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Dietary dependence of Williamson's Sapsucker nestlings on ants associated with dead and decaying wood in British Columbia

Les W. Gyug, Robert J. Higgins, Melissa A. Todd, Jeff M. Meggs, and B. Staffan Lindgren

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Abstract: Williamson's Sapsucker (*Sphyrapicus thyroideus* (Cassin, 1852)) breeds primarily in managed forests in Canada. Its status as endangered will require reliable information to develop habitat management guidelines. Adults provision nestlings with ants gleaned from tree trunks, so we estimated the preferred nestling diet by comparing nestling fecal sac composition with the ant fauna collected in tree trunk traps. For ants, we determined nest densities and substrates by counts along transects within sapsucker nest areas. Ants made up 98% of >10 000 arthropods identified in Williamson's Sapsucker fecal sacs. Of 11 ant taxa available, Williamson's Sapsucker consumed six, of which two large-bodied ant taxa, carpenter ants of *Camponotus* subgenus *Camponotus* and ants of the *Formica rufa* species group, were preferred. Together these two taxa averaged 80% of the nestling diet by biomass and formed >48% of the nestling diet at every nest examined (n = 89). Preference varied regionally: west of the Okanagan Valley, only the two large-bodied ant taxa already mentioned were preferred, in the Okanagan–Boundary and East Kootenay regions, smaller bodied ants of the genus *Lasius* were also preferred, although these comprised ≤5% of the nestling diet by biomass. *Camponotus* (*Camponotus*) spp. nests were 3.3 times more common in wood than soil, and the *F. rufa* species group were entirely dependent on dead or decaying wood for nest substrate. Given the dependence of Williamson's Sapsucker on these ants, retention and recruitment of dead and decaying wood should be considered a management priority for Williamson's Sapsucker breeding habitat.

Key words: ants, *Camponotus*, diet, Formicidae, *Formica*, myrmecophagy, Williamson's Sapsucker.

Résumé : Le pic de Williamson (*Sphyrapicus thyroideus* (Cassin, 1852)) niche principalement dans les forêts aménagées du Canada. Étant donné que cette espèce est en voie de disparition, des connaissances fiables sont requises pour établir des lignes directrices d'aménagement de son habitat. Sachant que les adultes nourrissent les oisillons de fourmis glanées sur les troncs d'arbres, nous avons pu étudier le régime alimentaire des oisillons en comparant le contenu de sacs fécaux d'oisillons aux fourmis recueillies dans des pièges installés sur les troncs. Pour les fourmis, nous avons déterminé la densité des nids et les substrats par décompte le long de transects positionnés près des nids de pics. Les fourmis totalisaient 98 % de >10 000 arthropodes identifiés dans les sacs fécaux des oisillons. Le pic de Williamson consommait six des 11 taxons de fourmis disponibles, avec une préférence pour deux taxons de grosses fourmis, soit des fourmis charpentières du genre *Camponotus* sous-genre *Camponotus* et des fourmis du groupe d'espèces *Formica rufa*. Ces deux taxons totalisaient en moyenne 80 % de la biomasse ingérée par les oisillons et constituaient >48 % de la diète de chaque nichée de pics étudiée (n = 89). Les préférences variaient selon les régions : à l'ouest de la vallée de l'Okanagan, seuls les deux taxons de grosses fourmis mentionnés ci-haut étaient préférés tandis que dans Okanagan–Boundary et Kootenay-Est, des fourmis plus petites appartenant au genre *Lasius* étaient aussi préférées, même si elles constituaient toujours ≤5 % de la biomasse apportée aux oisillons. Les nids de *Camponotus* sous-genre *Camponotus* étaient 3,3 fois plus communs dans le bois que dans le sol et ceux du groupe *F. rufa* étaient toujours construits dans du bois mort ou en décomposition. Étant donné que le pic de Williamson dépend de ces fourmis, la rétention et le recrutement de bois mort ou en décomposition devraient être considérés comme des objectifs prioritaires pour l'aménagement de l'habitat de reproduction du pic de Williamson. [Traduit par la Rédaction]

Mots-clés : fourmis, *Camponotus*, diète, Formicidae, *Formica*, myrmécophagie, pic de Williamson.

Introduction

Most woodpeckers (family Picidae) depend on dead and decaying trees for nest excavation and many forage for invertebrates found in dead and decaying wood. Maintenance of dead and decaying trees and wood in a forest managed for timber is not consistent with the objective of maximizing economic yield, making woodpeckers sensitive to habitat changes brought about by intensive forestry (Simberloff 1999; Virkkala 2006). An example in the southeastern United States (US) is the endangered Red-cockaded Woodpecker (*Picoides borealis* (Vieillot, 1809)), which requires live, old, large pines with internal decay for nesting and requires an open stand structure — neither of which were being provided by forest management (U.S. Fish and Wildlife Service 2003). In the

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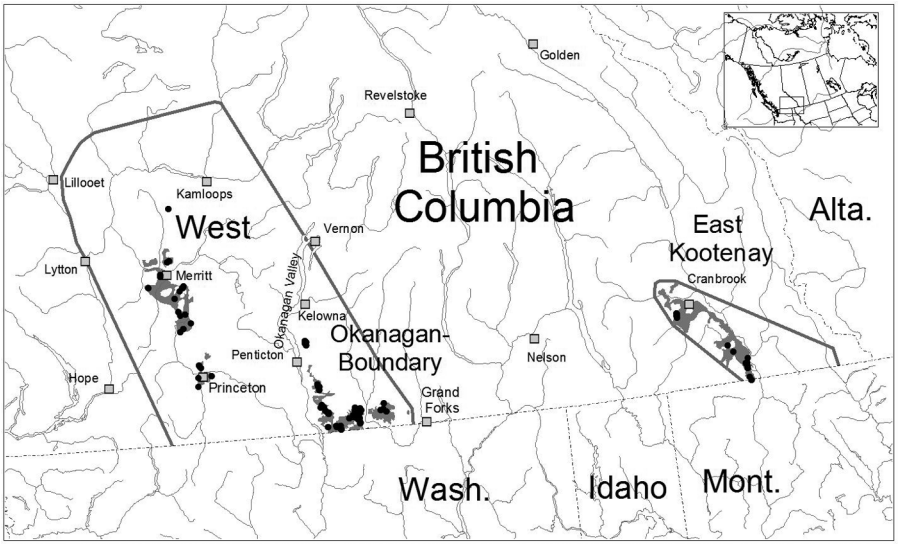
Fig. 1. Williamson's Sapsucker nest locations where nestling fecal sacs were collected (solid circles), 2006–2008. The extent of occurrence (heavy grey line encompassing all known breeding locations) and the area of occupancy (grey shaded areas of contiguous breeding habitat) of Williamson's Sapsucker in the southern interior of British Columbia are also shown (from Gyug et al. 2007, 2014).



