BioOne COMPLETE

Spatial Ecology of Migratory Passerines on Temperate and Boreal Forest Breeding Grounds

Authors: Whitaker, Darroch M., and Warkentin, Ian C.

Source: The Auk, 127(3) : 471-484

Published By: American Ornithological Society

URL: https://doi.org/10.1525/auk.2010.127.3.471

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

The Auk

An International Journal of Ornithology

Vol. 127 No. 3 July 2010



The Auk 127(3):471–484, 2010

© The American Ornithologists' Union, 2010.

Printed in USA.

PERSPECTIVES IN ORNITHOLOGY

SPATIAL ECOLOGY OF MIGRATORY PASSERINES ON TEMPERATE AND BOREAL FOREST BREEDING GROUNDS

DARROCH M. WHITAKER[1] AND IAN G. WARKENTIN[2,3]

[1]*Gros Morne National Park of Canada, P.O. Box 130, Rocky Harbour, Newfoundland and Labrador A0K 4N0, Canada; and*
[2]*Environmental Science—Biology, Memorial University of Newfoundland, Corner Brook, Newfoundland and Labrador A2H 6P9, Canada*

THE USE OF space reflects individual access to resources that are critical to survival and reproduction. Consequently, space use should be sensitive to a range of factors that have the potential to profoundly influence populations (e.g., Whitaker et al. 2007). The territory is one measure that has been employed to assess avian space use in the context of access to resources. In her seminal paper entitled "The Role of Territory in Bird Life," Margaret Morse Nice (1941) synthesized a then long-running discussion on patterns of space use by birds into a functional classification system for the types of territories used by various species. Among these was her "Type A" territory, which referred to a defended area used for mating, nesting, and as a feeding site for young; such territories are maintained by most breeding passerines and other noncolonial bird species that have socially monogamous breeding systems (Nice 1941). The territory has since been widely accepted as the fundamental unit of space use for most passerine species (e.g., Morse 1989, Barg et al. 2005, Fisher and Davis 2010), and the concept of the home range, which may include both defended and undefended areas, has been notably absent from many discussions of passerine spatial ecology (e.g., Cody 1981, Haila et al. 1996, Cornell and Donovan 2010a; see also many species accounts in Poole 2005). In large part, this is because technological limitations required, until recently, that most studies of space use employ passive methods, such as territory mapping, that focus on the visual observation of prominently displaying males (Bibby et al. 2000). However, this focus may have led to an incomplete understanding of space use if individuals make extensive movements beyond surveyed territorial areas into a broader home range, are nonterritorial (e.g., during the postbreeding period), or behave cryptically or are not equally detectable throughout the area they frequent.

Findings linked to recent technological progress and our growing knowledge of diverse aspects of avian ecology highlight the need to develop a more comprehensive understanding of passerine spatial ecology. Leading the way was the application of molecular genetics techniques to the study of avian breeding systems. This research revealed that extrapair mating was a regular occurrence in the vast majority of passerine species (Griffith et al. 2002), overturning assumptions that most socially monogamous birds were also sexually monogamous (Lack 1968). Because extrapair mates typically originate beyond territorial boundaries, this finding stimulated research into extraterritorial movements related to extrapair mating effort (e.g., Yezerinac and Weatherhead 1997, Stutchbury 1998, Woolfenden et al. 2005). During the same period, research in landscape ecology has revealed that individuals of many species are sensitive to habitat factors that occur beyond their territorial boundaries or at a scale larger than that of the territory (e.g., Hinsley et al. 1995; Betts et al. 2006, 2007). Similarly, ongoing research on other aspects of avian ecology, including dispersal, metapopulation dynamics, heterospecific attraction, and social information theory, has also led to greater understanding and recognition of the importance of extraterritorial movements by individuals, as well as interactions among birds distributed across a landscape (e.g., Hanski 1999, Walters 2000, Betts et al. 2008a). Field studies associated with these advances have been greatly facilitated by the development of miniaturized radiotransmitters, which allowed researchers to overcome many logistical hurdles that had hindered the collection of unbiased movement data. Use of radiotracking immediately demonstrated that individuals of some species make regular landscape-scale or extraterritorial movements (e.g., Hanski and Haila 1988, Williams 1990,

[3]Address correspondence to this author. E-mail: iwarkent@swgc.mun.ca

The Auk, Vol. 127, Number 3, pages 471–484. ISSN 0004-8038, electronic ISSN 1938-4254.

© 2010 by The American Ornithologists' Union. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, http://www.ucpressjournals.com/reprintInfo.asp.

DOI: 10.1525/auk.2010.127.3.471

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Smiseth and Amundsen 1995), and studies that explicitly distinguish territorial areas defended by singing males from their more expansive home ranges are beginning to appear (e.g., Leonard et al. 2008, Anich et al. 2009).

Information now available offers the hope of a more comprehensive and accurate understanding of the spatial ecology of breeding passerines. On the basis of recent research, we propose a model of space use in which individuals occupy defended territories embedded within potentially broader, multipurpose home ranges (Powell 2000) that are extensively traveled and for which they have a detailed cognitive map. However, there remains a substantial lack of basic knowledge regarding the overall spatial ecology of breeding passerines. Thus, our review focuses on recent research that provides insight into space use by passerines from the prebreeding through premigratory periods. Building on this, we offer general observations on the nature of passerine space use, assess the extent to which socially monogamous passerines use areas beyond the boundaries of their territories, and suggest some important future directions for research involving passerines and for conservation in temperate and boreal forests.

