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Facultative polygamy may influence post-fledging movements in a brood-splitting passerine

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Abstract

Animal space-use patterns can vary widely with age, sex, and stage of the annual cycle, but the factors that drive pattern shifts are poorly understood. Here, we provide preliminary evidence that mating strategy (*i.e*., polygamy) influences movements of parents attending recently-fledged young. We monitored the space-use during the post-fledging period for *Vermivora* spp. broods led by a male and female with a split brood in 2014 and the same male with 2 fledglings in 2015. We observed context- and sex-specific space use patterns that seemed to be driven by the male's attention to a secondary polygamous nest in 2014. When attending his secondary nest, the male restricted his primary brood's movements to within the nesting habitat close to his secondary nest until the nest failed. This pattern was distinct from movements of both the 2014 female and the same male in 2015 when he lacked a secondary nest. These observations may explain some reports from other studies that female-led broods disperse farther than male-led broods. Future work should explicitly consider the potential impacts of facultative polygamy on post-fledging space-use, especially in species traditionally considered monogamous.

Keywords: brood splitting, movement, polygamy, post-fledging, space-use, *Vermivora*

Habitat and space use often varies with breeding status and stage (Werner and Gilliam 1984), and this has been described for a variety of taxa including mammals (Adams 1996), fish (Werner and Gilliam 1984, Knip et al. 2011), squamate reptiles (Paulissen 1988), and even invertebrates (With 1994). The underlying causes of these shifts have been difficult to ascertain, particularly for small-bodied species, but recent advances in tracking technology have made possible more detailed examinations of space-use patterns of songbird fledglings (Barron et al. 2010, Cox et al. 2014), such as the Golden-winged Warbler *Vermivora chrysoptera* (8-9 g, Frantz et al. 2016). Because space-use patterns during the post-fledging period are frequently associated with movement away from nest site (Kreshner et al. 2004), habitat shifts (Anders et al. 1998, Vitz and Rodewald 2011), and low survival rates (Yackel Adams et al. 2006), understanding the factors motivating post-fledging movements have important conservation implications

Most studies of post-fledging movements suggest that spatial patterns result from individuals selecting habitats that promote survival of young, but alternative hypotheses have seldom been examined (McDermott and Wood 2010). One possibility is that post-fledging space-use reflects parental decisions that may be affected by multiple factors. For brood-splitting species, male-led broods may exhibit different space-use patterns than female-led broods (Nolan 1978, McLaughlin and Montgomerie 1985, Rush and Stutchbury 2008, Peterson et al. 2016). Moreover, species that exhibit facultative polygamy may also lead sub-broods differently depending on their mating-status (monogamous, polygamous, etc.; Peak et al. 2010). Given the level of complexity associated with space-use patterns for any species, motivations for making particular movement choices often remain unclear. In this paper, we report observations

of space-use patterns by 3 post-fledging sub-broods of a *Vermivora* spp. Warbler: one led by a female in 2014 and 2 led by a single male: in 2014 while attending a secondary nest and 2015 when he did not. We discuss these observations within the context of post-fledging space use by passerine birds, and consider the implications with respect to mating and parenting strategies.

Methods

In 2014-15, we studied movement ecology of *Vermivora* spp. nesting within early-successional forest patches created through silviculture within the Delaware State Forest of Pike and Monroe Counties in northeastern Pennsylvania, US. As part of a larger study, we banded resident *Vermivora* males with USGS aluminum bands and 1-3 colored plastic leg bands and monitored *Vermivora* nests at 2-4 day intervals. *Vermivora* are typically socially monogamous though polygamy has been reported (Confer et al. 2011), and young usually fledge at 8 days of age (Confer et al. 2011). Brood splitting is almost ubiquitous in *Vermivora* (Peterson et al. 2016), and sub-broods regularly – though not always - move from nesting habitat types (early-successional forest) to non-nesting habitat types (*e.g.*, older forest seral stages; Streby et al. 2016) during the post-fledging period. Young are nutritionally independent from parents ~25-30 days post-fledging (Streby et al. 2016).

We attached radio-transmitters to 2 random nestlings from each nest 1 day prior to fledging or early on the day of fledging. Radio transmitters were attached using a figure-eight harness (Rappole and Tipton 1991) and the combined mass of transmitter/harness was < 5% of the fledglings' mass (Fair et al. 2010). Upon fledging, we tracked each juvenile warbler/parent family unit each day using the homing method and collected location information using a hand-held GPS unit (Garmin eTrex 20, Garmin Ltd., Olathe KS). At each fledgling location we

recorded habitat cover type, sex of attending parent, and general fledgling behavior (*e.g.*, begging, foraging, etc.).