Pacific Northwest, ecological requirements including snag and woody debris retention have been mandated in forestry management since 1986 for the Pileated Woodpecker (*Dryocopus pileatus* (L.)) because of its position as either an indicator or a keystone species (Aubry and Raley 2002). In Canada, Williamson's Sapsucker (*Sphyrapicus thyroideus* (Cassin, 1852)) has been assessed as endangered due to habitat loss from harvesting of mature forests (Committee on the Status of Endangered Wildlife in Canada 2005). Its addition to Schedule 1 of the Species at Risk Act in 2006 required preparation of a recovery strategy in which cost effectiveness is a legislated consideration. Because breeding habitat occurs largely on provincial Crown land available for timber harvesting (B.C. Ministry of Environment 2012), recovery planning will rely heavily on stand-management objectives in managed forests. Objectives have been developed for nest trees (Gyug et al. 2009), but should maintenance of additional dead and decaying wood to meet foraging needs be required at the expense of wood suitable for timber harvest; solid ecological justification is needed.

Even though Williamson's Sapsuckers are specialized for feeding on sap, ants make up a large portion of the adult diet in the breeding season and of the prey brought to nestlings (Gyug et al. 2012). During the final three weeks of the approximately four-week nestling period, regurgitated sap or phloem fibers cannot form a large part of the nestling diet because adults only feed prey held in the bill to the nestlings (Wheelock 1905; Crockett and Hansley 1977). Ants made up 72%–86% of Williamson's Sapsucker adult stomach contents by volume (Beal 1911; Otvos and Stark 1985), 88%–96% of adult stomach contents by item count (Otvos and Stark 1985; Stanford and Knowlton 1942), and 99% of adult bill contents by item count (Crockett 1975). Of these studies, only Otvos and Stark (1985) identified ants to genus level (genera *Camponotus* and *Liometopum*), although Stanford and Knowlton (1942) observed many of the ants to be "carpenter ants" (genus *Camponotus*).

Williamson's Sapsucker forage primarily by gleaning ants from tree trunks as the ants travel up and down the trunks (Crockett 1975; Stallcup 1968). Many *Camponotus* and *Formica* ants forage extensively or tend aphids in the canopy of trees and shrubs (Hölldobler and Wilson 1990). Gyug et al. (2010) found a threshold of 85 mature trees/ha below which Williamson's Sapsucker nest success decreased. They hypothesized that limited access to foraging resources for nest provisioning, i.e., ants on tree trunks, may have resulted in reduced nest success. Without more detailed information on which species or genera of ants Williamson's Sapsucker preferred, Gyug et al. (2010) could not make further recommendations for habitat management beyond this single threshold. While many species of both *Camponotus* and *Formica* are known to be dependent on wood as a nest substrate (Hansen and Klotz 2005; Higgins and Lindgren 2006), many ants are commonly found in ground nests and would therefore not require maintenance of dead or decaying wood.

Analysis of adult feces has been used to determine the diet of Pileated Woodpeckers (Beckwith and Bull 1985; Bull et al. 1992; Raley and Aubry 2006), Eurasian Three-toed Woodpeckers (*Picoides tridactylus* (Linnaeus, 1758)) (Pechacek and Kristin 2004), and Northern Flickers (*Colaptes auratus* (Linnaeus, 1758)) (Gow et al. 2013). When coupled with data on relative prey availability (e.g., Wolda 1990), analysis of fecal sacs (the feces of nestlings, contained in gelatinous sacs) can be used to determine the preferred prey items on which the nestlings were reared. For example, Pechacek and Kristin (2004) used fecal sacs to show that Eurasian Three-toed Woodpeckers, considered an important predator of bark beetles, predominately shifted their diet to longhorn beetle larvae during the nesting season.

To manage commercial forests as critical habitat for Williamson's Sapsucker, we must quantify the relative importance of different ant genera or species to breeding Williamson's Sapsuckers and the types of nest substrates of these ants. For ant taxa present in Williamson's Sapsucker breeding range in Canada, we (*i*) identified the relative amounts consumed based on fecal sacs, (*ii*) quantified relative availability by passive collection on tree trunks, (*iii*) determined preference by comparing nestling consumption with availability using Johnson's (1980) index, and (*iv*) quantified nest substrate types.

Methods

Study area

The study area encompassed the three regions of Williamson's Sapsucker breeding range in British Columbia (B.C.) (Fig. 1) (Gyug et al. 2007, 2014). The region west of Okanagan Lake in the Merritt and Princeton areas (termed "West") was primarily mixed forests of ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and trembling aspen (*Populus*

Table 1. Ant taxa or species groups found in fecal sacs and trunk traps and during ant nest surveys, with their respective body sizes and nesting habits.

Ant taxon code	Ant species or species group included in taxon	Taxon occurrence by survey type*			Ant length† (mm)	Estimated biomass‡ (mg)	Nesting habit§			
		Fecal sacs	Trunk traps	Ant nest surveys			Dead or decaying wood	Rock	Soil	Thatch
Large-bodied ants										
CAM CAM	*Camponotus* (*Camponotus*) *herculeanus* (Linnaeus)	Y‖	Y	Y	6–13	8.5	Y	—	—	—
	Camponotus (*Camponotus*) *laevigatus* (Smith, F.)		Y	?	7–13	9.6	Y	—	—	—
	Camponotus (*Camponotus*) *modoc* Wheeler, W.M.		Y	Y	6–13	8.5	Y	—	—	—
	Camponotus (*Camponotus*) *novaeboracensis* (Fitch)		Y	Y	6–13	8.5	Y	—	—	—
CAM TAN	*Camponotus* (*Tanaemyrmex*) *semitestaceus* Snelling	Y‖	Y	Y	7–13	9.6	—	Y	Y	—
	Camponotus (*Tanaemyrmex*) *vicinus* Mayr		Y	?	6–13	8.5	Y	Y	Y	—
FOR RUF	*Formica rufa* sp. group	Y	Y	Y	7–10	6.5	—	—	—	Y
FOR SAN	*Formica sanguinea* sp. group	Y	Y	Y	8–9	6.5	Y	Y	Y	Y
Small- to medium-bodied ants										
APH SPP	*Aphaenogaster* spp. Mayr	—	R	—	3–5	1.1	Y	Y	Y	—
FOR FUS	*Formica fusca* sp. group	Y	Y	Y	4–6	1.9	Y	Y	Y	—
FOR NEO	*Formica neogagates* sp. group	—	R	—	4–6	1.9	—	Y	Y	—
LAS SPP	*Lasius* spp. Fabricius	Y	Y	Y	3–5	1.1	Y	Y	Y	—
LEP SPP	*Leptothorax* spp. Mayr	—	Y	Y	2–3	0.4	Y	Y	Y	—
MYR SPP	*Myrmica* spp. Latreille	—	Y	Y	3–5	1.1	Y	Y	Y	—
TAP SES	*Tapinoma sessile* (Say)	—	R	Y	2–4	0.6	Y	Y	Y	—

