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OCCURRENCE OF POLYGYNY AND DOUBLE BROODING IN THE EASTERN WOOD-PEWEE

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ABSTRACT.—We document the first confirmed cases of polygyny and double brooding in the Eastern Wood-Pewee (*Contopus virens*). During an intensive study of the effects of shelterwood harvesting on canopy-nesting songbirds in southeastern Ohio, 2007–2010, we color-banded 79 Eastern Wood-Pewees and monitored 237 pewee nests. In 2007, we confirmed a color-banded male provisioning at two concurrently active nests; the male was polygynous in at least two consecutive years. In 2009, we observed an unbanded female feeding fledglings and subsequently shaping a nest from which young had recently fledged; the female successfully fledged two broods from the same nest. In addition to confirmed observations, we identified several other probable cases of polygyny and double brooding. In our upland oak system, we estimated rates of polygyny from 6–22% with the greatest occurrence of polygyny during a dry spring in 2007; rates of double brooding may have been as high as 6–12%. Males appeared to benefit from polygyny, because males paired with two females fledged twice as many young compared to monogamous males, without any apparent negative effect on return rate. Overall, we did not find negative effects on reproductive success for females paired with polygynous males, although we were not able to consistently differentiate between primary and secondary females. Polygyny appeared to be related to either territory quality and/or male quality with nests of polygynous males located in preferred nest sites while provisioning rates were greater at polygynous compared to monogamous nests. In addition, we only found experienced males paired with two females. Both males and females benefited from double brooding, fledging twice as many young as single brooded pairs, but in our system double brooding appeared to be limited by high levels of nest predation early in the breeding season. *Received 3 August 2012. Accepted 11 December 2012.*

Key words: *Contopus virens*, double brooding, life history strategy, pewee, polygyny.

Long-term reproductive strategies tend to maximize biological fitness, which is determined by the number of young produced by an individual that can pass on their genes to future generations. Small passerines with relatively high mortality may maximize fitness by producing as many young as possible (Newton 1989). In the absence of additional costs, such as juvenile and adult mortality, a number of strategies may increase fitness including breeding with more than one individual or attempting multiple broods (Stearns 1992). Alternative strategies appear to be favored under different environmental conditions depending on trade-offs among clutch size, parental care, and future reproductive potential of the parent (Verhulst et al. 1997, Verhulst 1998).

For example, older males in high quality territories may be more likely to be polygynous (e.g., Petit 1991, Pribil and Searcy 2001), whereas older females in high quality territories may be more likely to attempt multiple broods (e.g., Holmes et al. 1996, Nagy and Holmes 2005). Males may increase fitness by pairing with additional mates, although parental care may be reduced, especially for the secondary female (Huk and Winkel 2006) who in some cases may be of lower quality (Grønstal et al. 2003). On the other hand, multiple brooding may increase fitness for both members of the pair. For females to initiate a second clutch, males generally have to take over care of dependent fledglings from the first brood, whereas single brooded pairs typically divide care of the fledglings among both parents (Evans Ogden and Stutchbury 1997, Vega Rivera et al. 2000). Alternatively, individuals may increase fitness through extra pair copulations which may be common in synchronously breeding populations (Vedder et al. 2011).

For many species, knowledge of the occurrence of life history strategies such as polygyny may be limited by the number of intensive studies (Ford 1983). Both facultative polygyny and double brooding continue to be documented in a number

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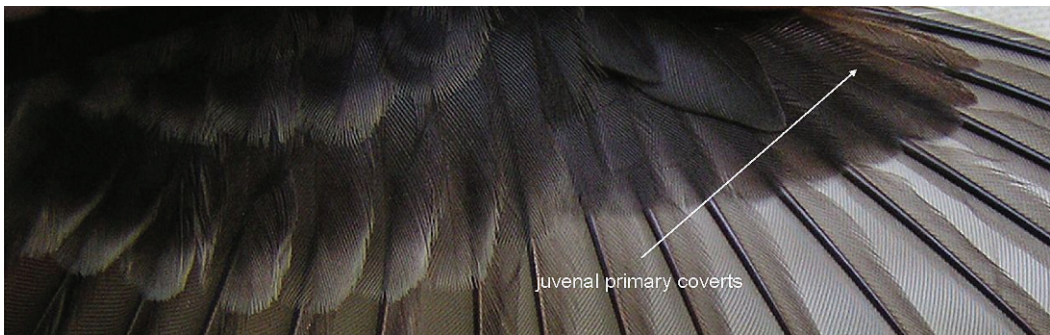[4] Corresponding author; e-mail: felicity.newell@gmail.com

