

Intersexual variation in the foraging ecology of sexually monochromatic Western Wood-Pewees

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ABSTRACT. Investigators generally pool observations of males and females in studies of the foraging behavior of sexually monochromatic songbirds. However, such pooling can obscure possible intersexual differences. We compared the foraging behavior of male and female Western Wood-Pewees (*Contopus sordidulus*), a sexually monochromatic species, in the Sierra Nevada Mountains of California during the breeding seasons of 2007 and 2008. We recorded 143 foraging observations (male $N = 74$, female $N = 69$). Overall, mean foraging rates of females (2.8 attacks/min) were higher ($P < 0.001$) than those of males (1.1 attacks/min). In addition, female foraging rates were significantly higher during incubation than during the nest building, nestling, and fledgling periods. When foraging, males perched higher above ground than females (means = 17.1 and 6.7 m, respectively). Differences between male and female Western Wood-Pewees in foraging rates and perch heights suggest that males may spend more time on vigilance while females focus on foraging quickly during incubation and when feeding nestlings. Because metrics such as foraging attack rates are sometimes used as indicators of habitat quality and we found that rates can differ between the sexes and among nesting stages, investigators should consider the possibility of such differences when assessing habitat quality, especially for sexually monochromatic species of birds.

RESUMEN. Variación intersexual en la ecología de búsqueda de alimento de *Contopus sordidulus* una especie sexualmente monocromática

Investigadores generalmente agrupan observaciones de machos y hembras en estudios de comportamientos de búsqueda de alimento en aves paseriformes sexualmente monocromáticas. Sin embargo, esta agregación puede estar ocultando posibles diferencias entre los sexos. Comparamos el comportamiento de búsqueda de alimento de machos y hembras de *Contopus sordidulus*, una especie sexualmente monocromática, en las montañas de la Sierra Nevada de California durante la temporada reproductiva del 2007 y 2008. Colectamos 143 observaciones de búsqueda de alimento (machos $N = 74$, hembras $N = 69$). En total, la tasa promedio de búsqueda de alimento de las hembras (2.8 ataques/min) fue mayor ($P < 0.001$) que la de los machos (1.1 ataques/min). Adicionalmente, la tasa de búsqueda de alimento por parte de las hembras fue significativamente mas altas durante la incubación que durante los periodos de construcción del nido, polluelos y volantones. Cuando buscan alimentos, los machos se perchan a mayores alturas respecto al suelo en comparación a las hembras (promedio = 17.1 y 6.7 m, respectivamente). Diferencias entre machos y hembras de *C. sordidulus* en tasas de búsqueda de alimento y altura de perchas sugiere que los machos pueden estar pasando mas tiempo vigilando mientras que las hembras se enfocan en buscar alimento rápidamente durante la incubación y cuando están alimentando a los polluelos. Debido a que medidas métricas como tasas de ataque durante la búsqueda de alimento son usadas ocasionalmente como indicadores de calidad del hábitat, y debido a que encontramos que las tasas de búsqueda de alimento pueden diferir entre sexos y etapas durante la anidación, investigadores deberían considerar la posibilidad de la existencia de estas diferencias cuando evalúen la calidad del hábitat, especialmente en especies de aves sexualmente monocromáticas.

Key words: *Contopus sordidulus*, foraging rate, habitat selection, montane meadow, perch use, Sierra Nevada mountains, tyrant flycatcher

Sex-specific differences in foraging behavior during the breeding season have been documented for many songbird species, most notably parulids (Morse 1968, Franzreb 1983, Holmes 1986, Petit et al. 1990). Intersexual differences in foraging behavior may result from a partitioning of resources due to intraspecific competition

(Rand 1952, Selander 1966) or constraints associated with reproductive behavior and parental care, such as females foraging near nests and males near song perches (Morse 1968, Franzreb 1983, Holmes 1986, Petit et al. 1990, Kelly and Wood 1996).