The Prenesting Period

Many migrants arrive at sites of higher latitude or altitude several weeks in advance of breeding (Benson and Winker 2001, Hahn et al. 2004, Hahn and Silverman 2007). Early arrival is associated with securing limited nest sites, high-quality territories, or mates (Francis and Cooke 1986, Cooper et al. 2009a), but availability of insect foods and favorable microclimates may be unpredictable at this time. For example, during late May and early June 2004, the weather was cold and wet at our study site in the mountains of western Newfoundland. Yellow-rumped Warblers (*Dendroica coronata*), among the first migratory songbirds to arrive at our study area, were dispersed throughout the landscape and singing on territory during warm days. However, inclement weather, including late snowfalls, was a regular occurrence in the area until mid-June, and during such conditions these warblers retreated to low-lying alluvial fens to forage on the ground; at these times, aggregations of up to 100 individuals were observed. Eventually, the weather warmed enough that birds were able to remain on their breeding territories, though nesting was delayed by approximately 9 days that year (Dalley et al. 2009). Limited attention has been paid to the ecology of migratory birds during the prebreeding period, but, as this anecdote suggests, there may be considerable stress on returning birds and local refugia may be important at this time (Morton 2002, Hahn et al. 2004; see also Williams 1990). Consequently, patterns of space use during the prebreeding period may differ in many important ways from those in the rest of the breeding season. For example, one could argue that if individual birds know the locations of such refugia and use them as needed, then these areas comprise very real and overlapping components of their individual home ranges (Powell 2000), even though such sites may not be visited during years with favorable spring weather. In addition, newly arrived birds must seek out available sites and establish a breeding territory, find a mate, and gather knowledge about the distribution, breeding status, and quality of neighboring conspecifics for possible use during future extrapair mating efforts (Hahn and Silverman 2006, Betts et al. 2008b). These activities require an extensive cognitive map of the landscape (e.g., Double and Cockburn 2000), which makes this a potentially important period for gathering and using information about the distribution of resources in the landscape.

Although it has been suggested that young birds search for future breeding sites during the postfledging period (i.e., from leaving the nest until departure on migration; Reed et al. 1999), some species postpone prospecting for breeding sites until their first breeding season (Reed and Oring 1992). The focus during such exploration may well be the presence of conspecifics, both for the inherent social message that their presence conveys regarding habitat quality (Nocera et al. 2009) and for their potential future importance in species with dispersed-lek breeding systems (Wagner 1998, Tarof et al. 2004). During natal dispersal, an optimal strategy may well involve returning to the natal site and then searching outward from that location to find suitable habitat, using singing males as a cue (Dale et al. 2005, Winkler et al. 2005). Clearly, the same social cues may be used by adults seeking new breeding opportunities (breeding dispersal) during the prebreeding, breeding, and postbreeding periods (Lang et al. 2002, Dale et al. 2005, Hahn and Silverman 2006).

As a result of the various factors affecting establishment, male territories are not static from initial establishment on arrival but can shift over time until settlement cues, such as the arrival of females in Cerulean Warblers (*D. cerulea*), signal the shift to breeding activities (Barg et al. 2005). This prebreeding period may last several weeks (Woolfenden et al. 2005) but can be shorter, depending on the degree of synchrony in arrival times between males and females (Roth et al. 1996). Hubalek (2001) indicated that the habitat associations of migratory songbirds differed during the prebreeding and breeding periods, and Dall et al. (2005) suggested that the capacity to shift territory location in response to changing perceptions of habitat quality may well be a common strategy during the prebreeding period. Betts et al. (2008b) have identified "apparent movement" in the prebreeding period, when males shift from initial locations to higher-quality sites as more information on habitat quality emerges and other individuals vacate sites as they also find better locations. It may also be that information is not immediately or readily available (Stamps 2006) and it takes time to collect appropriate information by assessing food resources (Rodenhouse et al. 2003) or monitoring the initial productivity of early breeders, which are typically the older, more experienced individuals that arrived first (Holmes et al. 1996). Cardinal (2005) found that prebreeding Southwestern Willow Flycatchers (*Empidonax trailli extimus*) held defended territories within home ranges that were highly variable in area but significantly larger, overall, than those in the breeding season (Table 1). Flycatchers that initially occupied multiple habitat patches separated by as much as 800 m were individuals that had not previously been encountered in the study area, whereas the prebreeding home ranges of returning flycatchers tended to be substantially smaller. This points to experience as a factor affecting space use during the prebreeding period.

The Nesting Period

A defining aspect of space use during the nesting period is that the movements of breeding birds must remain centered on their

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Table 1. Estimated mean (± SE) sizes of defended territories and home ranges, mean and maximum extraterritorial movement (ETM) distances and durations, and percentage of time spent off territory (percent ETT) for male temperate and boreal passerines monitored via radiotracking during the prebreeding and breeding periods. Scientific names not listed below are given in the text.

Species[a]	*n*	Stage[b]	Territory (ha)	Home range (ha)	ETM distance (m)	ETM duration (min)	Percent ETT	Source
Acadian Flycatcher (CF–P)		P–I	≈1	—	202, 1,500	10.2, 60	7.4	Woolfenden et al. 2005
Southwestern Willow Flycatcher (FF–U)	6	P	—	11.4 ± 10.8	178, 410[c]	—	—	Cardinal 2005
Southwestern Willow Flycatcher (FF–P)	12	L–N	—	0.4 ± 0.1	46, 85[c]	—	—	Cardinal 2005
Wood Thrush (CF–P)	41	P–N	—	—	107, 624	—	—	Lang et al. 2002
Wood Thrush (CF–P)	4	L	2.4 ± 0.8[d]	—	67, 350	7, 15	—	Evans et al. 2008
Wood Thrush (CF–P)	9	I	2.4 ± 0.8[d]	—	95, 200	12, 33	—	Evans et al. 2008
Blackpoll Warbler (FF–P)	35	P–F	3.0 e	4.3[e]	405, 1,448	—	—	Leonard 2007, Leonard et al. 2008
American Redstart (FF–P)	19	L–N			104, 1,170	17, 110	18	Churchill and Hannon 2010
Swainson's Warbler (CF–P)	28	L–I	6.48 ± 1.2	9.38 ± 1.2	—	—	—	Anich et al. 2009
Ovenbird (FF–P)	21	I–F	—	1.95 ± 0.85	—	—	—	Mazerolle and Hobson 2003
Ovenbird (FF–P)	12	L–F	1.3 ± 0.79[d]	3.14 ± 1.33[d]	—	—	—	Bayne et al. 2005
Ovenbird (CF–P)	5	L–I	—	1.6 ± 0.4[d]	—	—	—	Bayne 2000
Ovenbird (FF–P)	12	L–I	—	1.8 ± 0.8[d]	—	—	—	Bayne 2000
Northern Waterthrush (FF–P)	30	P–F	4.3[e]	13.3[e]	358, 987	—	—	Leonard 2007, Leonard et al. 2008
Common Yellowthroat (CF–P)	13	L–I	—	—	—	5.9, 9	2.3	Pedersen et al. 2006
Hooded Warbler (CF–P)	10	P–I	—	—	—, 150	6.7, 18	4.7	Stutchbury 1998
Hooded Warbler (FF–UP)	20	P–N	—	—	405, 2,500	29, 151	16.5	Norris and Stutchbury 2001
Hooded Warbler (CF–P)	19	L–I	—	—	—	8.57, 16.50	—	Pitcher and Stutchbury 2000
Scarlet Tanager (FF–P)	17	L–N	—	6.0 ± 0.8	—	—	—	Vega Rivera et al. 2003
Scarlet Tanager (CF–P)	12	P–F	0.9 ± 0.2	—	106, —	—	4.7	Fraser and Stutchbury 2004
Scarlet Tanager (FF–P)	11	P–F	1.6 ± 0.3	—	173, —	—	5.7	Fraser and Stutchbury 2004
Scarlet Tanager (FF–U)	8	P–F	3.2 ± 0.9	122 ± 99	793, —	—	32.3	Fraser and Stutchbury 2004
Common Chaffinch (CF)[f]	9	P–N	≈0.5 ha	2–4	—	—	16	Hanski and Haila 1988, Hanski 1992
Nightingale (*Luscinia megarhynchos*) (FF–P)	12	P–N	5.4 ± 1.6	11.5 ± 1.3	160, 350	8, 13	8	Naguib et al. 2001

