Extra-territorial Movements by Eastern Whip-poor-wills

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Abstract

In the course of conducting research into the habitat use of the Eastern Whip-poor-will (Antrostomus vociferus), I discovered two males that did not follow the typical pattern of remaining within a restricted territory during the breeding season. Over a six week tracking period, these two birds were detected at five different sites scattered across approximately 250 ha, with three of these sites being used by both birds at least once, sometimes simultaneously. Eight other males tracked in 2010-2012 never exhibited this wandering behavior, and instead remained faithful to territories of 1-12 ha (mean = 4.8). Because male Eastern Whip-poor-wills share in incubation and brooding duties, I assume that neither male had successfully obtained a mate. The reasons for this extra-territorial behavior remain unknown.

INTRODUCTION

Although the terms "territory" and "home range" are often used interchangeably, they do carry specific meanings that relate to their ecological function. A territory is generally defined as an area defended against conspecific intrusion, usually through some combination of vocalization, display, or physical interaction. In contrast, a home range is the area actually used by an individual (e.g., Naguib et al. 2001, Whitaker and Warkentin 2010). Home ranges can include locations outside the defended territory that are used for foraging or roosting and exclude areas within a territory that are not used, such as unsuitable habitat. Territories are usually represented by minimum convex polygons, whereas home ranges are defined by the intensity of use (e.g., through kernel analysis).

The Eastern Whip-poor-will (Antrostomus vociferus) is a crepuscular nightjar (Caprimulgiformes, Caprimulgidae) of open or disturbed forest habitats in the eastern United States and southern Canada. The species is socially monogamous, with males defending territories primarily through an onomatopoetic call. Both males and females share in incubation and brooding duties as well as in provisioning of young (Cink 2002, pers. obs.). In the context of the present study, I use the term territory because available data indicate that Eastern Whip-poor-wills restrict their activity to the area roughly delineated by calling locations (Cink 2002, Wilson 2003, Hunt unpubl. data). Although there is increasing evidence that home ranges may vary somewhat from territories as defined above (Hunt, unpubl. data), the overlap between the two is considerable. It is in the context of a traditional territory that the observations reported in this paper are the most intriguing.

METHODS

Study Site - Eastern Whip-poor-wills were studied in the Mast Yard State Forest in Hopkinton and Concord, Merrimack County, NH (43.239°N, -71.659°W). The state forest consists of 250 ha of primarily mature pine-oak forest dominated by white pine (Pinus strobus), red pine (P. resinosa), and northern red oak (Quercus rubra), with lesser amounts of pitch pine (P. rigida) and red maple (Acer rubrum). The understory is dominated by Vaccinium species. Embedded in the forest are several shrubby wetlands and areas of early successional habitat. The latter are the result of previous habitat management and are dominated by seedlings and saplings of the dominant tree species, plus extensive stands of aspen (*Populus* sp.) and birch (*Betula* sp.). Abutting the state forest on the north, east, and south are another 200 ha of both public and private lands of similar habitat that were also included in the study area, for a total area of approximately 450 ha. A 2000x100 m power line right-of-way passes through the eastern portion of the study site.

Telemetry - From 2010 to 2012, a total of 10 male whip-poor-wills were fitted with radio transmitters (Holohil BD-2: 1.5 g). Birds were caught in standard mist nets using a playback of conspecific calls, and transmitters attached using a modified leg harness design (Hallworth et al. 2009). Birds were tracked beginning at least 12 hr after transmitter attachment using a receiver and tri-element Yagi antenna. Locations were obtained both opportunistically (e.g., in the course of other research, or while tracking a different individual) and during longer periods when a single bird was tracked for one or more hours. In the latter cases, locations were obtained roughly every 10-15 minutes, or when the focal bird clearly shifted position. In cases where the bird moved, the interval between points was often longer due to the need to relocate the individual. Roost sites were usually determined upon arrival to the study site and prior to dusk, although a few were also found after dawn. When a bird's telemetry signal was detected, its location was estimated based on a combination of visual detection.

simultaneous auditory detection, and signal strength. For mapping purposes, locations were assigned low, moderate, or high confidence by the observer, and only the latter two categories used for habitat assessment. Low confidence locations are included in the discussion of extra-territorial movements because they provide valuable information on birds' movements away from the primary study area.

