Covert-Bratland et al. 2006). Although these larvae accounted for nearly 40% of identified prey fed to nestlings, they were only present in 22% of all nest visits. Wood-boring beetle larvae, which reside in dead wood for 2–3 years, may be low in abundance in our study areas, because unburned stands have low snag densities (Kozma 2011). Few nests in burned stands were monitored within 5 years of the fire when abundance of these larvae is thought to be highest (Murphy and Lehnhausen 1998, Covert-Bratland et al. 2006). Low snag density may explain why we observed Hairy Woodpeckers foraging for wood-boring beetle larvae in downed logs and cut stumps from previous harvests in addition to standing snags (JMK, unpubl. data). In addition to these larvae, ants and beetles are documented as important components of the diet of Hairy Woodpeckers (Koplin and Baldwin 1970, Crockett and Hansley 1978, Otvos and Stark 1985).

White-headed Woodpeckers also had a low dietary niche breadth. Wood-boring beetle larvae accounted for the highest percentage of identified prey brought to nestlings, which is surprising,

A



B

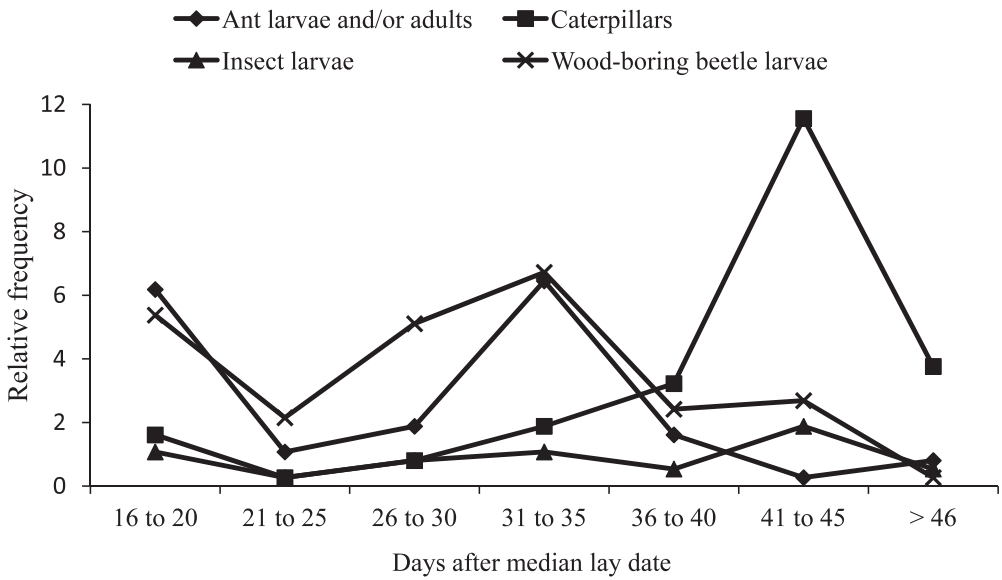


FIG. 3. Seasonal change in the four major prey types in the nestling diet of Hairy Woodpeckers (A; median laying date 4 May, $n = 72$ nests) and White-headed Woodpeckers (B; median laying date 28 May, $n = 77$ nests) in managed ponderosa pine forests of the east Cascade Range, Washington, 2009–2011. Laying date refers to the date the first egg was laid.

because the White-headed Woodpecker is thought to be limited in its ability to excavate into wood while foraging. Instead, it primarily probes into bark crevices, gleans bark surfaces, and chips away bark to find prey (Koch et al. 1970, Ligon 1973, Raphael and White 1984). Similar to Hairy Woodpeckers, we only observed White-headed Woodpeckers foraging for wood-boring larvae in cut stumps (JMK and T. Lorenz, unpubl. data). Wood-boring beetle larvae are found deeper in wood during the winter (Gardiner 1957) and therefore may be more accessible to White-headed Woodpeckers during the breeding season when larvae are located closer to the bark surface. This supposition is supported by the fact that we have not observed White-headed Woodpeckers foraging for wood-boring beetle larvae from October–January (JMK and T. Lorenz, unpubl. data), although snow cover may also limit the use of stumps as a winter foraging substrate. The Three-toed Woodpecker and Pileated Woodpecker also exhibit differential seasonal use of these larvae as food (Pechacek and Kristin 2004, Raley and Aubry 2006).