Observations

On 7 June 2014, we located a *Vermivora* nest along the edge of a timber harvest that was tended by an un-banded Golden-winged Warbler female (hereafter, "Female A") and a hybrid male ("Brewster's Warbler" phenotype) banded previously in the study (band no.: 2520-97742; hereafter, "hybrid male"). Female A's nest contained 5 hatchlings that were 1 day-old when first discovered. We monitored the nest until 15 June, when 2 nestlings were fitted with radio transmitters prior to fledging. The 2 marked fledglings (hereafter: "Fledgling A", and "Fledgling B") were located outside the nest the next day (day 1 post-fledging) and remained within 50 m of the nest through day 2 post-fledging when the brood was divided. Fledgling A was under the care of the hybrid male and Fledgling B was under the care of Female A. By day 3 post-fledging, the parents separated broods and traveled in different directions. Female A and Fledgling B entered the nearby closed-canopy forest whereas the hybrid male and Fledgling A remained within the timber harvest nesting habitat.

By day 4 post-fledging, the hybrid male led Fledgling A 166 m from the completed natal nest to an active nest (3 eggs) tended by a hybrid female *Vermivora* ("Brewster's Warbler" phenotype, hereafter, Female B). Over the next 12 days, the hybrid male regularly provisioned i) Fledgling A, ii) Female B and iii) Female B's nestling (hatch date: 28 June). Over this same period, Fledgling A (age: 4 – 15 days post-fledging) was a mean distance of 36 m from Female B's nest as the fledgling remained nutritionally-dependent upon the hybrid male's care. Also during this period, Female A and Fledgling B remained an average of 275 m from Female B's

nest. The final observation of Female B's nest where activity was confirmed by observers was 1 July 2014, after which time, the nest was depredated or abandoned (nest physically undamaged but dead nestling found 1-m away). After the failure of Female B's nest, we observed the hybrid male and Fledgling A directing space-use away from the failed nest location, and subsequent space use appeared unbiased by the nest's location after this time. Mean distance between the hybrid male/Fledgling A and Female B's nest after the last observed date of activity was 109 m (>3x the distance, pre-failure; Fig. 1). In contrast, Female A and Fledgling B remained a similar distance from Female B's nest, post-failure as they did pre-failure (mean post-failure: 285 m). Although both sub-broods travelled away from their natal nest location, the female-led sub-brood was on average 30% farther from the natal nest than was the male-led sub-brood. Moreover, Female A's sub-brood moved a mean distance of 122 m/day (SE: 18.28) over the post-fledging period whereas the hybrid male's sub-brood moved a mean distance of 86 m/day (SE: 12.73). Both fledglings (Fledgling A, Fledgling B) were successfully reared to independence.

On 31 May 2015, a primary nest tended by the hybrid male and an un-banded female Golden-winged Warbler was located (containing 5 eggs) within the timber harvest used in 2014. All 5 eggs were hatched and 2 nestlings were marked with radio transmitters 1 day before fledging. Upon fledgling, both marked juveniles (Fledglings "C" and "D") were under the provisioning care of the hybrid male. During the 2015 breeding season, the hybrid male was never observed tending any secondary nests. Consequently, we observed the hybrid male leading his 2015 brood into the adjacent closed-canopy forest, 1 day post-fledging. Fledglings C and D, because tended by the same parent, were typically found within 50 m of each other (Fig. 1). Unlike within the 2014 season when this male provisioned a secondary nest, the hybrid male's 2015 brood movement resembled those of Female A and her 2014 brood: patterns were

characterized by overall mean daily movements distances of 160 m (SE: 24.64) directed away from the nest site (Fig. 1). The distance the male moved his sub-brood in 2014 (mean: 86 m) were about half the mean distance in 2015 (160 m) when a secondary brood was provisioned.

Discussion

Our observations of a male *Vermivora* warbler biasing post-fledging movements around a secondary nest provide insight into sex-specific differences in post-fledging movements. Previous studies have reported that females often travel farther from the nest site with sub-broods than do males (Nolan 1978, McLaughlin and Montgomerie 1985, Rush and Stutchbury 2008, Peterson et al. 2016). Our observations suggest that males may constrain movements by ~50% when attending secondary nests. Because *Vermivora* spp. limit most extrapair copulations to ~100 m from their own nesting territories (Vallender et al. 2007), we expect that polygamous males attending both primary fledgling broods and secondary females/broods to remain closer to their primary territories (and nearby extrapair matings) during this portion of the post-fledging period. Post-fledging and brood movements generally are thought to be driven by predation risk, adult foraging efficiency, and juvenile foraging development (Harper 1985, McLaughlin and Montgomerie 1985, Byle 1990). However, our observations suggest that post-fledging movements also may be shaped by polygamy, an explanation that has not been previously reported in the literature.