Sex differences in the foraging behavior of monochromatic species have seldom been examined because of the difficulty of identifying males and females. As a result, investigators

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studying monochromatic species have generally either pooled foraging observations of males and females (Gabbe et al. 2002, Cumming 2004, Hartung and Brawn 2005, Rodewald and Brittingham 2007) or focused on one sex to control for sexual variation (Lovette and Holmes 1995, Meehan and George 2003, Kilgo 2005). However, averaging across sex can lead to results that do not represent the foraging patterns of either sex (Hanowski and Niemi 1990, Kelly and Wood 1996).

Western Wood-Pewees (*Contopus sordidulus*) are sexually monochromatic, Neotropical migrant songbirds that typically occur in open-canopy forests and riparian areas in western North America. Western Wood-Pewees occupy a variety of habitats that provide exposed perches both in the understory and high in the canopy, and are aerial insectivores, passively searching for and sallying to capture prey from perches (Bemis and Rising 1999). In previous studies of the foraging behavior of Western Wood-Pewees, investigators did not differentiate males and females (Beaver and Baldwin 1975, Verbeek 1975, Eckhardt 1979, Szaro et al. 1990).

We studied the foraging ecology of male and female Western Wood-Pewees (hereafter, pewees) and examined possible intersexual differences. During two breeding seasons in the southern Sierra Nevada, we used song, behavior, and color-bands to distinguish male and female pewees and examine possible differences in foraging behavior. Our objectives were to (1) compare foraging rates of male and female pewees during different nesting stages, (2) examine possible intersexual differences in perch substrates, and (3) compare distances between the foraging locations of male and female pewees and their nests.

METHODS

Our study was conducted from mid-May through early August in 2007 and 2008. Study sites were located along forest edges surrounding wet montane meadows on the western slope of the southern Sierra Nevada Mountains in Fresno County, California. Our study sites included seven meadows that averaged 15 ± 10 (SD) ha (range = 4–29 ha) in size and were between 1682 and 1828 m in elevation. Habitat surrounding the meadows consisted of montane hardwood-conifer, montane riparian, and Sierra

mixed-conifer forests (Mayer and Laudenslayer 1988). Common tree species included ponderosa pine (*Pinus ponderosa*), California black oak (*Quercus kelloggii*), incense-cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), sugar pine (*P. lambertiana*), and lodgepole pine (*P. contorta*). Several trees associated with wetter sites were also present, including willows (*Salix* spp.), white alder (*Alnus rhombifolia*), and quaking aspen (*Populus tremuloides*). The shrub layer was characterized by greenleaf manzanita (*Arctostaphylos patula*), whitethorn ceanothus (*Ceanothus cordulatus*), snowberry (*Symphoricarpos acutus*), and Sierra gooseberry (*Ribes roezlii*). Meadows were dominated by herbaceous cover, including forbs, grasses, rushes (*Juncus* spp.), and sedges (*Carex* spp.).

Foraging observations. We observed and recorded foraging behavior of pewees between sunrise and sunset (~06:00 and 20:00), with most observations before 11:00. We systematically searched meadow edges and located all breeding pairs and unmated males that defended a territory with the goal of observing both the male and female of each pair on the same day. Total meadow length surveyed (all meadows combined) was 20.7 km and territory density was two to five pairs per km of meadow edge. We completed 32 survey days in 2007 and 30 in 2008, with 1–5 individual observations per day. To ensure statistical independence, each individual was observed only once per day, with visits to each territory at least four days apart. The order in which meadows were visited and direction walked was rotated to reduce bias for particular birds within sites. Mean observation time was 753 s for males and 479 s for females. Observation times were generally shorter for females because observations ended when they returned to nests.

We quantified foraging rate using foraging attack rate (Hutto 1990). A foraging observation consisted of watching birds as they foraged and recording each attack and the duration of nonforaging behaviors (to the nearest second) on a portable digital recorder. An attack was defined as a sally (a wing-powered aerial strike; Remsen and Robinson 1990) toward a prey item, whether successful or not. An observation ended at 20 min or when we lost sight of a bird for more than 5 min. To calculate attack rate, we divided the total number of attacks by total time spent foraging. Time spent in

nonforaging behaviors, including preening, prey handling, nest building, feeding nestlings, and interacting with other birds or predators was subtracted from the observation period. Pewees are sit-and-wait foragers and, as they searched for insect prey, they may have also been searching for predators, conspecifics, or simply resting; thus, these behaviors may have been included in foraging rate calculations. All observations were made by A. M. Fogg.