In contrast to the diet of Hairy Woodpecker nestlings, caterpillars were an important component of the diet of White-headed Woodpecker nestlings later in the nestling period. Many of these were caterpillars of western spruce budworm moths (*Choristoneura occidentalis*) that adults collected from Douglas-fir needles, as well as caterpillars of the pine white butterfly (*Neophasia menapia*) taken from ponderosa pine foliage. White-headed Woodpeckers may switch to caterpillars, because they are often locally abundant (e.g., spruce budworms) and are much easier to capture than wood-boring beetle larvae (Rossmannith et al. 2007). White-headed Woodpeckers also fed more frequently on winged prey than Hairy Woodpeckers. This result was unexpected as the White-headed Woodpecker is rarely documented flycatching (Raphael and White 1984, Dixon 1995). White-headed Woodpeckers initiate nests 3 weeks later than Hairy Woodpeckers (Kozma and Kroll 2012) and may be taking advantage of caterpillars and flying insects that become more abundant and active as air temperatures increase (Markin 1982). Despite the differences we observed in the diets of nestlings of Hairy and White-headed woodpeckers, the high Morisita's index suggests that their nestling diets overlap to a considerable degree (Hanula et al. 2000b). High dietary overlap could result in

interspecific competition for food, which in addition to an overlap in nest-site characteristics (Kozma 2012) and foraging behaviors (Morrison and With 1987), may account for the different nest initiation periods of these two species (Kozma and Kroll 2012). Temporal partitioning of resources is one way ecologically similar species can coexist (Hooper and Brown 1968, Toft et al. 1982) and which has been observed in other sympatric woodpeckers (Ingold 1989, Vierling et al. 2009). In addition, these woodpeckers may avoid competition by using resources in different niche dimensions (e.g., one species may forage for food in the upper canopy while the other may forage lower on the tree bole; Hayward and Garton 1988).

We note that our results may be inherently biased towards larger prey, as the smallest prey items were often unidentifiable with the methods we used. We were able to identify <60% of prey brought to nestlings, which is lower than that reported by other studies using comparable methods (Moreno 1987, Hogstad and Stenberg 1997, Rossmannith et al. 2007). We recommend that future research investigate nestling diets of these woodpeckers by using more powerful optics or automated video recorders to allow for more accurate identification of prey items and longer observational periods. We also suggest additional research investigate quality of prey delivered to nestlings, because although we observed a trend for provisioning rate to decline with larger broods, prey quality (i.e., calories) may buffer this drop if fewer, but higher quality prey are delivered. Wood-boring beetle larvae are important prey for nestlings of both woodpecker species and they are only found in recently dead trees and downed wood. Although stumps contain wood-boring beetle larvae used by woodpeckers for food, stumps from previous harvests should not be considered substitutes for snags. To improve foraging habitat during the nesting season, land managers should retain as many snags with a diameter at breast height (dbh) >35 cm and defective (e.g., burn scars, heavy mistletoe infestation, frost cracks, dead tops, etc.) live trees as possible post-harvest. Retaining or creating snags >35 cm dbh will provide greater foraging surface area leading to increased arthropod abundance and more profitable foraging (Hanula et al. 2000a, Covert-Bratland et al. 2006) while also meeting the nesting snag requirements of these woodpeckers (Kozma 2012). We also

recommend that future research compare the foraging niches of both species to further investigate resource partitioning, as well as sample the availability of arthropod prey so that its influence on prey choice and the ability of adult woodpeckers to raise larger broods can be examined (Török 1990, Pechacek and Kristin 2004).

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