FIG. 1.   Retained juvenal primary coverts were used to age Eastern Wood-Pewees. Of the 22 pewees identified as second-year individuals, 8 retained 1–4 outer juvenal primary coverts, 2 retained all except one molted inner primary covert, and 12 appeared to have retained all juvenal primary coverts, including 4 birds that exhibited a fault bar across all primary coverts. Several individuals also had small windows <2 mm where the skull was incompletely pneumatized. We did not observe retained juvenal primary coverts on any of the polygynous males.

of species generally considered to be single-brooded and/or monogamous (e.g., Mulvihill et al. 2009, Small et al. 2009). Polygyny and double brooding have been documented in a number of flycatcher species (Prescott 1986, Briskie and Sealy 1987, Sedgewick and Knopf 1989, Mitrus and Socko 2005, Pearson et al. 2006). One case of polygyny has been documented in the Western Wood-Pewee (*Contopus sordidulus*) (Eckhardt 1976), although no evidence of double brooding has been reported (Bernis and Rising 1999). Based on reports of young fledged late in the season, Eastern Wood-Pewees (*Contopus virens*) have been thought to possibly double brood (McCarty 1996), and a male Eastern Wood-Pewee was seen with two females in his territory (W.J. Smith, pers. comm., cited in Eckhardt 1976). However, without previous studies of color-marked individuals, information on reproductive strategies of this species has been lacking (McCarty 1996). Our objectives of this study were to 1) document occurrence of both polygyny and double brooding in the Eastern Wood-Pewee based on color-marked individuals, 2) examine effects of these strategies on reproductive success, and 3) examine ecological correlates of these two strategies to provide some insight into factors influencing occurrence of polygyny and double brooding.

METHODS

From 2007–2010, we studied Eastern Wood-Pewees as part of a large–scale study on the effects of shelterwood harvesting on canopy-nesting songbirds. Study sites were located in upland mixed oak forest in 14 stands across three forests in Vinton and Jackson counties in southeastern Ohio. Half of the sites were recently harvested to approximately 50% stocking, and half were unharvested mature second-growth (see Newell and Rodewald 2011, 2012).

Color-Banding.—We uniquely color-banded 62 male and 17 female Eastern Wood-Pewees during the study. Mist-nets and song playback were used to capture birds throughout the breeding season. Response to playback varied among individuals, and we were not able to color-band birds in all territories. At least one adult was banded on approximately half of ~150 territories in which we found nests. Birds were weighed to the nearest 0.1 g using a digital scale, and we measured wing length to the nearest 0.5 mm; measurements were calibrated among observers. Males and females were identified based on breeding characteristics, occasionally in combination with wing length. We aged birds as second-year (SY) or after-second-year (ASY) individuals using wing molt limits (Mulvihill 1993, Pyle 1997). Retained juvenal primary coverts were identified on 22 individuals (Fig. 1). Similar molt patterns have been observed in Western Wood-Pewees (Wolfe and Frey 2011), although it remains unclear whether some individuals molt all primary coverts during the first prebasic molt (Pyle 1997). Individuals were uniquely color-banded and resighted throughout the breeding season; and we searched territories occupied by color-banded individuals in subsequent years (Newell and Rodewald 2012).

Nest Monitoring.—We monitored 237 Eastern Wood-Pewee nests during the study. We searched

for and monitored pewee nests from May through the end of August. Nests were checked every 2–3 days until failure or fledging. We watched nests until a parent was seen at or within one meter of the nest. If there was no activity, we watched for 20 mins (or 40 mins if the female could not be seen on the nest), and checked the nest on a second visit to confirm that it was inactive. A nest was considered to have failed if it was inactive prior to the earliest possible fledging date, estimated from known initiation dates for nests found during building. Additional behavioral observations, including absence of active provisioning and immediate re-nesting without any sign of young, were used for nests found later in the nesting cycle. We searched for a re-nest within a few days after a nest failed, which allowed us to find consecutive nesting attempts during building and estimate productivity. Some pairs re-nested at least 4 times, but most territories were successful later in the season. Productivity did not differ between territories with at least one banded adult, and territories in which we were not able to capture an adult (Wilcoxon rank sum test: $W = 1556$, $P = 0.82$), and we used all territories. We were able to determine productivity for about two-thirds of the territories in which we found nests. Once birds were actively feeding young 3–6 days after hatching, we conducted 30-min provisioning observations to estimate age of young and count brood size (Newell and Rodewald 2011, 2012); we watched nests every 1–3 days as time allowed. Vegetation data were collected at nests including basal area by tree species using a 2.3× metric prism (10× English), and topographic position of the nest including slope and aspect using a clinometer and compass (see Newell and Rodewald 2011 for more detailed description).