To reduce potential biases due to observability (Morrison 1984), we used the location of the second foraging sally for all habitat measurements even if a bird returned to the same perch. For the second foraging sally, we estimated sally length (m), recorded perch height, the perch substrate (tree species, snag [standing dead tree], log [dead tree on the ground], or fencepost), and the height (measured with a digital hypsometer; ± 0.1 m) of the perch substrate. During 2008, we collected data concerning tree species and snag availability by pairing used locations with nearby random locations (Fogg 2009). To locate random trees or snags, we chose a random distance (25–75 m) and azimuth from the foraging location, with the stipulation that the location was within 60 m of the meadow edge, and a foraging substrate (tree or snag) > 1.3 m tall was within 10 m of the random location. Data were collected for the tree or snag closest to the random location.

The locations of perch substrates used by foraging pewees were flagged and recorded using a global positioning system (GPS) unit to ensure that observations were not collected from the same individual in the same foraging substrate on subsequent visits. To avoid sampling the same individual on the same day, we walked at least 150 m (the average radius of a pewee territory; K. Purcell, unpubl. data) before recording another foraging observation. The only exception was if we positively identified the sex of the individual and observed an individual of the opposite sex on the same territory, in which case we recorded both observations.

Sex identification. The sex of focal pewees was determined using two methods. Pewees observed singing (either the dawn song, *Pee-pip-pip*, or *Pee-er* song; Bemis and Rising 1999) were identified as males. Female pewees are thought to be solely responsible for nest building and incubation, but both sexes are known to feed nestlings (Bemis and Rising 1999). A bird

was identified as a female only if we observed it nest building or incubating or if we knew the location of a singing male on the same territory while observing the female. Individuals that were generally silent or not engaged in breeding behavior were removed from the sample to avoid potentially confusing transient males with females. To verify these sex-identification methods, we color-banded several individuals in 2008. Birds were captured using mist nets (6 m long $\times$ 2.6 m high) and song playback. We sexed birds using the presence or absence of a brood patch. Brood patches were used as the defining characteristic because the cloacal protuberance is poorly developed in male pewees (Pyle 1997). We color-banded one female and seven males and observed their behavior and that of their mates throughout the summer to verify that only males sang and only females incubated; we later confirmed this to be true. Although this produced a male-biased sample of color-marked birds, it often allowed us to be certain that a non-marked bird was a female.

Foraging locations relative to nest sites.

While conducting foraging observations, we mapped territory boundaries and opportunistically searched for nests. At each nest, we recorded UTM coordinates with a handheld GPS. We recorded nest height and determined breeding stage by checking the contents with a mirror pole or observing the nest for at least 15 min (Martin and Geupel 1993). Behaviors used to determine nest stage included nest building (building), long periods of nest attendance without feeding nestlings (incubation), carrying fecal sacs from the nest and feeding nestlings (nestling), and feeding fledglings (fledgling). If we observed one or both members of the pair foraging nearby and could confirm breeding stage, we compared GPS locations of foraging perches with nest locations using the Euclidean Distance formula:

$$d = \sqrt{(\Delta x)^2 + (\Delta y)^2 + (\Delta z)^2},$$

where Δx = change in distance between the easting coordinates, Δy = change in distance between the northing coordinates, and Δz = change in distance between nest height and foraging height. All measurements were in meters.

Statistical analyses. We tested for differences between males and females in foraging attack rate (attacks/min) in both years using two-way analysis of variance (ANOVA). We

compared foraging rates between sexes and among nesting stages (building, incubation, nestling, and fledgling) using two-way ANOVA. Female sample sizes were sufficient to test for differences between breeding stages using Tukey's Honest Significant Differences test. Due to low sample sizes for males, we only used observations from the nestling stage to compare male and female foraging rate using a two-tailed *t*-test and were not able to compare rates by breeding stage for males. Euclidean distances between nest locations and foraging locations were compared between sexes, using a two-tailed *t*-test; sample sizes were too small to also compare distances by nesting stage. Distances were square-root transformed to improve normality; data transformation was evaluated for improved normality by inspecting histograms.