[a]Conditions experienced by monitored birds are indicated in parentheses: CF = continuous forest, FF = fragmented forest, P = paired, and U = unpaired.
[b]Stages of breeding season: P = prelaying, L = laying–fertile, I = incubation, N = feeding nestlings, and F = postfledging.
[c]Distances calculated as one half of the distance between the two most extreme locations.
[d]Standard deviation reported in source.
[e]Median value.
[f]Study conducted in Finland.

nest. This imposes a state of obligate fidelity to a central place that lasts, at a minimum, from the initiation of nest building, through egg laying and incubation, and until the young fledge and leave the nest. Over the past 20 years, researchers have increasingly employed radiotelemetry as a method to investigate the spatial ecology of passerines during the nesting period (e.g., Tables 1 and 2). These telemetry studies have demonstrated that, contrary to past concepts of spatial ecology, extraterritorial movements are a regular activity during the nesting period for both sexes of many passerine species. Breeding individuals have been observed from 2 to >25 territory diameters away from their own territories, spending from 2% to >50% of their time off territory, and in some cases making multiple extraterritorial moves per hour (Tables 1 and 2; see also Westneat 1988). However, these extraterritorial moves have often been referred to as "forays" (e.g., Stutchbury et al. 2005), which may reflect and perpetuate a perception that such movements are irregular or exceptional rather than commonplace.

The extent of off-territory movement has been corroborated by genetic studies that identified the paternity of extrapair young. Although such studies do not necessarily include direct monitoring of movements by individuals, they provide irrefutable evidence that some birds (potentially of both sexes) travel great distances off their territory during the fertile period to seek extrapair copulations. Although sires of extrapair young often occupy a neighboring territory, many are located two or three territories away, and some typically come from farther afield (Currie et al. 1998, Pedersen et al. 2006, Dolan et al. 2007). However, there are also examples of species in which the proportion of extrapair young sired by proximate neighbors is relatively small and some sires may well be from 10 or more territory-widths away (Woolfenden et al. 2005, Hung et al. 2009). As with resighting surveys, paternity studies necessarily have limited search areas and so are inherently biased against detecting distant extrapair sires at a scale greater than that of the most distal nests sampled (Koenig et al. 1996, Woolfenden et al. 2005). Consequently, they provide minimal estimates, and much larger movements may be occurring, as exemplified by Dolan et al. (2007), who documented a nestling Eastern Kingbird (*Tyrannus tyrannus*) that was sired by an extrapair male that occupied a territory >15 km away.

Extensive extraterritorial movements such as these are an important component of space use that went largely unrecognized before the advent of radiotelemetry. Most previous studies of the distribution and movements of breeding birds relied on passive techniques such as point counts, territory mapping, and mist netting to measure the distribution and movements of breeding birds (e.g., Ralph et al. 1995, Bibby et al. 2000). Surveys based on resightings are biased toward detecting territorial, displaying, or calling birds. In such research, intruders were likely to be identified as being of unknown origin or, worse, if individuals were not uniquely identifiable by sight, they may have been incorrectly identified as the territory holders. Furthermore, radiotelemetry studies have consistently reported that birds are typically silent and furtive during extraterritorial movements (e.g., Williams 1990, Neudorf et al. 1997, Mays and Ritchison 2004), which dramatically reduces their detectability and inevitably leads to underestimation of the incidence of territorial intrusions and extraterritorial movement in studies that employ passive techniques. Mark–recapture studies are less prone to these behavioral and misidentification biases but can detect movements only within a fixed and often relatively small study area, so the problems of reduced detectability of off-territory birds and underestimation of the scale of movement remain. The probability of failing to detect such extraterritorial movements increases with the scale at which such movements occur (Baker et al. 1995, Koenig et al. 1996), though some resighting surveys of color-banded individuals have yielded evidence that individuals regularly make large-scale extraterritorial movements. For example, male Northern Wheatears (*Oenanthe oenanthe*) made regular intrusions on territories up to 1.6 km from their own (Currie et al. 1998), and, at our study area in Newfoundland, >25% of resightings (4 of 15) of male White-throated Sparrows (*Zonotrichia albicollis*) were of individuals that were 1.1–2.8 km away from their territories (D. Whitaker unpubl. data).