*For "Taxon occurrence by survey type", Y indicates taxon found, dash (—) indicates taxon not found, R indicates taxon only rarely found with <10 ants total in trunk traps; question mark (?) indicates species was not found in ant nest surveys, but 18% of *Camponotus* nests were not identified to species, so these species could have been among those found.

†Ant taxa sizes (anterior of head to posterior of gaster) are approximations for workers (Hansen and Klotz (2005) for *Camponotus*; R. Higgins, unpublished data for others).

‡Biomass (dry mass) estimated from equations provided in Ganihar (1997) using the midpoint of the range of worker lengths.

§Nesting habits from Wheeler and Wheeler (1963, 1986) and from R. Higgins and S. Lindgren (unpublished data). Thatching for the two species of thatching ants is often associated with a stump or log (see text).

‖CAM CAM and CAM TAN were not identified below subgenus taxon level in fecal sacs so were grouped.

tremuloides Michx.) at elevations from 700 to 1250 m. The Okanagan–Boundary region on the eastern side of the Okanagan Valley, extending approximately from Penticton to Grand Forks, was primarily mixed western larch (*Larix occidentalis* Nutt.) and Douglas-fir forests at elevations from 860 to 1550 m. The East Kootenay region near Cranbrook was 200 km east of the Okanagan–Boundary region and was also primarily mixed western larch and Douglas-fir forests at similar elevations (830–1350 m). We examined regional diets separately because the regions are geographically separate and the West region was different in elevation and dominant vegetation.

Fecal sac collection and processing

We collected fecal sacs at the bases of nest trees occupied by Williamson's Sapsucker during other studies on nest productivity from 2006 to 2008 (Gyug et al. 2010). A single fecal sac collection consisted of at least 10 fecal sacs (whenever possible) made on a single nest visit. We sealed each fecal sac collection in a plastic bag, which was stored frozen until the time of processing for content identification. To determine nest productivity, we usually made repeat visits to each nest in a single breeding season. To better represent the nestling diet for any given nest, we made additional fecal sac collections on repeat visits. On a repeat visit within a single breeding season, we tried to collect only the most recent fecal sacs that represented the nestling diet over the preceding few days.

We developed an approach for extracting, sorting, and identifying invertebrates in fecal sacs based on Beckwith and Bull (1985) and Kleintjes and Dahlsten (1992). We thawed fecal sac collections, broke up clumps of material, and then mixed the fragments within the field collection bag prior to weighing a 200 mg subsample for processing. Each subsample was air-dried and weighed. We sorted the subsample under a stereomicroscope, where we separated identifiable body parts. Identifiable body parts included intact heads and alitrunks for ants and generally heads and elytra for non-ant arthropods. We made identifications using a combination of taxonomic keys and reference to the ant collection made during ant nest surveys (see below). As taxonomic keys are normally developed using whole specimens, limited taxonomic resolution was possible from separated ant body parts. We identified ants to the level of genus, subgenus, or species group (Table 1) based primarily on head structure. We identified non-ant arthropods to the lowest taxonomic level possible based on the sorter's experience, generally to the level of family (Table 2).

We used the Williamson's Sapsucker nest area as the sample unit, which we defined as 16 ha around an active nest. We based this on a 225 m radius, which was half of the mean distance between nearest-neighbor nests (Gyug et al. 2007). The nest area was used rather than nest tree because different nest trees within the same nest area might be used in different years. To determine nestling diet for a nest area, all fecal sac collections were analyzed separately, but multiple collections from the same nest area were averaged to provide a single estimate of nestling diet for each nest area. To test our assumption of relatively little change in nestling diet from year to year so that we could group across years, we used

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Table 2. Arthropod taxa observed in 200 mg wet-mass subsamples of 142 Williamson's Sapsucker fecal sac collections (of about 10 fecal sacs each) from 89 nest areas in British Columbia, 2006–2008. Non-ant taxa broken down by family or genus where easily identifiable.

Order	Family, subfamily, and genus	Common name(s)	Total individuals identified	% of all individuals
Hymenoptera	Formicidae	Ants	10 935	98.08
Coleoptera	Buprestidae	Metallic wood-boring beetle	8	0.07
	Carabidae	Ground beetle	2	0.02
	Cerambycidae	Longhorn beetle	3	0.03
	Cleridae	Checkered beetle	1	0.01
	Curculionidae	Weevil	11	0.10
	Elateridae	Click beetle	5	0.04
	Scarabaeidae			
	Melolonthinae			
	Dichelonyx spp.	Scarab, chafer, May or June beetle	109	0.98
	Polyphylla spp.	Lined June beetle*	—	—
	Staphylinidae	Rove beetle	1	0.01
	Oxyporinae			
	Oxyporus spp.	Cross-toothed rove beetle, fungus beetle	1	0.01
	Unidentified beetles		72	0.65
	Subtotal all beetles		213	1.91
Diptera	—	Fly	1	0.01
Total			11 149	100

*Identified during cursory examination of all fecal sac material but not contained within any subsamples analyzed.

a repeated-measure ANOVA design to compare annual nestling diets. We controlled for nest area differences using year as the repeated measure for the four most common ant taxa across the 16 nest areas where we had fecal sac collections from both 2006 and 2007.

Ant availability

We used Wolda's (1990) definition of availability as "the abundance of potential prey items in microhabitats used by an insectivore when searching for food." From the available pool of nests with fecal sacs collected in 2006 and (or) 2007, we randomly selected 10 nest areas in the West region, nine in the Okanagan–Boundary region, and seven in the East Kootenay region for ant sampling in 2008.