Perch heights, tree heights, and distances to capture (sally length) of male and female pewees were compared with two-sample *t*-tests. Perch substrate use (tree, snag, log, or fencepost) by males and females was compared using a *G*-test, and a chi-square goodness-of-fit analysis was used to evaluate specific perch substrate snag or tree species selection separately for males and females. We then used a Bonferroni correction to calculate 95% confidence intervals around the proportion of tree species used and examined whether the proportion of tree species available fell within the confidence interval (Neu et al. 1974). We acknowledge that multiple observations of the same individual are not truly independent and may have increased sample sizes and led to a higher Type I error rate (Hurlbert 1984). To examine whether repeated observations of the same individual may have influenced our results, we excluded duplicate observations of the same individual in 2008 (when birds were color-banded) and our results did not differ. As a result, we included all observations in our analyses. We used $\alpha < 0.05$ as indicating a significant difference, all data used in parametric statistical tests were normally distributed. Results are reported as means $\pm$ SE. All statistical analyses were conducted using program R (R Development Core Team 2008).

RESULTS

Foraging rates. We recorded 143 foraging observations, including 54 in 2007 (male $N = 29$, female $N = 25$) and 89 in 2008 (male

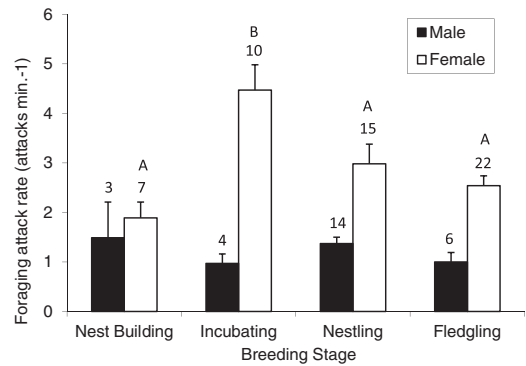


Fig. 1. Foraging attack rates (mean $\pm$ SE) during different nesting stages for male and female Western Wood-Pewees breeding along edges of montane meadows in the southern Sierra Nevada Mountains in 2007 and 2008. Numbers of foraging observations are indicated above each bar. For males, sample sizes were too small to compare rates among nesting stages. Female foraging rates differed with nesting stage (two-way ANOVA; $P = 0.02$); different letters above columns indicate a significant difference (adjusted P values < 0.05 ; post-hoc Tukey HSD tests).

$N = 45$, female $N = 44$). Territory mapping resulted in an estimate of 30 pairs sampled in 2007 and 60 pairs in 2008. Mean foraging rates of females (2.83 ± 0.18 attacks/min) were > 2.5 times higher than those of males (1.09 ± 0.06 attacks/min; $F_{1,140} = 92.0$, $P < 0.001$). Foraging rates did not differ between years ($F_{1,140} = 2.1$, $P = 0.15$) and the interaction between year and sex was not significant ($F_{1,140} = 0.8$, $P = 0.38$). The mean pooled foraging rate for males and females combined was 1.92 ± 0.12 attacks/min.

Nests were located and breeding stage confirmed for 81 of 143 foraging observations (27 male and 54 female). For those observations, foraging rates differed among breeding stages ($F_{3,73} = 7.7$, $P < 0.001$; Fig. 1), and the interaction between sex and breeding stage was significant ($F_{3,73} = 3.5$, $P = 0.02$). Female foraging rates were higher during incubation than during the nest building, nestling, or fledgling stages (Tukey HSD test, all $P < 0.05$). During the nestling stage, the mean foraging rate of males (1.34 ± 0.13 attacks/min) was lower than that of females (3.01 ± 0.42 attacks/min; $t_{1,28} = 3.4$, $P = 0.001$).