Data Analysis.—Statistical analysis was conducted using Program R (R Development Core Team 2012). We compared brood size, male and female productivity, male body condition, and nest placement between monogamous and polygynous territories with two-sampled *t*-tests or Wilcoxon rank sum tests; Fisher's Exact tests or chi-squared tests were used to compare annual rates of polygyny, male return rate, and topographic position of the nest. To examine nestling provisioning, we used generalized linear mixed effects models with a negative binomial distribution for overdispersed count data in the glmmADMB package in Program R (Fournier et al. 2012, Skaug et al. 2012). Nest was included as a random effect to account for repeated observations at the same nest, and we examined the interaction between breeding strategy and nestling age, controlling for brood size, time of day and time of season as fixed effects. Nesting success was calculated according to the Mayfield method (Mayfield 1975, Johnson 1979), and based on our data we used a nesting cycle of 29 days. We compared reproductive success between monogamous and polygynous males using chi-squared tests in Program CONTRAST (Hines and Sauer 1989).

RESULTS

Polygyny.—We confirmed polygyny when a male was seen feeding nestlings at two concurrently active nests. We confirmed consecutive years of polygyny for a color-banded male in 2007 and 2008. During the first year of the study, the male was color-banded with all red bands on 30 May 2007 near a recently completed nest. The red male was recaptured 5 June 2007 near another recently completed nest 174 m away. Both nests failed during laying or incubation and re-nests were found in each area. On 6 July 2007, the red male was seen provisioning young at each re-nest in the two different areas. Color-bands were confirmed by several observers and no other pewees had red bands at the site. Provisioning observations were conducted at both nests which successfully fledged a combined total of five young. In 2008, the red male was resighted with two females and provisioning observations again confirmed that he was polygynous. The same male also returned in 2009 and 2010, although due to limited field time at the study site, we were not able to confirm polygyny beyond the first 2 years.

We identified five other probable cases of polygyny based on nests of color-banded males. We considered polygyny probable when the male was seen regularly singing and interacting with the female around two concurrently active nests. Because nests often failed prior to hatching, we were not able to confirm the male at the nest. In one case, an unbanded male was followed between two nests during provisioning; the male and one female were later banded after the nests fledged. For the three polygynous territories in which we were able to identify timing of nesting, we estimated 5–10 days between first laying dates for nests of primary and secondary females. In 2007, we estimated 21.7% (5/23) of color-banded

TABLE 1.   Comparison of monogamous and polygynous Eastern Wood-Pewees in southeastern Ohio, 2007–2010. We observed potentially greater fitness for six polygynous males who fledged greater numbers of young each year than monogamous males. Significance from Wilcoxon rank sum, Fisher's Exact or chi-squared tests.

	Monogamous			Polygynous			
	Mean	SE	*n*	Mean	SE	*n*	*P*-value
Brood size							
First nest	2.35	0.10	31	2.50	0.29	4	0.70
Re-nest	2.10	0.07	60	2.33	0.17	9	0.29
Reproductive success							
Daily nest survival	0.965	0.003	213	0.962	0.011	23	0.77
Nest success (%)[1]	36.0	3.4	213	32.1	10.5	23	0.71
Fledglings/female	2.03	0.08	97	2.23	0.21	14	0.30
Fledglings/male	**2.03**	**0.08**	**97**	**4.46**	**0.36**	**7**	**<0.001**
Male quality							
Return rate (%)	42.6		61	57.1	18.7	7	0.69
Male wing length (mm)	84.4	6.3	56	85.1	0.7	6	0.43
Male body mass (g)	14.1	0.1	53	14.5	0.3	5	0.21

[1] Based on a 29 day nesting cycle.

males were polygynous, but in 2008 we identified polygyny in only 6.3% (2/32) of color-banded males (Fisher's Exact Test: $P = 0.11$); one was the same male confirmed polygynous in 2 consecutive years, and the other a new male in a territory occupied by a polygynous male the previous year. In 2009, we focused less extensively on pewees, and did not identify any cases of polygyny. Greater occurrence of polygyny in one year could have been related to weather, which in 2007 was hot and dry during May and June when pewees were establishing territories; in 2007 Ohio received 12 cm of rainfall in May–June compared to 29 cm in 2008.

In our system, males paired with two different females appeared to increase fitness. Polygynous males fledged twice as many young as males not known to be polygynous without any apparent negative effect on return rate (Table 1). Because site fidelity of returning males was 100% in our system (Newell and Rodewald 2012), this likely indicates high survival. Brood size and nesting success were similar for polygynous and monogamous nests and, with on average similar numbers of fledglings/female, we did not find any apparent negative effect of polygyny on overall female reproductive success (Table 1). However, we were not able to consistently differentiate between primary and secondary females, and there was some indication that earlier nesting females might have been more successful than later nesting females for three territories in which we were able

to identify timing of breeding (primary: 2.33 ± 0.33 fledglings/female, secondary: 1.33 ± 0.66 fledglings/female, Wilcoxon rank sum test $P = 0.27$).