While most wood warblers of Parulidae are socially monogamous, polygamy has been previously described for a handful of species within the family (Stewart 1953, Ford 1983, Secunda and Sherry 1991, Peak et al. 2010), including Golden-cheeked Warbler (*Setophaga chrysoparia*, Peak et al. 2010), Common Yellowthroat (*Geothlypis trichas*, Stewart 1953), and

American Redstart (*S. ruticilla*, Secunda and Sherry 1991). Although prevalence of obligate and facultative are poorly documented, Ford (1983) detailed > 55 North American passerine species known to engage in polygamy and noted that a similar number of species had been reported in Palearctic systems. For promiscuous species, sires generally provide fertilization without parental investment (Ford 1983, Westneat and Stewart 2003). Socially monogamous birds that regularly engage in polygamy, in contrast, may provide some level of parental care to secondary females and young (Martin 1974, Slagsvold and Lifjeld 1994, Confer et al. 2011). For many Parulids, polygamy may be relatively common within some populations (*e.g.*, 16% of males; Secunda and Sherry 1991), even approaching the 20% threshold set by Ford (1983) for defining "truly polygamous" populations (also see Vernor and Wilson 1969). That said, the extent of polygamy can vary widely across years (Secunda and Sherry 1991) and sites (Verner 1964). *Vermivora* typically have only a single social mate and thus are not considered to be truly polygamous (Vallender et al. 2007). However, polygamous behavior occurs fairly regularly (at least 3% of males; Confer et al. 2011), and the species is best considered "facultatively polygamous" (Ford 1983). Our study sites supported at least 1 male *Vermivora* engaging in polygamy annually (2012-14; McNeil, unpub. data), which when adjusted for breeding densities (5 – 8 males per year; McNeil, unpub. data) suggests polygamy rates ranging from 13 – 20%. Future work examining the relationship between i) species likelihood of splitting broods and ii) species rates of polygamy would be valuable toward exploring this topic further.

Given that facultative polygamy may be fairly common in Parulids, it seems surprising that few studies on post-fledging movement ecology report its impact on sub-brood movement (King et al. 2006, Rush and Stutchbury 2008, Streby et al. 2016). While our observation is not the first report of a facultatively polygamous species dividing parental duties between primary fledglings

and secondary nestlings (Peak et al. 2010), we are the first to report an association between polygamy and post-fledging movements of a facultatively polygamous passerine. Given the increasing prevalence of avian post-fledging studies (Cox et al. 2014), we propose that future studies of post-fledging movement ecology explicitly consider the effects of polygamy on sub-brood space-use.

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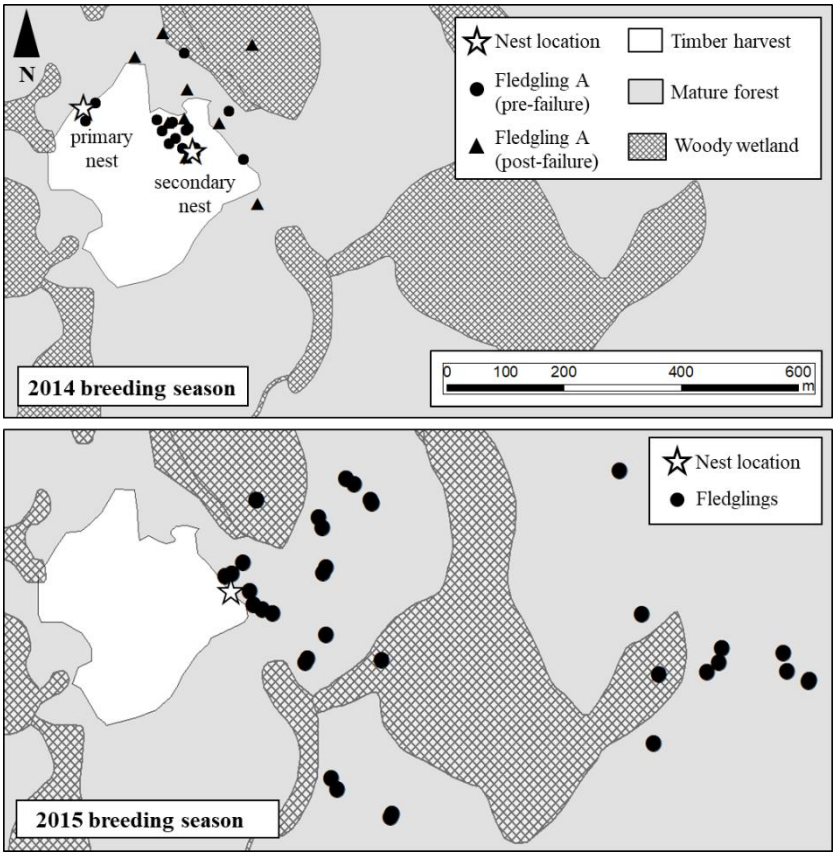

Figure 1. Daily locations of 2 sub-broods of a hybrid male *Vermivora* sp. in a year when the male attended a secondary nest (2014; top) and in a year when no polygamy was observed for the male (2015; bottom). In 2014, the male reared a single fledgling to independence ("Fledgling A"). In 2015, the male reared 2 fledglings to independence.

Figure