RESULTS

Data from the ten birds are summarized in Table 1. For eight of these, all locations consistently fell within a fairly well-defined territory, and birds were never detected outside of these core areas (Hunt, unpubl. data). In 2012, however, two individuals consistently left their territories for extended periods of time, as described below and in Table 2. Locations mentioned in these summaries are indicated by capital letters A-E as identified in Fig. 1. Note that the two birds were not monitored every day, and thus gaps or omissions in date ranges do not imply the bird's absence from a location, but merely the absence of data from that time period.

Table 1. Telemetry data for eight male Eastern Whip-poor-wills (two birds were tracked in two years) at Mast Yard State Forest, NH, in 2010-2012.

			Number of Locations ¹	
Bird ID	Date Range	# Days with Data	All	High Conf. ²
2010-2	25 May to 21 June	13	106	84
2010-3	28 May to 15 July	13	107	72
2011-2	30 May to 19 July	11	69	40
2011-3	6 June to 13 August	14	72	57
2012-4	24 May to 11 July	26	89	63
2012-5*	25 May to 19 July ³	12	44	14
2012-6 (= 2011-2)	26 May to 7 July	18	85	43
2012-7	1 June to 17 July	12	60	20
2012-8*	7 June to 17 July	21	96	69
2012-9 (=2011-3)	19 June to 8 August	18	72	45

^{*} Birds exhibiting extra-territorial behavior as described in this paper.

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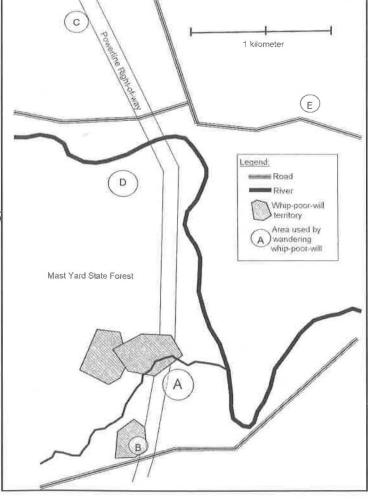
Table 2. Overview of movements and behaviors of two male Eastern Whip-poor-wills exhibiting extra-territorial behavior at Mast Yard State Forest, NH. The first date listed for each bird is the date of initial capture. See Fig. 1 for locations.

	Bird 2012-5			Bird 2012-8	
Date(s)	Area	Behavior	Area	Behavior	
25 May to 1 June	A	roost, nocturnal activity			
26 and 31 May	В	silent			
8-27 June		not detected	A	roost, nocturnal activity	
27 June		not detected	В	roost, then moved north of A and out of range	
28 June to 7 July		not detected	A	nocturnal activity	
7 July	С	roost, calling at dusk	Е	roost	
7 July	D	moved here after dusk, silent			
9-10 July	Е	roost, nocturnal activity	Е	roost, nocturnal activity	
12-19 July	В	roost, calling	Е	roost ²	
12-19 July	D	moved here after dusk, silent	A	nocturnal activity 2	

¹ Bird was not detected on 15, 18, and 25 June.

Fig. 1. Generalized map of the eastern portion of Mast Yard State Forest and surrounding area, showing locations used by two wandering Eastern Whip-poor-wills in the summer of 2012.

Letters refer to general areas used by birds 2012-5 and 2012-8 (see text and Table 2).



Jul. - Sep. 2016

Numbers of locations have not been adjusted to eliminate locations that were clearly auto correlated.

² High conf(idence) includes only those locations where the observer felt the bird was within 20 m of the recorded point, including exact locations based on visual detection.

³ Two discontinuous periods: 25 May to 1 June and 7-19 July.

² Actual end date for 2012-8 was 17 July.