Territory quality could have been a factor influencing polygyny for Eastern Wood-Pewees, and nests of polygynous males were located in preferred nest sites. In our system, pewees selected nest sites on xeric ridgetops (Newell and Rodewald 2011). Consistent with this, nests of polygynous males were located in areas with significantly greater basal area of xerophytic oaks, including black oak (*Quercus velutina*), scarlet oak (*Q. coccinea*), and chestnut oak (*Q. prinus*), compared to nests of males not known to be polygynous (polygynous: 11.2 ± 1.0 m²/ha xerophytic oaks, $n = 24$; monogamous: 7.7 ± 0.4 m²/ha xerophytic oaks, $n = 254$; Wilcoxon rank sum test, $P = 0.001$). However, there were no differences in topographic slope position (Bonferoni adjusted chi-squared test all $P > 0.05$). Partial harvesting also did not appear to be a factor and three territories of polygynous males were located predominantly in shelterwood stands, whereas four were located in unharvested stands.

Polygyny may also have been related to male quality, and males paired with two different females appeared to be experienced breeders. We identified all six polygynous males as ASY birds with broad glossy primary coverts and none showed retained coverts or windows in the skull.
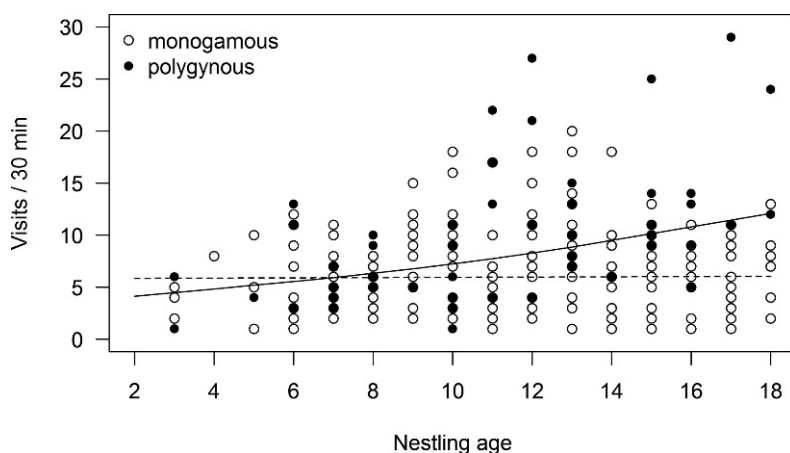
FIG. 2.   Provisioning rates at nests of Eastern Wood-Pewees in southeastern Ohio, 2007–2010. At nests of 5 polygynous males (58 observations at 11 nests), provisioning rates increased with nestling age compared to 73 males not known to be polygynous (204 observations at 73 nests).

On the other hand, we identified one female, which we were able to capture paired with a polygynous male, as a SY bird based on retained primary coverts. Interestingly, overall we captured a greater proportion of SY females at 53% (9/17) compared to SY males at 21% (13/62) (Fisher's Exact test: $P = 0.01$). Experienced males may be better able to defend a large territory that can support two females. Although we did not measure territory size, polygynous males averaged 110 ± 18 m ($n = 9$) between concurrently active nests of different females compared to consecutive re-nests of other color-banded pewees which averaged 66 ± 5 m ($n = 33$) (Wilcoxon rank sum test $P = 0.02$). This would suggest that polygynous males were defending a larger area than monogamous males.

Either related to territory or male quality, provisioning rates at nests of polygynous males were 7% greater per day with nestling age compared to individuals not known to be polygynous (Likelihood-ratio test: Deviance$_{1,10}$ = 5.5, $P = 0.01$) (Fig. 2). We confirmed one male provisioning at nests of both females in his territory, but we were not able to examine male contribution towards feeding young, because color-bands were often difficult to identify on pewees at the nest. Provisioning rates at nests of both females were especially high for one male polygynous in 2 consecutive years. Overall high provisioning rates are consistent with high reproductive success for polygynous males in our system.

Double Brooding.—Direct behavioral observation confirmed a case of double brooding in 2009. On 15 July 2009, an unbanded female was seen feeding fledglings from a successful nest, then subsequently she returned to reshape the nest from which three young had fledged 10 days previously (DLN, pers. obs.). On 24 July 2009, the female was observed sitting on her previous nest, and she continued to sit on the nest until several small downy young were visible. On 17 August 2009, 33 days after the female was seen feeding young from the previous nest, three young were large and close to fledging in the second nest. The color-banded male for the territory was seen provisioning at both nesting attempts. The pair fledged five young from two clutches in the same nest.