We estimated ant availability by collecting arboreal-foraging ants in trunk traps (Fig. 2) set from 9 June – 8 July 2008 to coincide with the chick-rearing period of Williamson's Sapsucker (Gyug et al. 2007). We made trunk traps from clear plastic 2 L pop bottles by cutting out the bottom and one side of each. We then set out 12 of these trunk traps in the vicinity of each selected Williamson's Sapsucker nest by screwing the inverted 2 L pop bottle to the tree trunk at 1.75 m height. Urine sample vials partially filled with 25% propylene glycol and 75% water were attached to the bottom of each trap by a hole drilled into the cap of each vial that fit tightly over the screw threads of the pop bottle neck. Traps were randomly placed on live trees within 225 m of each selected Williamson's Sapsucker nest. Traps were open for 21–23 days after which the sample vials were removed and capped and the traps were taken down.

Ant nest type and relative abundance

Relative density of ant nests by taxon and substrate type was estimated on transects at 24 of the 26 sites where availability was also estimated. Surveys were completed from 13 to 28 August 2008 to avoid disturbance to ants during the trunk trapping and nesting birds during the nestling period. We established 1500 m belt transects oriented to stay within the 225 m radius of each Williamson's Sapsucker nest area (Fig. 3), consistent with line-intercept sampling principles for large logs where long lines are needed to sample a naturally patchy distribution (e.g., Marshall et al. 2000). A section of each transect (900 m) was surveyed by randomly allocating 100 m skips where no sampling was done to allow completion of two sites by a team of two in one day.

We identified six classes of ant nest substrate: (1) decaying live trees, (2) snags, (3) stumps, (4) logs, (5) soil, and (6) rock. The term "coarse woody debris" is considered downed and dead wood > 7.5 cm in diameter and is often synonymous with logs (e.g., Marshall et al. 2000). Here we sampled a much wider range of dead and decaying wood in which ants will nest and have used specific terms for each class of dead or decaying woody structure, e.g., stumps, logs, or snags. The area of transect surveyed for each substrate varied in length and width to optimize field survey effort with the expected high densities of ant nests, e.g., in soil and small logs. Large woody structures were searched for ant nests over the 900 m transect length using 4 m total width for logs with large end diameter (LED) > 22.5 cm and 2 m total width for stumps > 22.5 cm diameter-at-stump-height, snags (standing dead trees) > 22.5 cm diameter-at-breast-height (DBH), and large live trees with obvious rots or defects > 37.5 cm DBH. A set of six 10 m × 2 m subplots were randomly located within each leg (Fig. 3) of the 900 m belt transect to survey small logs with 7.5–22.5 cm LED and to survey soil- and rock-associated ant nests. Logs were only searched within the belt transect if they crossed the transect line and were >7.5 cm in diameter at the point of intercept. We searched for ant nests using a hatchet in wood and with a trowel for soil- and rock-associated nests. To avoid double counting *Camponotus* satellite nests as >1 nest (Hansen and Klotz 2005), *Camponotus* nests of the same species within 25 m of each other were only tallied once.

Ant reference collection

To facilitate identification of ants in fecal sacs, we compiled an ant reference collection from the specimens collected during ant nest surveys and trunk trapping. We collected at least six ants (biased towards major workers, as keys are generally based on this caste) from each *Camponotus* spp. nest encountered during ant nest surveys. For other ant groups, we collected one sample of at least six ants per genus or species group per nest area. Additional ant specimens from the trunk trap samples were added to the reference collection as needed.

For ant identification, we followed the keys of Wheeler and Wheeler (1963), Francoeur (1973), Wheeler and Wheeler (1986), Naumann et al. (1999), and Hansen and Klotz (2005). Ant species nomenclature followed Bolton et al. (2007). We identified *Camponotus* ants to species whenever possible, although heads were the most

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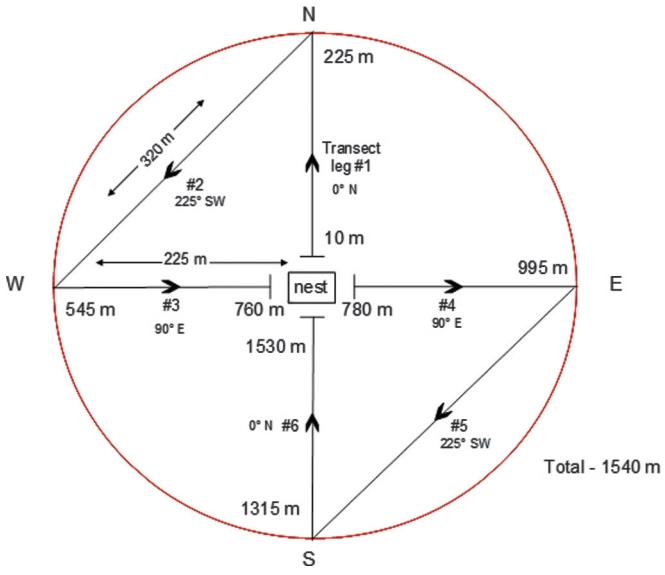
Fig. 2. Examples of ant trunk traps made from 2 L plastic bottles cut to the shape of a funnel and attached inverted to tree trunk. Photos by Okanagan Wildlife Consulting (left) and R. Higgins (right).

Fig. 3. The hourglass configuration of the 1500 m ant nest transect within a 16 ha Williamson's Sapsucker nest area. The transect began 10 m north of the nest following a due north bearing, with 45° turns at the 225 m radius from the nest. To avoid transect overlap at the centre, the 10 m closest to the nest was not sampled in any direction.



useful body part for identification in fecal sacs and usually allowed identification only to subgenus. We identified other ants only to either genus or species groups in all sample types. Ants were appropriately mounted and labeled following the Ant Leaf Litter Protocol (Agosti et al. 2000). Specimens have been stored at Thompson Rivers University in Williams Lake.

Data analysis

We used Johnson's (1980) index of use–availability preference (or consumption–availability in this case) based on Waller and Duncan's (1969) Bayesian multiple comparison procedure. Based on ranks, it is not as sensitive to outliers or to absolute levels of availability as other indices. The procedure was implemented using PREFER v5.1 software (Pankratz 1994) using K = 50, which approximates an alpha of 0.10. While we write of this as nestling diet preference, it is understood that results represent preference in adult provisioning.

To estimate consumption, we used the number of individual ants by taxon/100 mg dry mass of fecal sacs averaged over the collections made for each nest area. Biomass (dry mass) of each ant taxon was predicted using the equations of Ganihar (1997) using the midpoint of the range of worker lengths (Table 1). To estimate the relative amount of biomass contributed by each ant taxon for each nest area, we multiplied individual biomass times the number of individuals/100 mg dry mass for each taxon, summed these for the nest area, and then divided the biomass of each taxon by the nest area sum. Where regional or total means are presented, variance is presented as the standard error (SE).