Bird 2012-5-This individual was captured at A (Fig. 1) on 25 May, and roosted here on 26 May, 27 May, and 1 Jun. He was also present here well after sunset on 27 May. On 26 and 31 May he was found between midnight and dawn 0.5 km to the southwest at B, within the territory of a different radio-tagged whip-poor-will (2012-4). He disappeared from both A and B after 1 Jun, and scans for his radio frequency elsewhere in the study area failed to detect it. A whip-poor-will was still singing at the capture site however, suggesting that the transmitter had failed. In attempting to recapture 2012-5 I instead caught a new bird (2012-8, below), and assumed that 2012-5 had been a transient and had departed the study area.

In the course of following 2012-8 during the pre-dawn hours of 7 Jul. 2012-5 was relocated well to the north of the study area at C, approximately 2.5 km from where he was banded. More detailed observations the evening of that same day revealed his roost site. At sunset, 2012-5 called and moved around the roost area for about 10 minutes until the radio signal was lost again. The signal was relocated 1.3 km south of that day's roost, in a section of Mast Yard State Forest (D) where whip-poor-wills had not previously been detected. The bird was not calling at this location at this time. When next searched for on 9 Jul, 2012-5 was at neither C nor D, but was found at roost in a new area (E) 1.6 km east of D and 2.1 km northeast of A. He remained here through at least the evening of 10 Jul, but was not present the morning of 12 Jul.

Shortly after dusk on 12 Jul, 2012-5 was relocated to the south at B (2012-4 also still present). This was apparently a roost site, since after a brief bout of calling he moved north between 2100 and 2130 and eventually ended up back at D (1.6 km away). This pattern of roosting and calling in the south and shifting north after dark continued until 19 Jul, after which point the radio ceased transmitting or the bird completely departed the study area.

Bird 2012-8 - This bird was captured on 7 Jun in the same location as 2012-5 (A in Fig. 1). Until 26 Jun he generally exhibited typical territorial behavior in this area: roosting there during the day and actively calling and foraging at night. On three occasions, however (after 2230 on 15 Jun, 2328 on 18 Jun, and 2305 on 25

Jun), his signal was not detected near A during incidental radio checks. Before sunset on 27 Jun he was located roosting 0.5 km south at B, where 2012-5 had been in late May. After departing the roost, he spent a brief period calling at A before continuing north and out of receiving range. From this point through 7 Jul, he was absent from both A and B during roost checks but present at A during the normal evening activity period. On 3 Jul he was again detected north of his usual territory shortly after sunset.

In an attempt to determine this bird's location during the day, we tracked him immediately prior to sunrise on 7 Jul, again finding him heading north from A. He ended up roosting at E, roughly 2.1 km to the northeast of his territory. He was found only here (along with 2012-5) through the evening of 10 Jul, and still present the morning of 12 Jul. He had returned to his original territory (A) by the evening of 12 Jul, and through 17 Jul settled into a pattern of being active at night at A and returning to roost at E during the day. He was not detected after 17 Jul, at which point the transmitter was assumed to have failed.

Four of the five areas used by these two birds were in habitats typically used by the species in NH. Locations A, B, and C were in mixed pine-oak forest adjacent to a shrubby powerline right-of-way, and E was in an area of forest bordering two open fields. In contrast, location D was in the mature pine-oak matrix forest of Mast Yard State Forest, a habitat disproportionately avoided by territorial males (\sim 30% of habitat within territories vs. \sim 75% of entire study site; Hunt, unpubl. data). The habitat within the core territory of 2012-8 (location A) was split roughly evenly between mature pine-oak and low shrubs (the right-of-way).

DISCUSSION

The behavior of whip-poor-wills 2012-5 and 2012-8 was completely unlike any other birds in the study area (Hunt, unpubl. data) and to the best of my knowledge has not previously been reported for the species (Mills 1986, Cink 2002, Wilson 2003, P. English pers. comm.). There is evidence of similar extra-territorial movements in the European Nightjar (*Caprimulgus europaeus*), although these appear primarily for foraging purposes and the birds involved all remained

associated with a nest site for the bulk of their activity (Alexander and Cresswell 1990). Because male whippoor-wills share incubation and brooding duties with females, extended absences from a core territory clearly indicate that neither bird successfully bred in 2012. It is also likely that neither male obtained a mate, which was independently suspected for 2012-8 based on his elevated singing rates well into June.