We identified a second probable case of double brooding in 2008. The male was color-banded, and the female unbanded. The timing and proximity of two successful nests in the territory, in conjunction with behavioral observations, indicate likely double brooding. We confirmed the color-banded male provisioning at two consecutive nesting attempts located 52 m apart. This distance was consistent with re-nesting, whereas we measured a minimum of 58 m between nests of different females in polygynous territories, which did not fledge consecutively. Although we often heard and saw the male calling and flying between different areas in polygynous territories, in the territory with two successful nests we found no evidence of a second female. On 11 July 2008, the unbanded female was found

building a re-nest about 30% complete 4 days after the previous nest in the territory had fledged. Typically pewee nests were built in 6 days (range: 4–10 days), and the female was seen sitting on the nest on 21 July 2008. On 16 August, 2008, 36 days after the female was first seen building, two young were large and close to fledging in the second nest. The male, apparently paired with one female, fledged four young from two successful nesting attempts.

High nest predation early in the season, when nesting overlapped with other forest songbirds, could have been a constraint limiting the occurrence of double brooding in our system. Success increased later in the season (Newell and Rodewald 2011), and only 32 first nesting attempts were successful; at least one adult was color-banded at 17 of these nests. We found a second nesting attempt for two of the color-banded birds, suggesting double brooding could be as high as 6–12%. Although we were not specifically looking for re-nests after a nest was successful, we visited sites every 3 days and spent extensive time searching for nests of several canopy species. Similar to the double brooding case in which a bird re-used the same nest, we observed several other pewees returning to previously successful nests, then sitting and spinning around in the nest, although no other nests were active on subsequent checks. We also did not find any other indication of re-nesting in the area.

Because of small sample size, we were not able to examine factors related to double brooding in the Eastern Wood-Pewee. However, double brooding appeared to be successful for pewees, and both attempts at a second nest were successful after fledging a first nest; double-brooded pairs fledged 4–5 young, twice as many as single-brooded pairs (Wilcoxon rank sum test $P = 0.009$). First laying dates of 3–4 June for double-brooded pairs were similar to average first laying dates of 4 June (22 May–22 Jun, $n = 100$) for pairs not known to double brood. Second nesting attempts of double-brooded pairs fledged 18–19 August and were within the range of re-nesting dates; 20% (12/62) of re-nesting attempts fledged after this date, and the last nest fledged 4 September for a >100 day breeding season from the first laying date on 24 May. Sample size was too small to examine provisioning rates of the two double brooded pairs, but a few observations generally appeared to be within the range for single brooded pairs. Both double-brooded males appeared to be ASY birds, and one returned to the same territory the following year; we were not able to color-band either female. Both double brooding attempts were located in shelterwood stands.

DISCUSSION

Through intensive color-banding and nest monitoring, we confirmed both polygyny and double brooding in the Eastern Wood-Pewee. Occurrence of both life history strategies was relatively rare in our system (<22%) with some variation among years. By pairing with more than one mate, males increased productivity without any apparent negative effect on return rates or overall female productivity. Polygyny appeared to be related to either a high quality territory or high quality male, and polygynous nests were located in preferred habitat with greater provisioning rates than monogamous nests. All polygynous males appeared to be experienced breeders, whereas at least one female paired with a polygynous male was an inexperienced breeder. Both males and females increased productivity by double brooding, but high nest predation early in the breeding season may have limited the occurrence of double brooding in our system. With only two observations, we were not able to examine other factors related to double brooding. Overall, our observations suggest low occurrence of a range of breeding strategies influenced by a combination of territory and male quality, as well as weather conditions and nest predation rates.

Estimates of polygyny ranging from 6–22% are typical for a number of species, although under certain conditions polygyny may be as high as 40–50% (Table 2). Our observations of polygyny are similar to the Western Wood-Pewee, in which males provision at both nests, but females occupy separate adjacent areas in contiguous forest (Eckhardt 1976). However, we did not observe clear polyterritoriality and we do not know if females were aware of the additional mate. In our system, occurrence of polygyny tended to vary between years. In 2007 a hot, dry period in May and June when pewees were establishing territories may have increased occurrence of polygyny; interestingly no cases of double brooding were observed in 2007. Pewees are aerial insectivores and drier years could result in greater variation in territory quality with clumped resources which could be more easily monopolized by a single

TABLE 2. Rates of polygyny in several facultatively polygynous passerines, that have been extensively studied in North America and Europe.

Species	Polygyny (%)	Reference
Eastern Wood-Pewee	6–22	This study
Willow Flycatcher (*Empidonax traillii*)	10–50	Review in Pearson et al. 2006
Eurasian Blue Tit (*Cyanistes caeruleus*)	20	Kempenaers 1994
House Wren (*Troglodytes aedon*)	10–40	Johnson et al. 1993
European Pied Flycatcher (*Ficedula hypoleuca*)	7–39	Alatalo and Lundberg 1984
Collared Flycatcher (*Ficedula albicollis*)	6	Garamszegi et al. 2004
Prothonotary Warbler (*Protonotaria citrea*)	9	Petit 1991
American Redstart (*Setophaga ruticilla*)	5–l6	Secunda and Sherry 1991

male. During the non-breeding season, pewees may be in better condition in dry years (Wolfe and Ralph 2009), and in our system pewees preferentially located nests in xeric microhabitats on ridgetops (Newell and Rodewald 2012). This is consistent with predictions that pewees may benefit from warmer drier climate (Matthews et al. 2004).