Behavioral motivations for extraterritorial movements in the breeding season differ among species, between sexes, and with stage of breeding. We have already made reference to the role of such movements in extrapair mating systems, and much of the recent work on passerine spatial ecology has been directed at this subject (e.g., Stutchbury et al. 2005). However, extraterritorial movements also often include foraging activity, and, although it is true that most passerines forage almost continuously while active, in some cases individuals have been observed carrying food from off-territory foraging sites to feed nestlings (Zach and Falls 1979, Williams 1990, Fraser and Stutchbury 2004). Another potential benefit of moving off territory is the acquisition of socially derived information on the quality of habitat in the surrounding area (Reed et al. 1999, Bayne and Hobson 2001, Betts et al. 2008a). However, many extraterritorial movements are strongly focused on searching for potential mates and obtaining extrapair mating opportunities (Stutchbury 1998, Westneat and Stewart 2003, Humbird and Neudorf 2008), though our perception of the relative importance of this motivation may be somewhat exaggerated by the research interest this topic has generated. For males, the benefits of additional fertilizations may offset the potential risks of cuckoldry while they are off territory during periods when their mate is fertile, particularly when both breeding synchrony for the population and the potential to obtain extrapair matings are high (Birkhead and Møller 1992, Stutchbury et al. 2005). For females, benefits of extrapair mating are less apparent (Magrath et al. 2009, Townsend et al. 2010), but various studies indicate that female behavior will strongly influence this process through their choice of which visiting males they copulate with (Dolan et al. 2007, Webster et al. 2007) and the nature of their own off-territory movements (Smiseth and Amundsen 1995, Double and Cockburn 2000, Dolan et al. 2007, Chiver et al. 2008). Indeed, in some species, females have been found to select extrapair mates that are of equal or higher quality than their social mates, which suggests that mate choice is an important motivation (Smith 1988, Kempenaers et al. 1992, Stutchbury 1998). Females of some species may even monitor or incite encounters between intruding males and social mates to assess their relative quality (Neudorf et al. 1997, Currie et al. 1998, Stutchbury 1998).

In Acadian Flycatchers (*E. virescens*), only males make extraterritorial moves (Woolfenden et al. 2005, Hung et al. 2009), but both males and females of many other species visit adjacent territories on independent forays (Smiseth and Amundsen 1995, Neudorf et al. 1997, Pedersen et al. 2006). However, although extraterritorial

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

TABLE 2. Estimated mean (± SE) sizes of defended territories and home ranges, mean and maximum extraterritorial movement (ETM) distances and durations, and percentage of time spent off territory (percent ETT) for female temperate and boreal passerines monitored via radiotracking during the prebreeding and breeding periods. Scientific names not listed below are given in the text.

Species[a]	*n*	Stage[b]	Territory (ha)	Home range (ha)	ETM distance (m)	ETM duration (min)	Percent ETT	Source
Acadian Flycatcher (CF–P)	12	P–I	—	—	0	0	0	Hung et al. 2009
Wood Thrush (CF–P)	45	P–N	—	—	136, 539	—	—	Lang et al. 2002
Wood Thrush (CF–P)[e]	4	L	2.4 ± 0.8	—	113, 550	16, 60	—	Evans et al. 2008
Common Yellowthroat (CF–P)	15	L–I	—	—	—	29.2, 75	6.1	Pedersen et al. 2006
Hooded Warbler (CF–P)	14	P–I	≈1 ha	—	120, —	23, 56	15	Neudorf et al. 1997
Hooded Warbler (FF–P)	9	L–I	—	—	73, 130	29, —	4	Norris and Stutchbury 2002
Hooded Warbler (CF–P)	17	L	—	—	—	9.7, 14	3.5	Chiver et al. 2008
Yellow-breasted Chat (*Icteria virens*) (FF–P)	20	P–L	—	—	—	—	10	Mays and Ritchison 2004
Northern Cardinal (CF–P)	4	L	0.5	1.1	—	—	31	Humbird and Neudorf 2008
Northern Cardinal[d]	3	L	0.3	1.0	—	—	54	Humbird and Neudorf 2008
Scarlet Tanager (FF–P)	2	L–N	—	3.2 ± 1.0	—	—	—	Vega Rivera et al. 2003
Dark-eyed Junco (*Junco hyemalis*) (CF–P)	13	L	—	1.45[e]	—	14.2, 180	—	Neudorf et al. 2002
Bullock's Oriole (*Icterus bullockii*) (FF–P)	13	P–I	—	—	—, 1,000	—	15[f]	Williams 1990
Bluethroat[g]	5	P	≈1.1 ha	—	331, 571	—	41	Smiseth and Amundsen 1995

[a] Conditions experienced by monitored birds are indicated in parentheses: CF = continuous forest, FF = fragmented forest, P = paired, and U = unpaired.
[b] Stages of breeding season: P = prelaying, L = laying–fertile, I = incubation, N = feeding nestlings, and F = postfledging.
[c] Females did not leave territory alone during the nonfertile period.
[d] Territories supplied with supplemental food.
[e] Median.
[f] Percentage of time spent >100 m from the nest.
[g] Bluethroats live in brushy tundra habitat, and this study was conducted in Norway.

movements of female Hooded Warblers (*Wilsonia citrina*) and Common Yellowthroats (*Geothlypis trichas*) seem largely restricted to the fertile period, males make such moves throughout the breeding season (Pitcher and Stutchbury 2000; Norris and Stutchbury 2001, 2002; Pedersen et al. 2006). Similarly, Humbird and Neudorf (2008) found that female Northern Cardinals (*Cardinalis cardinalis*) were very active during the fertile period and spent 30–50% of their time off territory. They consistently visited the territories of other males during these forays, and food supplementation led to more frequent extraterritorial movements, which suggests that the potential motivation for these moves was to seek extrapair copulations (see also Evans et al. 2008). It also appears that females collect information on the distribution of potential extrapair mates and actively assess the quality of neighboring males (Neudorf et al. 1997). In some cases, females likely begin collecting this information before they become fertile, as in female Bluethroats (*Luscinia svecica*), which make regular, furtive visits to extrapair males' territories at this time (Smiseth and Amundsen 1995). However, although female Common Chaffinches (*Fringilla coelebs*) also initiated many extraterritorial movements during the preincubation period, their social mates followed them on most trips, which indicates that mate guarding may also motivate individuals to leave their territories (Hanski 1992; see also Mays and Ritchison 2004, Evans et al. 2008).