To estimate availability, we used the average number of each ant taxon caught per trunk trap in each nest area. For any trunk traps open for >21 days, the number of ants caught per trap was reduced proportionally to an equivalent 21-day period. We compared availability of each ant taxon by region using the nonparametric Kruskal–Wallis test of ranks, so we did not have to assume normal distributions of the trunk trap capture data. We assumed that the probability of capture of each ant taxon in trunk traps was independent of the capture of other ant taxa so did not adjust for possible type I error inflation in the series of Kruskal–Wallis tests.

Availability was estimated at a subset of 26 nest areas in 2008, while most fecal sacs were collected in 2006 and 2007. We assumed that ant abundance, at least for ants that live in large colonies, is unlikely to vary markedly from year to year. Most large

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Table 3. Regional frequency of occurrence (percentage of nest areas where taxa occurred in fecal sacs), fecal sac composition (mean individuals/100 mg dry mass), and relative contribution (mean percent biomass of nestling diet) of ant taxa found in Williamson's Sapsucker fecal sacs from the 89 nest area samples collected between 2006 and 2008.

	Frequency of occurrence (%)			Fecal sac composition (individuals/100 mg fecal sacs)			Relative biomass contribution (%) to nestling diet		
	West (n = 22)	Ok–Bdy (n = 52)	EK (n = 15)	West (n = 22)	Ok–Bdy (n = 52)	EK (n = 15)	West (n = 22)	Ok–Bdy (n = 52)	EK (n = 15)
Large-bodied ants									
Camponotus (*Camponotus*) spp.	100	98	100	14.3 (0.43)	25.6 (0.20)	15.19 (0.36)	46.2 (5.5)	72.1 (2.4)	44.8 (2.9)
Camponotus (*Tanaemyrmex*) spp.	55	38	60	1.25 (0.07)	0.92 (0.04)	0.97 (0.09)	3.3 (0.8)	2.7 (0.8)	2.8 (0.9)
Formica rufa sp. group	91	77	93	18.58 (0.80)	3.70 (0.09)	15.95 (0.67)	39.4 (6.3)	8.2 (1.7)	33.4 (5.0)
Formica sanguinea sp. group	64	54	73	1.49 (0.08)	1.64 (0.04)	3.38 (0.20)	4.3 (1.1)	3.6 (0.7)	7.8 (1.9)
Small- to medium-bodied ants									
Formica fusca sp. group	95	94	93	9.23 (0.36)	14.72 (0.23)	11.78 (0.58)	7.1 (1.5)	8.9 (1.0)	8.1 (1.6)
Lasius spp.	50	81	73	1.61 (0.14)	12.81 (0.35)	7.49 (0.70)	0.1 (0.4)	4.5 (0.8)	3.0 (1.1)

Note: Values for fecal sac composition and relative biomass contribution are means with SE in parentheses. n, number of nest areas. Regional abbreviations: West, west of Okanagan Lake; Ok–Bdy, Okanagan–Boundary region; EK, East Kootenay region.

Camponotus colonies take a number of years to establish and are relatively long-lived (Hansen and Klotz 2005).

Relative ant nest densities for each ant taxon were estimated from transect surveys. For stumps, live trees, snags, thatch, soil, and rock nests, the relative density was the number of nests divided by the area sampled in the belt transects. For logs, ant nest relative abundance was not directly comparable to other nest types because nests were only searched for in logs intercepting the line; logs within the 4 m transect width that did not intercept the line were not searched. From other log transect surveys in 2007 (L.W. Gyug, unpublished data), 165 of 613 logs with LED > 22.5 cm were within a 4 m plot width but did not intercept the transect centre line. So, we applied an adjustment factor of 1.37 to each ant nest tallied in logs before estimating density using the 4 m plot width.

Nests under rocks were grouped with soil nests for all analyses. Ant nests in stumps, snags, and live trees were grouped for analysis. Large, mounded thatch nests were most often associated with a large piece of dead wood — either stump or log — so were subsequently rolled up with stumps, snags, and live trees and with large and small logs for comparison of wood nests to soil nests.

Results

Overall, we identified 15 ant taxa in Williamson's Sapsucker nest areas (Table 1). All 15 taxa were detected among the 9536 ants captured in trunk traps, but only 11 taxa were found in the 463 ant nests found on nest transects, and only six taxa were found in the 142 fecal sac collections from 89 nest areas. Because 18% of *Camponotus* nests were not identified to species, the two species of *Camponotus* nests found in trunk traps may have been among those unidentified nests on nest transects. In fecal sac analyses, we could distinguish *Camponotus* only to subgenus rather than to species as for nest surveys and trunk traps. This simplified our taxonomic groupings to 11 taxa detectable by each of our three methods. This included four large-bodied ant taxa and seven small- to medium-bodied ant taxa (Table 1). All four large-bodied ant taxa were found in fecal sacs, trunk traps, and ant nest surveys. All seven small- to medium-bodied ant taxa were found in trunk traps, but only five of seven were found in ant nest surveys, and only two of seven were found in fecal sacs.

Ant consumption — fecal sacs

We made 142 fecal sac collections containing approximately 1420 fecal sacs in total from 89 Williamson's Sapsucker nest areas between 2006 and 2008. Average dry mass of each 200 mg wet-mass subsample was 143 mg (SD, 18 mg; range, 85–198 mg), with an average of 78 prey items per subsample (SD, 32; range, 25–214). Fecal sac composition did not vary significantly between 2006 and 2007 for any of the four most abundant ant taxa in fecal sacs ($F_{[1,15]}$ ranged from 0.002 to 1.18; p ranged from 0.29 to 0.96).

Ants comprised 98% of the 11 149 arthropods identified from fecal sacs (Table 2). All other arthropods identified were beetles, except for one fly. Within the limits of our taxonomic classification (Table 1), the level of identification success of ants was very high: only 0.2% of specimens could not be identified to any taxonomic level, and 0.5% of *Camponotus* spp. and 1.0% of *Formica* spp. could not be identified below the level of genus. Non-ants and the few ants that could not be identified to a sufficient taxonomic level were not included in analyses and not presented in tables.