Estimates of the extent of double brooding within our population around 6–12% are within the range for the Acadian Flycatcher (*Empidonax virescens*) at 3–14% (Mumford 1964). Despite a long breeding season for the Eastern Wood-Pewee, double brooding was less common than for a number of warbler species which regularly double brood at 35% (Holmes et al. 1992, Evans Ogden and Stutchbury 1996), but similar to species which occasionally double brood at 6% (Mulvihill et al. 2009). However, in our system high nest predation early in the breeding season may have limited the occurrence of double brooding, and several pairs re-nested at least four times after nest failure. In addition to our observations, recent work has also found a number of cases of Eastern Wood-Pewees double brooding in the Ozarks, including reuse of the same nest (Kendrick 2012), supporting occurrence of this strategy in different regions.

Male Eastern Wood-Pewees increased annual productivity by pairing with more than one mate, whereas female pewees increased annual productivity by double brooding. Unlike some species, in which clutch size, reproductive success and/or provisioning rates may be reduced at nests of females paired with polygynous males (Johnson et al. 1993, Mulvihill et al. 2002, Ferretti and Winkler 2009), we found similar brood size and reproductive success, but greater provisioning rates at nests of both females, especially for one territory in which the male was polygynous in at

least 2 consecutive years. Thus in one year, males appeared to be able to fledge greater numbers of young without decreasing the overall number fledged by females, except perhaps if polygyny limited the occurrence of double brooding. We do not know if secondary females had lower success than primary females, which may be less related to polygyny than to female quality and settlement patterns (Grønstal et al. 2003). However, although fecundity and return rates of polygynous males were high during several years in our system, recent work suggests associations between polygyny and lifetime reproductive success may not be supported when data on the full lifespan are available (Herényi et al. 2012). Thus with limited observations over a few years, trade-offs in adult, as well as juvenile survival, are difficult to determine.

Our results do not differentiate between models to explain polygyny based on an abundance of resources (Orians 1961, Verner and Willson 1966, Ewald and Rohwer 1982) or male quality (Weatherhead and Robertson 1979, Wingfield 1984, Petrie and Lipsitch 1994). It remains unclear whether provisioning rates were greater because polygynous males occupied high quality territories, or because they were experienced breeders. High quality males often obtain the best territories (e.g., Petit 1991), thus female selection may be based on a number of characteristics, although recent work continues to highlight the importance of territory quality (Alatalo et al. 1986, Hasegawa et al. 2012).

Anecdotal observations did not suggest other models to explain polygyny, such as female site fidelity (Eliason 1986) or a skewed sex ratio (Smith et al. 1982, Kempenaers 1994). Compared to 100% site fidelity for males in our system (Newell and Rodewald 2012), only two females returned to the same territory and the third female moved >400 m between years (out of 16 banded

females). There also did not appear to be a shortage of unpaired males, as we banded several *floater* males early in the season that did not remain on territory. On the other hand, polygyny could provide an additional advantage for females through increased opportunity for extra pair mating while the male is occupied at the second nest (Vedder et al. 2011). Although occurrence of extra pair paternity in pewees remains unknown, we found female pewees actively engaged in territory and nest defense. Unlike other canopy-nesting species in our study, female pewees often responded to song playback within the territory (which allowed us to color band some females), and gave a loud two-note *pewee* alarm call in response to predators, as well as during nest building. Further work is needed to examine occurrence of extra pair mating in this species in relation to different life history strategies.

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LITERATURE CITED

ALATALO, V. R. AND A. LUNDBERG. 1984. Polyterritorial polygyny in the Pied Flycatcher *Ficedula hypoleuca* – evidence for the deception hypothesis. Annales Zoologici Fennici 21:217–228.

ALATALO, R. V., A. LUNDBERG, AND C. GLYNN. 1986. Female pied flycatchers choose territory quality not male characteristics. Nature 323:152–153.

BERNIS, C. AND J. D. RISING. 1999. Western Wood-Pewee (*Contopus sordidulus*). The birds of North America. Number 451.

BRISKIE, J. V. AND S. G. SEALY. 1987. Polygyny and double-brooding in the Least Flycatcher. Wilson Bulletin 99:492–494.

ECKHARDT, R. C. 1976. Polygyny in the Western Wood Pewee. Condor 78:561–562.

ELIASON, B. C. 1986. Female site fidelity and polygyny in the Blackpoll Warbler (*Dendroica striata*). Auk 103:782–790.

EVANS OGDEN, L. J. AND B. J. M. STUTCHBURY. 1996. Constraints on double brooding in a neotropical migrant, the Hooded Warbler. Condor 98:736–744.