The fact that males of several species focus their extraterritorial activities primarily on the territories of fertile females (e.g., Currie et al. 1998, Stutchbury 1998) is additional evidence of the importance, and detail, of information held on individual cognitive "extraterritorial maps." Male American Redstarts (*Setophaga ruticilla*) were most likely to visit females on other territories during nest building but avoided cuckoldry by not venturing out when their own mate was building its nest early in the fertile period (Churchill and Hannon 2010). Similar observations have been reported for Indigo Buntings (*Passerina cyanea*) and Wood Thrushes (*Hylocichla mustelina*), in which males rarely make solitary extraterritorial moves while their mate is fertile but frequently do so when their mate is not fertile (Westneat 1988, Evans et al. 2008).

A home range has been defined as a repeatedly traversed area where an animal has a predetermined probability of occurring during a given period; a territory is an area within an individual's home range over which it has exclusive or priority use (Powell 2000, Kenward 2001, Kernohan et al. 2001). The observations presented here make it clear that the most appropriate model of breeding-season space use for many temperate and boreal migratory passerines is that pairs occupy a relatively small defended territory, typically ranging from about 0.5 to 5 ha, embedded within a larger multipurpose home range of about 0.5 to 15 ha (Tables 1 and 2). This model is appropriate even when individuals do not make extraterritorial moves; in such cases, the home range and territorial boundaries are one and the same. Few studies have measured both territory and home-range size, but those that did reported home ranges that were, on average, 1.4–3.1 times the size of territories (Leonard et al. 2008, Anich et al. 2009). As reported in many of the studies discussed here, the portion of the home range that falls outside the defended territory typically overlaps the home ranges of neighboring conspecifics and often encompasses portions of their territories. This spatial overlap affords opportunities for direct social interaction and facilitates gathering of social

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

information, but it also compels individuals moving about their home range to forgo the highly visible and vocal behaviors associated with territories and instead make more discrete or furtive movements.

Perhaps more significant than the size difference between territories and home ranges is the extreme range in the extent of space use that has been reported across individuals of various species. For example, in Blackpoll Warblers (*D. striata*), Northern Waterthrushes (*Seiurus noveboracensis*), and Swainson's Warblers (*Limnothlypis swainsonii*), the largest territories observed were 15.8, 77.5, and 23.4 times larger than the smallest territories, respectively (Leonard et al. 2008, Anich et al. 2009; see also Fraser and Stutchbury 2004). Similarly, the largest home ranges were 10.3–27.7 times larger than the smallest home ranges in these species (Leonard et al. 2008, Anich et al. 2009). This plasticity is also reflected in the high variability in space use that a given individual may exhibit through the course of a breeding season. For example, Cardinal (2005) reported that home ranges of Southwestern Willow Flycatchers were, on average, 0.4 ha during nesting but increased to an average of 143.2 ha during the postbreeding period. Consequently, study of variation in space use can lead to the identification of factors that limit populations while also providing insight into diverse aspects of a species' ecology (e.g., Smith and Shugart 1987, Brooker and Rowley 1995, Whitaker et al. 2007).

Various studies have shown that breeding-territory vacancies are quickly filled (Marra and Holmes 1997, Cooper et al. 2009b), which suggests the widespread presence of broadly moving floaters in many breeding populations. Floaters (i.e., nonterritorial individuals) are difficult to monitor because of their secretive nature (Zack and Stutchbury 1992), and their existence has been explained by a number of mutually exclusive hypotheses (Sergio et al. 2009). However, the pursuit of a floater strategy may also be viewed as part of a continuum of space-use patterns. Floaters, which either wander with little site fidelity or move widely throughout a home range without establishing a defended territory (Reed et al. 1999), occupy one end of that spectrum. Other unpaired males may establish and defend a territory, though even these individuals may either exhibit a high degree of territory fidelity or move extensively through a large home range, seemingly employing a mixed floater–territorial advertisement strategy (Fraser and Stutchbury 2004). Floaters may be successful in terms of surviving from one year to the next, but this may also be a successful reproductive strategy for individuals that seek out extrapair copulations and potential mates by moving widely through a home range rather than defending a breeding territory (Shuster and Wade 2003; cf. Cooper et al. 2009b). Individuals that adopt this strategy may monitor territories of multiple pairs (Smith 1984) and, in so doing, move across the broader landscape at greater spatial scales than individuals that are tied to a breeding territory. However, in some cases, floaters are more common around high-quality habitat and may remain within a local area (Brown and Long 2007).

Adults and Juveniles during the Postnesting Period

Compared to the nesting period, limited information is available on the ecology and movements of adult passerines during the postfledging period leading up to migration (Faaborg et al. 2010). Given that adults are no longer attending to an immobile nest, it is logical to expect that the range of movement patterns will be more varied than during the nesting period. Banding data have made it clear that some portion of adults leave their breeding territories and are later found in other habitats or even outside of their species' typical breeding range (Cherry 1985, Rappole and Ballard 1987, Vitz and Rodewald 2006). More recently, the application of radiotelemetry to the study of postbreeding movements has demonstrated that individuals within a breeding population often exhibit a broad range of residency and more extensive movement patterns (Table 3). In some species, a portion of adults with dependent fledglings remain on the breeding territory while other family groups steadily drift away from the natal area (Anders et al. 1998, Vega Rivera et al. 2000, White and Faaborg 2008). In many species, parents typically split broods after fledging (e.g., Evans Ogden and Stutchbury 1997, Tarwater and Brawn 2008), and in Hooded Warblers it was found that these family subgroups moved farther when the attending parent was the female (Rush and Stutchbury 2008). Patterns of adult movement become even more diverse if one considers events that occur after fledglings become independent and family groups disperse. Vega Rivera et al. (1999) tracked 48 Wood Thrushes through the postbreeding period and reported that 23% molted on their breeding territories, 8% moved to habitat patches adjacent to their territories, 31% moved to molting sites 545–7,291 m away, and 37% left the study area altogether (i.e., moved >10 km). Similar results were reported for Scarlet Tanagers (*Piranga olivacea*), in which 45% of 20 individuals remained on their breeding home ranges during the postbreeding period and 55% relocated to other areas (Vega Rivera et al. 2003). However, several of the individuals that relocated made return visits to their breeding territories, which indicates that these areas still constituted a portion of their home ranges at that time. This is similar to observations of adult male Southwestern Willow Flycatchers, in which all individuals occupied expanded home ranges with multiple centers of activity during the postbreeding period (Cardinal 2005).