We identified six ant taxa from fecal sacs, all of which were present in all three regions (Table 3). *Camponotus* (*Camponotus*) spp. was the most common taxon found in fecal sacs, being found in all but one nest area. The *Formica fusca* sp. group was next most prevalent, found in 93%–95% of nest areas in each region. The *Formica rufa* and *Formica sanguinea* sp. groups were found in fewer fecal sacs in the Okanagan–Boundary region than in other regions.

Fecal sacs were proportionally dominated (first or second highest item counts) by *Camponotus* (*Camponotus*) spp. in each region (Table 3). The *F. rufa* sp. group was the most numerous taxon present in fecal sacs collected in the West region and in the East Kootenay region, but only fourth highest in the Okanagan–Boundary region. The *F. fusca* sp. group was consistently either second- or third-ranked in numbers present in fecal sacs in each region. *Lasius* spp. were either third- or fourth-ranked in each region but were proportionally much lower by item count in the West region than in other regions. The *F. sanguinea* sp. group and *Camponotus* (*Tanaemyrmex*) spp. ranked second lowest and lowest by item count, respectively, in fecal sacs in all regions.

Estimated biomass was dominated by two large-bodied ant taxa, *Camponotus* (*Camponotus*) spp. and the *F. rufa* sp. group, which made up 78%–85% of the ant portion of the nestling diet in each of the three regions (Table 3). These two taxa combined formed a minimum of 48% of the nestling diet by biomass at every Williamson's Sapsucker nest area examined in B.C. (n = 89) and averaged 80% (SE 1.2%) of the biomass. *Camponotus* (*Camponotus*) spp. formed the highest percentage (72%) in the Okanagan–Boundary region of any single taxon in any region. Two other large-bodied ant taxa, *Camponotus* (*Tanaemyrmex*) spp. and the *F. sanguinea* sp. Group, were <8% of the ant portion of the nestling diet by biomass in all regions. Small- to medium-bodied ants of the *F. fusca* sp. group and *Lasius* spp. were <9% of the nestling diet by biomass in all regions.

Ant availability — trunk traps

Ants of the *F. fusca* sp. group were captured in trunk traps at every Williamson's Sapsucker nest area (Table 4). Next most

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Table 4. Frequency (Freq.) of occurrence by nest area (%) and availability (mean number of ants/trunk trap standardized to 21-day trapping period followed by SE in parentheses) of ant taxa for three regions in B.C., 2008. Totals and Kruskal–Wallis contrasts only made across regions for taxa occurring in all regions.

	West (n = 10)		Okanagan–Boundary (n = 9)		East Kootenay (n = 7)		Total (n = 26)		Kruskal–Wallis statistics	
Ant species group	Freq.	Ants/trap	Freq.	Ants/trap	Freq.	Ants/trap	Freq.	Ants/trap	H	p
Large-bodied ants										
Camponotus (*Camponotus*) spp.	100	2.59 (1.25)	100	3.23 (2.23)	86	1.23 (0.40)	96	2.50 (0.92)	0.11	0.95
C. (*C.*) *herculeanus*	100	0.77 (0.20)	67	0.34 (0.17)	71	0.50 (0.20)	81	0.55 (0.11)	4.08	0.13
C. (*C.*) *modoc*	50	1.81 (1.17)	67	0.53 (0.35)	43	0.50 (0.38)	54	1.01 (0.48)	0.48	0.79
C. (*C.*) *laevigatus*	10	0.01 (0.01)	22	0.05 (0.04)	43	0.23 (0.12)	23	0.08 (0.04)	3.17	0.20
C. (*C.*) *noveboracensis*	0	0	11	2.30 (2.30)	0	0			—	
Camponotus (*Tanaemyrmex*) spp.	50	0.35 (0.14)	11	0.01 (0.01)	57	1.15 (0.68)	38	0.45 (0.20)	5.53	0.06
C. (*T.*) *vicinus*	50	0.35 (0.14)	11	0.01 (0.01)	57	0.97 (0.68)	38	0.40 (0.20)	5.21	0.07
C. (*T.*) *semitestaceus*	0	0	0	0	14	0.18 (0.18)			—	
Formica rufa sp. group	30	24.91 (24.73)	56	2.23 (1.62)	43	5.64 (4.58)	42	11.87 (9.52)	0.86	0.65
Formica sanguinea sp. group	60	2.47 (2.02)	56	3.50 (2.42)	71	1.81 (0.88)	62	2.65 (1.13)	0.40	0.82
Small- to medium-bodied ants										
Aphaenogaster spp.	20	0.03 (0.02)	0	0	0	0			—	
Formica fusca sp. group	100	5.56 (2.24)	100	29.17 (12.99)	100	4.42 (1.02)	100	13.43 (4.97)	0.95	0.63
Formica neogagates sp. group	10	0.05 (0.05)	0	0	29	0.05 (0.04)			—	
Lasius spp.	70	0.28 (0.08)	78	0.60 (0.20)	57	0.23 (0.10)	69	0.38 (0.08)	2.32	0.32
Leptothorax spp.	40	0.17 (0.10)	33	0.14 (0.07)	86	0.48 (0.17)	50	0.24 (0.07)	5.24	0.07
Myrmica spp.	60	0.11 (0.03)	22	0.39 (0.35)	71	0.32 (0.09)	50	0.25 (0.12)	5.62	0.06
Tapinoma sessile	0	0	0	0	43	0.12 (0.08)			—	

Note: n, number of nest areas.

prevalent was *C. herculeanus*, found at 81% of all nest areas. The *F. fusca* and *F. rufa* sp. groups were the most abundantly caught ants in trunk traps, averaging >10 ants/trunk trap. The *F. sanguinea* sp. group and *Camponotus* (*Camponotus*) spp. averaged >2 ants/trunk trap, and all others averaged <1 ant/trunk trap. Five taxa (*Myrmica* spp., *Leptothorax* spp., the *F. neogagates* sp. group, *Tapinoma sessile*, and *Aphaenogaster* spp.) were found only rarely in trunk traps, comprising 1.6% of the total ants collected but none of which was found in Williamson's Sapsucker fecal sacs. There were no significant regional differences in availability for any ant taxa that occurred in all regions (Table 4).

Diet preference

Camponotus (*Camponotus*) spp. and the *F. rufa* sp. group were preferred in every region and were the only two taxa preferred in the overall sample (Fig. 4). *Camponotus* (*Camponotus*) spp. was highly preferred (preference index < −0.5) in every region. The level of preference for the *F. rufa* sp. group varied regionally, being highly preferred in the West region and in the East Kootenay region, but not as preferred in the Okanagan–Boundary region. The *F. fusca* sp. group was not preferred in any region (avoidance indicated by preference index > 0.5 in all regions; Fig. 4), forming 7%–9% of the nestling diet by biomass in each region (Table 3). Large-bodied ants of *Camponotus* (*Tanaemyrmex*) spp. and the *F. sanguinea* sp. group were not preferred in any region and comprised <8% of the nestling diet by biomass in any region.