EVANS OGDEN, L. J. AND B. J. M. STUTCHBURY. 1997. Fledgling care and male parental effort in the Hooded Warbler (*Wilsonia citrina*). Canadian Journal of Zoology 75:576–581.

EWALD, P. W. AND S. ROHWER. 1982. Effects of supplemental feeding on timing of breeding, clutch-size and polygyny in red-winged blackbirds *Agelaius phoeniceus*. Journal of Animal Ecology 51:429–450.

FERRETTI, V. AND D. W. WINKLER. 2009. Polygyny in the Tree Swallow *Tachycineta bicolor*: a result of the cost of searching for an unmated male. Journal of Avian Biology 40:290–295.

FORD, N. L. 1983. Variation in mate fidelity in monogamous birds. Current Ornithology 1:329–356.

FOURNIER, D. A., H. J. SKAUG, J. ANCHETA, J. IANELLI, A. MAGNUSSON, M. MAUNDER, A. NIELSEN, AND J. SIBERT. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software 27:233–249.

GARAMSZEGI, L. Z., J. TÖRÖK, G. MICHI, AND A. P. MØLLER. 2004. Female survival, lifetime reproductive success and mating status in a passerine bird. Oecologia 138:48–56.

GRØNSTAL, G. B., I. BYRKJEDAL, AND Ø. FIKSEN. 2003. Predicting polygynous settlement while incorporating varying female competitive strength. Behavioral Ecology 14:257–267.

HASEGAWA, M., E. ARAI, M. WATANABE, AND M. NAKAMURA. 2012. Female mate choice based on territory quality in Barn Swallows. Journal of Ethology 30:143–150.

HERÉNYI, M., G. HEGYI, L. Z. GARAMSZEGI, R. HARGITAI, G. MICHLS, B. ROSIVALL, AND J. TÖRÖK. 2012. Lifetime offspring production in relation to breeding lifespan, attractiveness, and mating status in male Collared Flycatchers. Oecologia 170:935–942.

HINES, J. E. AND J. R. SAUER. 1989. Program CONTRAST—a general program for the analysis of several survival or recovery rate estimates. Fish and Wildlife Technical Report 24. USDA, Fish and Wildlife Service, Washington, D.C., USA.

HOLMES, R. T., T. W. SHERRY, P. P. MARRA, AND K. E. PETIT. 1992. Multiple brooding and productivity of a neotropical migrant, the Black-throated Blue Warbler (*Dendroica caerulescen*) in an unfragmented temperate forest. Auk 109:321–333.

HOLMES, R. T., P. P. MARRA, AND T. W. SHERRY. 1996. Habitat-specific demography of Black-throated Blue Warblers (*Dendroica caerulescens*): implications for population dynamics. Journal of Animal Ecology 65:183–195.

HUK, T. AND W. WINKEL. 2006. Polygyny and its fitness consequences for primary and secondary female Pied Flycatchers. Proceedings of the Royal Society B 273:1681–1688.

JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651–661.

JOHNSON, S., L. H. KERMOTT, AND M. R. LEIN. 1993. The cost of polygyny in the House Wren *Troglodytes aedon*. Journal of Animal Ecology 62:669–682.

KEMPENAERS, B. 1994. Polygyny in the Blue Tit: unbalanced sex ratio and female aggression restrict mate choice. Animal Behavior 47:943–957.

KENDRICK, S. W. 2012. Winter bird densities and Eastern Wood-Pewee breeding demography across a savanna-

woodland-forest gradient in the Missouri Ozarks. Thesis, University of Missouri, Columbia, USA.

MATTHEWS, S., R. O' CONNOR, L. R. IVERSON, AND A. M. PRASAD. 2004. Atlas of climate change effects on 150 bird species of the Eastern United States. USFS General Technical Report NE-318. USDA Forest Service, Newtown Square, PA, USA.

MAYFIELD, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

MCCARTY, J. P. 1996. Eastern Wood-Pewee (*Contopus virens*). The birds of North America. Number 245.

MITRUS, C. AND B. SOCKO. 2005. Polyterritoriality and the first record of polygyny in the Red-breasted Flycatcher *Ficedula parva* in a primeval forest. Acta Ornithologica 40:170–172.

MULVIHILL, R. S. 1993. Using wing molt to age passerines. North American Bird Bander 18:1–10.

MULVIHILL, R. S., A. CUNKELMAN, L. QUATTRINI, T. J. O'CONNELL, AND T. L. MASTER. 2002. Opportunistic polygyny in the Lousiana Waterthrush. Wilson Bulletin 114:106–113.

MULVIHILL, R. S., S. C. LATTA, AND F. L. NEWELL. 2009. Temporal constraints on the incidence of double brooding in the Louisiana Waterthrush. Condor 111:341–348.