Adult passerines face several demands during the postbreeding period, potentially including the rearing of dependent fledglings, maintenance of an existing territory or home range, prospecting for future breeding sites, partial or complete prebasic molt, and accrual of energy reserves needed for migration (premigratory fattening). The need to balance these competing needs likely explains the diverse range of patterns of space use observed among individual adults of a given species at this time. For example, energetic demands associated with molt and premigratory fattening may compel some individuals to move to more productive foraging sites, but if flight performance is compromised during molt, individuals may seek out dense escape cover to reduce predation risk (Rappole and Ballard 1987; Vega Rivera et al. 1999, 2003; Vitz and Rodewald 2007). Some studies have linked patterns of postbreeding movement to the reproductive success of individual birds: successful parents often remain on their territories and may even sing frequently, whereas failed breeders are more likely to move extensively or relocate during the postbreeding period (Vega Rivera et al. 1999, Bayne and Hobson 2001, Betts et al. 2008a). This fits the suggestion that for migratory birds the brief postbreeding period can be important both for the maintenance of an existing, proven territory (Vega Rivera et al. 2003) but also as

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

TABLE 3. Estimated mean (± SE) home-range sizes and displacement distances (mean, maximum) for adult and juvenile passerines in temperate and boreal forests during the postfledging period. Displacement distances are from start point to end point or two most distal points. Scientific names not listed below are given in the text.

Species	*n*	Sex	Natal home range (ha)	Postbreeding home range (ha)	Displacement (m)	Source
Adults						
Southwestern Willow Flycatcher	4	M	—	143 ± 83	1,558; 2,851	Cardinal 2005
Wood Thrush	30	M, F	2.6 ± 0.5	1.4 ± 0.3	1,997; 7,291[a]	Vega Rivera et al. 1999
Wood Thrush	63	M, F	—	—	3,353; 17,000	Lang et al. 2002
Ovenbird	22[b]	M	2.2	7.2	455; 5,630	Bayne and Hobson 2001
Scarlet Tanager	13	M	6.0 ± 0.8	17.4 ± 7.2	1,264; 7,100[c]	Vega Rivera et al. 2003
Scarlet Tanager	1	F	3.9	6.14	11,100	Vega Rivera et al. 2003
Juveniles						
Wood Thrush	18	—	—	2.8 ± 0.5	1,500; 5,300	Vega Rivera et al. 1998
Wood Thrush	34	—	—	—	2,189; 6,524	Lang et al. 2002
Wood Thrush	15	—	8.76 ± 8.05[d]	1.53 ± 1.60[d]	2,080; 4,680	Anders et al. 1998
Swainson's Thrush (*Catharus ustulatus*)	35	—	—	2.58 ± 0.52	598; 2,624	White and Faaborg 2008
Yellow-rumped Warbler	39	—	—	—	4,071; 9,468	Mitchell et al. 2010a
Blackpoll Warbler	30	—	—	—	3,076; 16,082	Mitchell et al. 2010a
Worm-eating Warbler (*Helmitheros vermivorum*)	60	—	10.4 ± 1.5	—	1,141; 3,695	Vitz and Rodewald 2010
Ovenbird	51	—	5.0 ± 0.56	—	1,314; 1,799	Vitz and Rodewald 2010

[a] Vega Rivera et al. (1999) indicated that an additional 18 individuals left the study area before molting, all of which moved >10 km.
[b] Sample size for displacement distance is 44.
[c] Vega Rivera et al. (2003) indicated that an additional 11 individuals left the study area before molting, all of which moved >10 km.
[d] Standard deviation.

a time to prospect for future breeding sites (Reed et al. 1999). Betts et al. (2008a) reported that many Black-throated Blue Warblers (*D. caerulescens*) visited sites where conspecific songs were broadcast during the postbreeding period and that, though deliberately located in low-quality habitat, many of these experimental sites were occupied during the following breeding season.

As with adult passerines, limited attention has been directed at studying the spatial ecology of fledgling and juvenile birds prior to migration (Faaborg et al. 2010). Where they have been studied, radiotagged independent juveniles typically remained on their natal territory for some time and then dispersed to other areas hundreds of meters to a few kilometers away, where they once again set up residency (Table 3). A subset of juveniles repeat this process two to four times, creating a stepped pattern of dispersal (Anders et al. 1998, Mitchell et al. 2009, Vitz and Rodewald 2010). Broad-scale movements by young birds shortly after they gain independence from adults have been hypothesized to reflect five possible behavioral patterns: (1) initial displacement associated with commencement of migration (Rappole and Ballard 1987), (2) habitat selection to locate and use productive foraging sites (Rappole and Ballard 1987, Morton et al. 1991), (3) prospecting for future breeding sites (Brewer and Harrison 1975), (4) location of landmarks that can be used to return to the natal territory the following spring (Wiltschko and Wiltschko 1978, Baker 1993), and (5) socialization (Morton et al. 1991). In regard to socialization, Vega Rivera et al. (1998) pointed out that it is often unclear whether juvenile passerines are actively flocking or simply co-occur at a commonly sought resource. Further, some movements may result because dominant (probably adult) individuals supplant subordinate juveniles that then gather in unproductive areas (Winker et al. 1995). However, Mitchell (2007) reported that the probability of individual independent juvenile Blackpoll and Yellow-rumped warblers being associated with a flock increased through the postbreeding period, approaching 100% immediately before migration. These aggregations typically included multiple species, and later in the season they comprised as many as 100 individuals (D. Whitaker pers. obs.). Given that these flocks were highly mobile, it is hard to imagine that membership was not voluntary and motivated by factors such as social learning, foraging efficiency, or reduction of predation risk.