Perch height, sally distance, and substrate selection. Males perched higher ($t_{1,142} = 7.4$, $P < 0.001$) in taller perch substrates

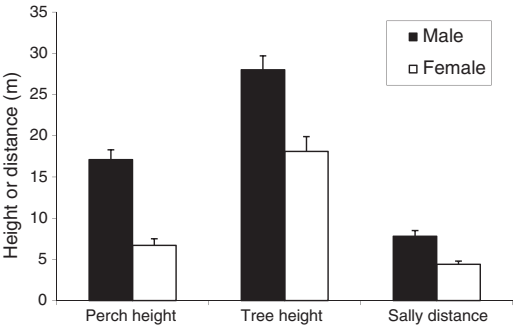


Fig. 2. Mean perch site characteristics and foraging sally distances (mean $\pm$ SE) for male ($N = 74$) and female ($N = 69$) Western Wood-Pewees breeding along edges of montane meadows in the southern Sierra Nevada Mountains in 2007 and 2008. All differences between males and females were significant (two-sample t -tests, $P < 0.0001$).

($t_{1,142} = 4.0$, $P < 0.001$) and sallied further distances to capture prey than females ($t_{1,142} = 4.7$, $P < 0.001$; Fig. 2). Perch height and sally distance were positively correlated for males (Pearson's correlation; $r = 0.41$, $P < 0.001$), but not for females ($r = 0.12$, $P = 0.31$). Males and females also chose different general perch substrates ($G_3 = 13.7$, $P = 0.003$). Trees were the most frequently used perch substrates for both sexes (males: 65% vs. females: 61%) and fenceposts were used only infrequently (both sexes: 2%). However, females used dead branches that protruded from logs as perches more than males (22% vs. 4%), and males used snags as perch substrates more than females (29% vs. 15%).

Both male ($\chi^2_7 = 135.3$, $P < 0.0001$) and female ($\chi^2_7 = 46.1$, $P < 0.0001$) pewees exhibited selective use of snags and some species of trees as perch substrates (Table 1). Confidence intervals around the proportions of tree species or snags used indicated that males used snags and sugar pines more than expected based on availability, incense-cedar and ponderosa pine less than expected, and used all other conifer and hardwood species in proportion to their availability. Females used snags more than expected based on availability, white fir and incense-cedar less than expected, and used all other species in proportion to their availability.

Foraging location. We located 42 nests (13 in 2007, 29 in 2008) and all nests were within 25 m of meadow edges. Mean nest height was 9.7 ± 1.1 m (range = 2.2–29.5 m).

Table 1. Selection of trees and snags as perch substrates by male and female Western Wood-Pewees breeding in montane meadows in the southern Sierra Nevada (Fresno County, California) during the summers of 2007 and 2008. The number and proportion of used and available trees are shown and 95% confidence intervals around proportion used. Significance can be evaluated by examining whether the proportion of available trees falls outside of 95% confidence intervals of proportion used.

Perch substrate	Number of times used		Frequency of use (proportion, or p_i)		95% Confidence Interval (p_i)		Number available	Proportion of available trees
	Male	Female	Male	Female	Male	Female		
White fir	9	6	0.13	0.11	$0.22 \leq p_1 \leq 0.03$	$0.20 \leq p_1 \leq 0.01^a$	17	0.21
Incense-cedar	21	16	0.30	0.29	$0.42 \leq p_2 \leq 0.16^a$	$0.43 \leq p_2 \leq 0.14^a$	38	0.47
Lodgepole pine	2	2	0.03	0.04	$0.07 \leq p_3 \leq 0.00$	$0.09 \leq p_3 \leq 0.00$	2	0.03
Sugar pine	8	3	0.11	0.06	$0.20 \leq p_4 \leq 0.02^b$	$0.12 \leq p_4 \leq 0.00$	1	0.01
Ponderosa pine	7	7	0.10	0.13	$0.18 \leq p_5 \leq 0.01^a$	$0.23 \leq p_5 \leq 0.02$	15	0.19
Black oak	1	3	0.01	0.06	$0.05 \leq p_6 \leq 0.00$	$0.12 \leq p_6 \leq 0.00$	0	0
Willow spp.	1	6	0.01	0.11	$0.05 \leq p_7 \leq 0.00$	$0.20 \leq p_7 \leq 0.01$	2	0.03
Snags	22	11	0.31	0.20	$0.44 \leq p_8 \leq 0.18^b$	$0.32 \leq p_8 \leq 0.07^b$	5	0.06