MUMFORD, R. E. 1964. The breeding biology of the Acadian Flycatcher. University of Michigan Museum of Zoology Miscellaneous Publications, 125. Ann Arbor, MI, USA.

NAGY, L. R. AND R. T. HOLMES. 2005. To double-brood or not? Individual variation in the reproductive effort in Black-throated Blue Warblers (*Dendroica caerulescens*). Auk 122:902–914.

NEWELL, F. L. AND A. D. RODEWALD. 2011. Role of topography, canopy structure, and floristics in nest-site selection and nesting success of canopy songbirds. Forest Ecology and Management 262:739–749.

NEWELL, F. G. AND A. D. RODEWALD. 2012. Management for oak regeneration: short-term effects on the bird community and suitability of shelterwood harvests for canopy songbirds. Journal of Wildlife Management 76:683–696.

NEWTON, J. 1989. Lifetime reproduction in birds. Academic Press, London, UK.

ORIANS, G. H. 1961. The ecology of blackbird (*Ageliaus*) social systems. Ecological Monographs 31:285–312.

PEARSON, T., M. J. WHITFIELD, T. C. THEIMER, AND P. KEIM. 2006. Polygyny and extra-pair paternity in a population of Southwestern Willow Flycatchers. Condor 108:571–578.

PETIT, L. J. 1991. Experimentally induced polygyny in a monogamous bird species: Prothonotary Warblers and the polygyny threshold. Behavioral Ecology and Sociobiology 29:177–187.

PETRIE, M. AND M. LIPSITCH. 1994. Avian polygyny is most likely in populations with high variability in heritable male fitness. Proceedings of the Royal Society of London 256:275–280.

PRESCOTT, D. R. 1986. Polygyny in the Willow Flycatcher. Condor 88:385–386.

PRIBIL, S. AND W. A. SEARCY. 2001. Experimental confirmation of the polygyny threshold model for Red-winged Blackbirds. Proceedings of the Royal Society of London, B. 268:1643–1646.

PYLE, P. 1997. Identification guide to North American birds. Slate Creek Press. Bolinas, California, USA.

R DEVELOPMENT CORE TEAM. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

SECUNDA, R. C. AND T. W. SHERRY. 1991. Polyterritorial polygyny in the American Redstart. Wilson Bulletin 103:190–203.

SEDGEWICK, J. A. AND F. L. KNOPF. 1989. Regionwide polygyny in Willow Flycatchers. Condor 91:473–475.

SKAUG, H., D. FOURNIER, A. NIELSEN, A. MAGNUSSON, AND B. BOLKER. 2012. Generalized Linear Mixed Models using AD Model Builder. R package version 0.7.4.

SMALL, D. M., M. E. GIMPEL, J. PARKS, J. B. GUERARD, AND D. E. GILL. 2009. First documented cases of polygyny in the Grasshopper Sparrow. Wilson Journal of Ornithology 121:822–825.

SMITH, J. N. M., Y. YOM-TOV, AND R. MOSES. 1982. Polygyny, male parental care, and sex ratio in Song Sparrows: an experimental study. Auk 99:555–564.

STEARNS, S. C. 1992. The evolution of life histories. Oxford University Press, New York, USA.

VEDDER, O., J. KOMDEUR, M. VAN DER VELDE, E. SCHUT, AND M. J. L. MAGRATH. 2011. Polygyny and extra-pair paternity enhance the opportunity for sexual selection in Blue Tits. Behavioral Ecology and Sociobiology 65:741–752.

VEGA RIVERA, J. H., C. A. HAAS, J. H. RAPPOLE, AND W. J. MCSHEA. 2000. Parental care of fledgling Wood Thrushes. Wilson Bulletin 112:233–237.

VERHULST, S. 1998. Multiple breeding in the Great Tit, II. The costs of rearing a second clutch. Functional Ecology 12:132–140.

VERHULST, S., J. M. TINBERGEN, AND S. DAAN. 1997. Multiple breeding in the Great Tit. A trade-off between successive reproductive attempts. Functional Ecology 11:714–722.

VERNER, J. AND M. F. WILLSON. 1966. The influence of habitats on mating systems of North American passerine birds. Ecology 47:143–147.

WEATHERHEAD, P. J. AND R. J. ROBERTSON. 1979. Offspring quality and the polygyny threshold: ''the sexy son hypothesis.'' American Naturalist 113:201–208.

WINGFIELD, J. C. 1984. Androgens and mating systems: testosterone-induced polygyny in normally monogamous birds. Auk 101:665–671.

WOLFE, J. D. AND C. J. RALPH. 2009. Correlations between El Niño-Southern Oscillation and changes in Nearctic-Neotropical migrant condition in Central America. Auk 126:809–814.

WOLFE, J. D. AND B. I. FREY. 2011. Primary covert replacement patterns in the Western Wood-Pewee. North American Bird Bander 36:113–115.