Movements of postfledging birds likely reflect the need to acquire energy for the maintenance of body temperature and to support molt and premigratory fueling for autumn migration, as well as to avoid predation (Weathers and Sullivan 1989, Morton et al. 1991, Kershner et al. 2004). Several studies have documented broad and extensive landscape-level postfledging movements on a scale of kilometers before migration (Table 3). Although such movements may be associated with meeting these immediate resource needs, their functions remain poorly understood (Vega Rivera et al. 1998, Kershner et al. 2004), and they may also be a means to search for sites that will be used in the future (e.g., breeding areas). Attempts to distinguish between food- and predator-driven hypotheses have produced equivocal results (Vega Rivera et al. 1998, Lang et al. 2002, Vitz and Rodewald 2007), though some studies have documented habitat-mediated differences in juvenile survival (King et al. 2006, Berkeley et al. 2007) linked to the propensity to seek out dense cover and thereby reduce predation risk (Anders et al. 1998, Rush and Stutchbury 2008, Vitz and Rodewald

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

2010). However, Mitchell et al. (2010b) found that postfledging birds either made directed landscape-level movements toward and down river valleys, which supports the "habitat optimization" hypothesis, or moved in close association with river valleys but with an orientation that lent support to the hypothesis that they were forming a homing target for spring migration. These results suggest the importance of meeting immediate needs for food and minimizing predation risk, but they do not support other hypotheses focused on short-term drivers (e.g., intraspecific competition and migration initiation; Morton 1991, Baker 1993, Vega Rivera et al. 1998). At the same time, they leave open the possibility that individuals are meeting longer-term needs by developing a homing target and building a cognitive map of the natal landscape. The observation that broadcasting conspecific vocalizations during the postbreeding period compelled many first-time breeders to settle in unsuitable habitat the following year also indicates that juvenile birds use postbreeding social cues to gather information on potential future breeding sites (Betts et al. 2008a; cf. Cornell and Donovan 2010b).

Interannual Movements: Natal and Breeding Dispersal

It is well known that many migratory passerines show high fidelity to breeding territories, returning to nest year after year (e.g., Hoover 2003). It may also be the case that individuals show interannual fidelity to extraterritorial sites used after the nesting period and before migration (e.g., White and Faaborg 2008). A review of patterns of natal and breeding dispersal is beyond the scope of this paper and has been done elsewhere (e.g., Greenwood and Harvey 1982, Paradis et al. 1998). However, in the present context, it is important to note that if individuals occupy large home ranges, then establishing a new territory that falls within that home range represents an ecologically distinct process from dispersal to a new site beyond the old home-range boundary. Such movements do not represent "breeding dispersal" in the true sense of the term, but rather a shift in a focal area or center of activity while philopatry toward a home range is maintained.

An Expanded View of Space Use and Its Implications

Because they typically fly at speeds of 25–50 km h^{-1} (e.g., Evans and Drickamer 1994), passerines are highly mobile and can make relatively efficient landscape-scale movements in minutes. This enables them to range over large areas daily to acquire such resources as food, nesting materials, and mates and to get information on habitat quality and the distribution and status of resources and conspecifics in the surrounding landscape. Clearly, there are still potential costs associated with large-scale movements, including predation risk and the energetic cost of flight. Several studies have shown that songbirds, notably parids, adjust their use of open habitat to reduce predation risk (Desrochers and Hannon 1997, Rodríguez et al. 2001, St. Clair 2003). Likewise, high breeding-season survival rates indicate that predation risk to adults is low or at least successfully avoided during the breeding season in general (Leonard et al. 2008, Whitaker et al. 2008) and during extraterritorial movements in particular (Norris and Stutchbury 2001, Woolfenden et al. 2005). Passerines are also capable of traveling hundreds of kilometers per day during migration (e.g., Stutchbury et al. 2009), which indicates that travel via sustained flight is relatively cheap in terms of time and energy (see also Tarof et al. 1998, Nudds and Bryant 2000). Thus, in many cases, the greatest cost of extensive movement during the breeding period may be time away from a nest or mate, which can lead to increased risk of nest predation, nest parasitism, or cuckoldry (e.g., Westneat and Stewart 2003, Brylawski and Whittingham 2004).

Although high mobility allows daily exploitation of large areas, our review makes it clear that an individual bird may exhibit several different patterns of movement over the course of a breeding season. Moreover, different individuals in a population often employ strikingly different patterns of space use at any one time. This highlights the importance of temporal scale when considering patterns of space use, which are clearly dynamic and affected by a broad range of individual, social, and environmental factors during the course of a breeding season. However, much of this seemingly chaotic array of spatial behaviors fits within the broader definition of a home range, if considered at an appropriately broad temporal scale. Movements that seem transient or that could perhaps be classified as dispersal within a given period may in fact constitute use of different parts of an individual's overall breeding-season home range. For example, White and Faaborg (2008) reported that Swainson's Thrushes with dependent young often moved their family to the same off-territory postfledging sites in different years. Similarly, individuals may make seemingly transient movements to gather spatially referenced social information during the postbreeding period. However, if they then use this cognitive map when selecting future breeding sites (Reed et al. 1999, Betts et al. 2008a), it seems reasonable to view these areas as constituting part of the individual's "perceptual" home range (*sensu* Powell 2000).

Given this broader view of passerine space use during the breeding period, it is clear that quantifying and describing space use presents an intellectual challenge. The fact that most breeding passerines make routine extraterritorial movements during the nesting period suggests that adopting a "territory–foray" view of space use is inappropriate. This is logically overcome by shifting to a more generalized model in which breeding individuals typically defend a territory embedded within a larger home range that they regularly travel for a variety of reasons, and for which they maintain a detailed cognitive map. Behaviors restricted to or more prevalent within territories include predator mobbing, territorial singing, and physical aggression toward conspecifics (e.g., Betts et al. 2005); birds typically exhibit more furtive behavior while off territory (e.g., Stutchbury 1998). However, maintenance of a territory may occur during only part of the breeding season, typically spanning the prebreeding and nesting periods, and many individuals relocate one or more times throughout the course of a breeding season. Sometimes, this involves a shift to another site within the breeding landscape, after which an individual once again exhibits residency (e.g., Vega Rivera et al. 1999, Cardinal 2005). In other cases, individuals make seemingly transient movements, including dispersal, exploratory forays, drift, and possibly even vagrancy (e.g., Rappole and Ballard 1987, Vega Rivera et al. 1998, Mitchell et al. 2009). Rigorously distinguishing between and quantifying these classes of space use requires a broad view of the range of

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

patterns of movement possible and consideration of how the time scale in which they are measured may affect the inferences made (White and Garrott 1990, Powell 2000, Kernohan et al. 2001).