^aUsed less than expected based on availability

^bUsed more than expected based on availability

Nests were located and breeding stage confirmed for 50 foraging observations (18 male and 32 female; nests with fledged young excluded). Overall, males and females foraged at similar distances from nests ($t_{1,49} = 0.4$, $P = 0.66$), with mean distances of 25.1 ± 3.3 m for males and 23.0 ± 3.0 m for females. Mean nest height and foraging height were not correlated for either male (Spearman rank correlation; $r = -0.04$, $P = 0.86$) or female ($r = 0.02$, $P = 0.91$) pewees. On average, males foraged from perches higher than nests (mean height = 17.1 ± 1.2 m) and females from perches lower than nests (mean height = 6.7 ± 0.8 m).

DISCUSSION

Foraging rates. Attack rates of female pewees averaged >2.5 times those of males and the pooled average value of 1.9 attacks/min was not representative of either sex. Female foraging rates were highest during incubation, with similar rates during the nest building, nestling and fledgling stages. Females may be under greater energetic stress during incubation and may, therefore, require higher rates of energy intake (Merila and Wiggins 1997, Nagy et al. 2007). In addition, among species where only females incubate, females might be expected to forage rapidly during their short bouts off the nest (Dobbs and Martin 1998). In many species of birds, males feed females during incubation (Ricklefs 1974). However, male pewees were never observed either feeding females or incubating. Thus, female pewees may need to forage rapidly during short bouts to meet their nutritional needs and return to their nests to avoid chilling the eggs and reduce the risk of predation (Conway and Martin 2000).

We found that foraging rates of female pewees were higher than those of males during the nestling stage. In contrast, foraging rates of males and females were found to be similar in Mountain Bluebirds, (*Sialis currucoides*; Power 1980), Pied Flycatchers (*Ficedula hypoleuca*; Post and Gotmark 2006), and Prothonotary Warblers (*Protonotaria citrea*; Lyons 2005). The higher foraging rates of female pewees during the nestling stage may be a result of their need to balance time on the nest, at least early in the nestling period when brooding young, with the need to provision nestlings. In addition, females were frequently observed shielding nestlings

from the sun while males were singing, foraging, and, presumably, monitoring the area for the presence of potential nest predators (A. Fogg, pers. obs.). Because they need not spend time at nests brooding or shading young and have more time to forage, male pewees may be able to provision nestlings without needing to spend as much time foraging as females.

Perch height, sally distance, and substrate selection. Male pewees in our study foraged from perches, on average, more than 10 m higher than those used by females. Males may forage further above ground than females to enhance territory vigilance, that is, to better monitor potential predators and conspecific males and females. In addition, male pewees may use higher perches because they represent better song post locations, as has also been reported for males in several species of warblers (Morse 1968, Holmes 1986, Petit et al. 1990, Kelly and Wood 1996). There have been few sex-specific studies of the foraging behavior of flycatchers, but male and female Scissor-tailed Flycatchers (*Tyrannus forficatus*) were also found to differ in mean foraging height, with females foraging from lower perches than males (Teather 1992). Female Olive-sided Flycatchers (*Contopus cooperi*) were also found to use perches closer to the ground than those used by singing males (Robertson 2012). Foraging at different heights may also reflect different foraging opportunities for males and females and reduce intersexual competition for food (Robinson and Holmes 1982).