Ant nest surveys

Ant taxa found in nest surveys included the same taxa found in fecal sacs and trunk traps with the exception of two taxa: *Aphaenogaster* spp. and the *Formica neogagates* sp. group were found rarely in trunk traps but were not found in the ant nest surveys (Table 1). *Myrmica* spp, *Leptothorax* spp., and *Tapinoma sessile* were found commonly in ant nest surveys but only rarely in trunk traps and never in fecal sacs.

In total, 463 ant nests were tallied on 21 583 m of ant nest transects (Table 5). For the two most highly preferred ant taxa in the diet of Williamson's Sapsuckers, wood was more commonly used as a nesting substrate than soil: nest density of *Camponotus* (*Camponotus*) spp. nests was 3.3 times higher in wood than soil, and the *F. rufa* sp. group nests were only found associated with stumps (n = 2) and thatch-mound nests (n = 4). The thatch-mound nests were assumed to have been associated with wood buried underneath the thatch (e.g., McIver et al. 1997; Wheeler and Wheeler 1963). *Lasius* spp. was the only preferred ant taxon in two of the regions that was more abundant in soil than in wood. For ant taxa that were present but not preferred in the nestling diet of Williamson's Sapsuckers, the *F. fusca* sp. group and *Camponotus* (*Tanaemyrmex*) spp. nests were more abundant in soil than in wood, whereas the *F. sanguinea* sp. group nests were only found in wood (Table 5).

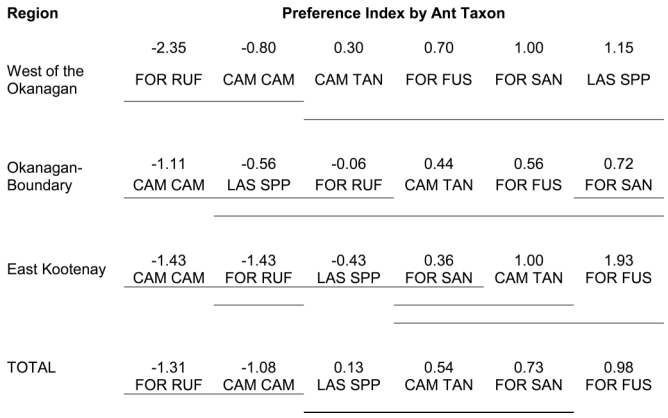

Fig. 4. Preference index by ant taxon by region. FOR RUF, *Formica rufa* sp. group; CAM CAM, *Camponotus* (*Camponotus*) spp.; CAM TAN, *Camponotus* (*Tanaemyrmex*) spp.; FOR FUS, *Formica fusca* sp. group; FOR SAN, *Formica sanguinea* sp. group; LAS SPP, *Lasius* spp.

Discussion

Our analysis of fecal sacs from 89 Williamson's Sapsucker nest areas support the observations from four other studies that the arthropod diet in the breeding season is mainly ants. Previous work had been based on adult stomach contents (Beal 1911; Stanford

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Table 5. Ant nest relative densities (number/ha) by nest substrate type.

	Large logs	Stumps, snags, live trees	Thatch	Small logs	All wood	Soil and under rocks
Total number nests found	120	139	4	35		165
Total area searched (ha)	8.6332	4.3166	4.3166	0.2760		0.2760
Large-bodied ants						
Camponotus (*Camponotus*) spp. subtotal	3.0	3.5	0.0	21.7	36.2	10.9
C. (*C.*) *herculeanus*	2.5	3.0	0.0	29.7	35.3	3.6
C. (*C.*) *modoc*	0.5	0.5	0.0	0.0	0.9	0.0
C. (*C.*) *noveboracensis*	0.0	0.0	0.0	0.0	0.0	7.2
Camponotus (*Tanaemyrmex*) *vicinus*	0.0	0.7	0.0	0.0	0.7	10.9
Camponotus spp.*	0.8	1.4	0.0	0.0	2.2	0.0
Formica rufa sp. group	0.0	0.5	0.9	0.0	1.4	0.0
Formica sanguinea sp. group	1.1	2.8	0.0	0.0	3.9	0.0
Small- to medium-bodied ants						
Formica fusca sp. group	6.2	6.0	0.0	44.6	56.8	83.3
Lasius spp.	5.7	12.0	0.0	34.7	52.5	195.7
Leptothorax spp.	1.4	1.2	0.0	24.8	27.4	10.9
Myrmica spp.	0.6	2.5	0.0	25.4	37.9	221.0
Tapinoma sessile	0.2	1.6	0.0	5.0	6.7	65.2
Total	13.9	32.2	0.9	173.5	225.7	597.8

*18% of *Camponotus* nests were not identified to subgenus so have been retained as separate row in this table.

and Knowlton 1942; Otvos and Stark 1985) and on counts of prey items in bills of adults returning to feed nestlings (Crockett 1975). This study confirms through direct examination of fecal sacs that adults provision nestlings almost entirely with ants.

The relatively detailed level of taxonomic identification in our study allows for a finer quantification of diet choice and the habitat associations of preferred prey than other studies. In California, Otvos and Stark (1985) found only two ant taxa in five Williamson's Sapsucker stomachs, with small- to medium-bodied *Liometopum* spp. (worker length 2.5–6 mm; Wheeler 1905) equal in volume to large-bodied *Camponotus* spp. but much higher in item count (103 vs. 16). No other study besides Otvos and Stark (1985) provided a breakdown of any taxonomic grouping below "ant". Working with nestling fecal remains in our study, where heads tended to remain intact, likely made it easier to identify ants to the subgenus or species group than if we had used adult fecal remains, where only mandibles would likely have remained intact (e.g., Beckwith and Bull 1985).

It is never possible to completely or perfectly measure availability of insect resources for birds (Hutto 1980). In this case, Williamson's Sapsucker appeared to have a relatively simple foraging system with quantifiable behavior (84%–97% of foraging on tree trunks; Crockett 1975; Stallcup 1968) and a limited range of taxa eaten (98% ants, this study and others). While analysis of fecal sacs will tend to be biased to the hard-bodied organisms that have more identifiable parts that survive the digestive process, other studies found Williamson's Sapsucker adults to provision nestlings predominantly with ants even when looking at prey items contained in the bill (Crockett 1975). This suggests that our results should not be significantly biased by using analysis of fecal sacs over direct interception of undigested prey items.