This behavior is similar to that exhibited by "floaters" in territorial songbirds (Whitaker and Warkentin 2010, Lenda et al. 2012), except that floaters typically do not maintain territories. It also resembles the behavior of mated males seeking extra-pair copulations (e.g. Norris and Stutchbury 2001) with females in neighboring territories, or birds foraging at more distant locations (Whitaker and Warkentin 2010), although in both cases males are mated and associated with a nest site. The shift from territorial to wandering behavior observed in whip-poor-wills is typical of unmated males in several species. Churchill and Hannon (2010) documented two yearling male American Redstarts (Setophaga ruticilla) that briefly defended territories before becoming floaters. Mated males also left territories, in which cases they were either silent (when in a neighboring male's territory) or actively singing (when in an unoccupied area), but they retained their connection to their core territory throughout the breeding season. In a long-term study of Ortolan Buntings (Emberiza hortulana) in Norway, Dale et al. (2006) documented multiple cases of within-breeding season long-distance movements. Birds usually moved from one traditional territory to another, with up to four patches visited in the course of a season. These movements appeared to be in response to either a failure to attract a mate, or the loss of a mate or nest in the original territory. The closest other documentation of such multisite behavior comes from a study of Scarlet Tanagers (Piranga olivacea) in a fragmented forest landscape (Fraser and Stutchbury 2004). In this study, unmated males exhibited two strategies: 1) sedentary with high song rates and 2) mobile with multiple singing sites, neither of which is typical of floaters as usually characterized (i.e., they do not sing).

The extraterritorial movements of the two male Eastern Whip-poor-wills in the present study share some features of all the preceding examples. First, the birds

were presumed unmated, which freed them up to undertake such movements in the first place. Secondly, they performed territorial behaviors (e.g., calling) at some of the extra-territorial sites. In the case of 2012-8, the bird retained a connection to its original territory for most of the season, which is analogous to the redstarts of Churchill and Hannon (2010). Male 2012-5 is most similar to the Scarlet Tanagers, in that he had multiple sites, some of which were repeatedly visited over the course of the season. Neither bird followed the pattern of sequential territories observed in Ortolan Buntings.

Another similarity between these whip-poor-wills and typical extraterritorial birds is that both were known to spend time in the territory of a known mated male (2012-4). Intrusions by unmated males into this territory may have represented attempts to mate with the female, although most of the behavior occurred late in the breeding season. Alternatively, the wandering males may have been prospecting for future territories (e.g., Lenda et al. 2012) and using the presence of a female as an indicator of higher quality habitat. Similar behavior, wherein multiple apparently non-breeding males are found in the vicinity of active nests, has been observed in Common Nighthawks (Chordeiles minor, R. Suomala pers. comm.). However, neither whippoor-will in the present study was ever detected in a second neighboring territory with a mated pair (northwest of area A in Fig. 1).

One important deviation from typical extraterritorial behavior was 2012-5's overnight use of a portion of the study area (D) where whip-poor-wills were never detected over the five years of habitat-use research. This bird was never detected singing at that location, suggesting that his use of the site was not associated with attempts to find a mate. The behavior of 2012-5, in general, is highly unusual, given the number of sites used in a short amount of time, highly variable behavior among sites, and the fact that the bird went undetected for over a month. He may have been prospecting over an even larger area, only to circle back to where he started toward the end of the season.

In general, the extraterritorial behavior shown by two male whip-poor-wills in this study is most consistent with their attempting to find mates. There are no data on the numbers of whip-poor-wills, or their mating status, at the two peripheral sites found during this study. So while mate-seeking is likely involved, the overall pattern of habitat use by these birds may also be influenced by additional factors that would require further investigation. Still in need of explanation is the congruence of the two birds' specific locations, including co-habiting the same remote site for multiple days. The latter suggests that some form of conspecific attraction could be involved, a pattern borne out by the dispersion of whippoor-will territories at Mast Yard over the five-year study period (Hunt, unpubl. data).

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Eastern Whip-poor-will by George West