We found that the mean sally distances were 7.8 m for males and 4.4 m for females, and sally distance was positively correlated with perch height for males, but not for females. Similarly, male Scissor-tailed Flycatchers were found to sally up to 2 m further than females and this was attributed to differences in foraging heights and tail length; sally distance was positively correlated with perch height for both sexes (Teather 1992). Mean sally distances of Western Wood-Pewees reported in previous studies (both sexes combined; 3.8 m, Verbeek 1975; 4.4 m, Eckhardt 1979) were similar to those of females in our study, but shorter than those of males. Mean perch heights of pewees in these previous studies were also lower than in our study (<5 m). Avian aerial insectivores on higher perches can scan a larger area for insect prey than when on lower perches and thus

may detect prey at, and sally, greater distances (Andersson 1981). Thus, female pewees in our study may have sallied shorter distances because they perched lower and were more likely to detect closer prey. Vegetation density can also affect the ability of aerial insectivores to detect prey, and perches in more open areas may allow flycatchers to detect prey at greater distances (Troy and Baccus 2009). By perching higher in the canopy, male pewees may be foraging in areas where vegetation is less dense than where females forage in the understory. Thus, males may detect insect prey at, and sally, greater distances than females.

We found that female pewees used dead branches that protruded from logs as perches more than males, and males used snags more than females. Logs used as perches by females were usually in meadows and perpendicular to meadow edges. The dead branches that protruded from logs usually provided perches unobstructed by dense meadow vegetation, allowing females to more effectively scan for aerial insect prey (Troy and Baccus 2009). Snags can also provide unobstructed views to scan for aerial insects and males may have also used snags more than females because they provided higher perches for better territory vigilance (see above).

To examine specific substrate preferences, we used snag and tree species selection analysis and found that, based on availability, male and female pewees used snags as perch substrates more than expected and incense-cedars less than expected. Males also used sugar pines more and ponderosa pines less than expected, and females used white firs less than expected. However, confidence intervals for proportion of substrates used by male and female pewees overlapped, suggesting that their use of tree species and snags was similar. Male and female Olive-sided Flycatchers were also found to selectively use snags rather than live trees as perch substrates in conifer forests (Robertson 2012). Live conifers, especially firs and cedars, often have dense foliage that may not provide the openings that pewees need to scan for insect prey (Hager et al. 2004). Many sugar pines, often the tallest trees in the forest canopy, suffer from the white pine blister rust pathogen (*Cronartium ribicola*; Storer et al. 2004), and the resulting dead tops or dead branches were often used as perches by male pewees (A. Fogg, pers. obs.).

Foraging location. The reproductive constraints hypothesis (Morse 1968) proposes that intersexual differences in foraging behavior result when both sexes forage near their primary zone of reproductive activity to reduce the time and energy costs associated with these activities (i.e., song posts for males and nests for females). Such differences have been documented for numerous songbird species, but most often for warblers (Franzreb 1983, Holmes 1986, Hanowski and Niemi 1990, Petit et al. 1990). We tested this hypothesis by measuring the distance from foraging locations to nest locations and hypothesized that females would forage closer to nests than males. We also examined the possible relationship between nest height and foraging height. However, we found that male and female pewees foraged at similar distances from nests and foraging height was not correlated with nest height for either males or females. We did not have the sample sizes needed to compare the foraging distance of males and females from nests during different nest stages, and half of our observations were made during the nestling period. Thus, male and female pewees may have foraged at similar distances from nests because many of our observations were made during the nestling period when both were feeding nestlings. Foraging locations of males and females may differ during other nest stages. For example, although sample sizes were small (male $N = 4$, female $N = 10$), Fogg (2009) found that the mean distance of female pewees from nests during incubation was closer than that of males (21 m vs. 34 m).

Attack rates and habitat quality. Metrics such as foraging attack rate have been used as indicators of habitat quality and to assess the effectiveness of habitat restoration or land conservation efforts (Gabbe et al. 2002, Pomara et al. 2003, Lyons 2005, Lindell 2008, Morrison et al. 2009). Researchers often observe only males because they are more conspicuous and thus easier to watch (Lovette and Holmes 1995, Kilgo 2005) or do not account for sex in their analyses (Gabbe et al. 2002, Pomara et al. 2003, Morrison et al. 2009). We found that foraging attack rates can differ between the sexes and, for females, among nesting stages. The possibility of such differences should be taken into consideration if attack rates are being used to assess habitat quality, especially for sexually monochromatic species of birds.

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