Camponotus (*Camponotus*) spp. and the *F. rufa* sp. group were preferred in all regions, but *Lasius* spp. were preferred in only two of three regions. The two most preferred taxa nested primarily in all classes of wood substrate, including large and small logs, stumps, snags, and live trees, and in thatch associated with stumps or logs. Taxonomic diet preferences may be expected to vary regionally depending on the composition of local ant communities. In our study, the biomass consumed was mostly *Camponotus* (*Camponotus*) spp. in one region but was split almost equally between *Camponotus* (*Camponotus*) spp. and the *F. rufa* sp. group in two other regions. *Camponotus* spp. ants may compete with the *F. rufa* sp. group ants for honeydew aphids, but it is not known to what extent one species group might limit the other (Jurgensen et al. 2005).

Camponotus (*Camponotus*) spp. ants made up the largest proportion of the nestling diet by biomass across all regions, and the majority of their nests are found in wood. *Camponotus* (*Camponotus*) spp. typically form large nests of 3000 – 12 000 workers for *Camponotus* (*Camponotus*) *herculeanus* and 50 000 workers or more for *Camponotus* (*Camponotus*) *modoc* (Hansen and Klotz 2005) that may forage over a wide area, perhaps as much as 100 m (Sanders 1972). Satellite nests may arise in materials not suitable for the natal nest, e.g., in small pieces of wood, under rock, or in soil (Wheeler and Wheeler 1986), complicating interpretation of nest locations. This would explain why a large number of *Camponotus* (*Camponotus*) *herculeanus* nests were found in small logs and why some *Camponotus* (*Camponotus*) spp. nests were found in soil (Table 5).

Large-bodied ants of the *F. rufa* sp. group made up the second highest proportion of the nestling diet in this study, and nests for this group were only found in thatch or in stumps. These ants usually initiate nests in wood (McIver et al. 1997), piling thatch against and around the wood, such that a mature colony will appear to be entirely thatch and the initial wood may be a small portion of the nest and have almost entirely decayed (Wheeler and Wheeler 1963). Their nests tend to be very large, with up to 400 000 workers in a single nest and foraging trails up to 100 m from the nest (Collingwood 1979; Sorvari 2009). McIver et al. (1997) estimated 57 000 000 *F. rufa* sp. group workers in a "supercolony" consisting of 210 active nests and covering 4 ha but found no other nests in 181 km of 10 m wide belt transect. Risch et al. (2008) found very low densities (0.11 to 0.17 *F. rufa* sp. group mounds/ha) in Wyoming, finding only 85 nests over a total of 507 km of transect. We found nests of this taxon at only 13% of Williamson's Sapsucker nest areas and in trunk traps at 42% of nest areas but in fecal sacs at 83% of nest areas. This would indicate that Williamson's Sapsuckers are far more effective at finding *F. rufa* sp. group ants to feed their nestlings than were either of our direct survey methods and that they are a preferred prey.

Observations suggest that the *F. rufa* sp. group forms trails that are more concentrated and active compared with the other ants under consideration here (R.J. Higgins, personal observations). Given the patchy distribution of their large nests and their tendency to travel on concentrated trails to foraging areas, Williamson's Sapsucker may specifically search out occurrences of the *F. rufa* sp. group on tree trunks and return to them repeatedly.

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Williamson's Sapsucker are known to forage up to 500 m from the nest (Gyug et al. 2007), so they may also have been finding the *F. rufa* sp. group outside our 225 m radius survey areas. If that was the case, then the *F. rufa* sp. group would be preferred prey that they may travel longer distances to find. Their apparent scarcity highlights the importance of maintaining large thatch nests of this taxon during timber harvest.

Ants of the *F. fusca* sp. group comprised the third largest component of the nestling diet, even though they were not preferred in any region. These are medium-sized ants ubiquitous in most habitats where ants are found within B.C. (Naumann et al. 1999). The *F. fusca* sp. group ants were the most abundantly captured ants in trunk traps in the Okanagan–Boundary region and second to the *F. rufa* sp. group in the other regions. Given their relatively high abundance, widespread distribution, and smaller size, it seems likely that Williamson's Sapsucker would take them opportunistically while foraging but they were not a preferred species group.

Lasius spp. ants were a preferred ant taxon in the Williamson's Sapsucker nestling diet in the Okanagan–Boundary and East Kootenay regions, where they comprised a substantial part of the nestling diet by number, but not by biomass. *Lasius* spp. ants create small nests in a variety of substrates, though nests occur primarily in soil and under rocks. Their nests were the second most abundant after *Myrmica* spp., but they were the least common ant taxon in the tree trunk samples of the six ant taxa consumed by Williamson's Sapsucker. This may reflect a lower tendency for arboreal foraging and (or) an ability to avoid the trunk traps. We do not know the relative susceptibility of ant taxa to falling into the trunk traps but have assumed it is equal among taxa. Clearly, a higher measure of confidence (as discussed by Wolda 1990) could be given to our availability estimates if we could define the probability of capture for each ant taxon in the trunk traps. Regardless, Williamson's Sapsuckers appear to be able to find them and select them preferentially relative to this apparent limited availability. As with the *F. fusca* sp. group ants, these ants are widespread and small and may be taken opportunistically or preferred, possibly for their thinner exoskeleton (R.J. Higgins, personal observations) wherever they may be particularly abundant. However, *Lasius* spp. did not form >5% of the estimated nestling diet in any region by biomass and nest primarily in soil or under rocks, so they would not be a priority for habitat management for Williamson's Sapsucker.

This study suggests that retention and recruitment of dead and decaying wood will be an important component of stand-level management within Williamson's Sapsucker breeding and foraging habitat. The two most preferred ant taxa comprising 80% of the nestling diet biomass, *Camponotus* (*Camponotus*) spp. and the *F. rufa* sp. group, demonstrated a high dependence on dead and decaying wood for nesting. *Camponotus* (*Camponotus*) spp. establish natal nests in larger woody features including logs, stumps, snags, and decaying live trees, with many smaller satellite nests. The *F. rufa* sp. group nest specifically in thatch nests constructed around or over dead or decaying wood. The findings of this study strongly support the need to manage dead and decaying wood within Williamson's Sapsucker breeding and foraging habitat and will allow us to focus management efforts for these two preferred ant taxa in particular, rather than for ants in general.

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