These ideas highlight the importance of employing appropriate quantitative methods to delineate home ranges and other used areas. The simplistic minimum-convex-polygon estimator has been widely employed (e.g., Bayne and Hobson 2001, Vitz and Rodewald 2010) but is highly sensitive to sample size, often includes large areas of unused habitat, and offers no information on the distribution of activity within the home range (White and Garrott 1990). Instead, researchers should quantify home ranges in terms of probabilistic utilization distributions, which allow a used area to be modeled in terms of the individual's probability of being in different places (Seaman and Powell 1996, Barg et al. 2005). A variety of estimation techniques have been developed, and useful reviews have been published elsewhere (Powell 2000, Kenward 2001, Kernohan et al. 2001). In particular, the fixed-kernel method has gained widespread acceptance, has many desirable quantitative traits (Seaman and Powell 1996, Powell 2000), and is well suited for use with passerines (e.g., Barg et al. 2005, Leonard et al. 2008, Anich et al. 2009). However, even these methods are inappropriate when individuals are not exhibiting residency, in which case a dynamic quantitative approach is necessary (e.g., Mitchell et al. 2010a).

Conservation Applications and Future Directions: Linking Space Use to Landscapes

Although a great deal of information on the spatial ecology of passerines has been gathered in the past 20 years, significant gaps remain. Smith (1988) commented that considerably less attention had been paid to female strategies in extrapair mating systems, the prevailing belief being that females rarely move beyond territorial boundaries. More studies have focused on females since that time, and this research indicates substantial mobility in females of most species, but there are still comparatively few studies to match our knowledge of male movements (there have also been relatively few studies of juveniles; cf. Tables 1, 2, and 3). Females certainly exert a high degree of control over extrapair mating (Neudorf et al. 2002, Woolfenden et al. 2005, Chiver et al. 2008), but the selective advantages to females are unclear (Townsend et al. 2010), as are many of the details behind the mate selection process that the females use during breeding. A historical focus on assessment of habitat use through surveys of displaying males (e.g., Whitaker and Montevecchi 1999) may also mean that important habitat needs of females have been overlooked in the development of conservation prescriptions.

Comparing across a broad range of studies on temperate and boreal passerines, one of the most consistent and striking aspects of space use is the extreme variation in the observed scale of breeding-season movements. This is true whether one compares different individuals during a given period or observes a single individual between different periods of the breeding season. Clearly, the high mobility of passerines allows them to modify the extent of their movements to suit their daily physiological, social, and reproductive needs and constraints. The range of this ability to compensate for habitat disturbance or loss is critical to conservation, as this is likely one of the primary behavioral mechanisms that birds employ to respond flexibly to environmental change (Schmiegelow et al. 1997, Walters 1998). Elucidating the mechanisms that underlie such variability (e.g., Schmiegelow et al. 1997, Whitaker et al. 2007, Leonard et al. 2008) and their associated fitness costs (e.g., Convery 2002) presents a current challenge to ornithologists, but doing so may facilitate a greater understanding of the degree of resilience to environmental change displayed by different species. There is a growing body of evidence that landscape-scale habitat characteristics directly affect the movement behavior of forest passerines. Hooded Warblers, Swainson's Warblers, Ovenbirds (*S. aurocapilla*), Northern Waterthrushes, and Scarlet Tanagers have all been found to make much more extensive movements in anthropogenically fragmented landscapes than in intact temperate and boreal forest landscapes (Bayne and Hobson 2001, Norris and Stutchbury 2001, Fraser and Stutchbury 2004, Anich 2008, Leonard et al. 2008). However, when severe fragmentation leads to the creation of habitat islands, only species able to cross habitat gaps can compensate for a loss of forest cover in this manner (e.g., Bélisle et al. 2001, Gobeil and Villard 2002), and doing so undoubtedly affects a broad range of other aspects of an individual's activities, as well as time and energy budgets and, possibly, fitness. Consequently, even when individuals can use small patches, these may still be of low habitat quality (e.g., Hinsley 2000, Bayne and Hobson 2002), and there may be thresholds of habitat loss or fragmentation beyond which individuals can no longer compensate (e.g., Betts et al. 2007, Cornell and Donovan 2010a); it may even be possible to directly link these thresholds to the movement capacity and time budgets of individual birds. For example, extraterritorial foraging may be more likely when the habitat is patchy or of variable quality, such that males occupying home ranges in fragmented forest may need to exploit multiple habitat patches to collect sufficient food (Fraser and Stutchbury 2004, Leonard et al. 2008). This would necessitate a time and energy tradeoff between foraging and paternity assurance strategies or defense of young (Hinsley 2000, Norris and Stutchbury 2002, Evans et al. 2009).

Also important to conservation is an improved understanding of landscape-scale habitat needs that could result from more thorough investigations of individual space use. During the nesting period, home ranges of paired adult male forest passerines may be 1.5× to more than 3× larger than territories (Leonard et al. 2008, Anich et al. 2009). This difference becomes greater still for unpaired individuals, or if one considers the pre- and postbreeding movements of adults (Tables 1–3). Use of large home ranges, in some cases exceeding 1 km^2 (e.g., Fraser and Stutchbury 2004, Cardinal 2005), offers a direct mechanism to explain the landscape-scale habitat sensitivity observed in many species of songbirds (e.g., Hinsley et al. 1995, Taylor and Krawchuk 2005, Betts et al. 2006). Although placement of territories is clearly affected by habitat use patterns, considering the broader home range that an individual uses is also critical for understanding the species' habitat ecology. It is important that we understand the placement of home ranges within landscapes and of territories within home ranges—similar to Johnson's (1980) hierarchical framework for habitat selection. However, few studies of passerines have explicitly studied habitat selection at the home-range scale or compared habitat in territories with that in broader home ranges. Given the potential importance of extraterritorial habitat for at least some

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

species in terms of predator avoidance, foraging, and extrapair mating opportunities, strong but variable selective pressure may be conveyed by the availability of suitable habitat at the home-range scale. Likewise, the manner in which juveniles explore and use the broader landscape has direct links to both individual survival and future population dynamics (Robinson et al. 2004).

Summary

Much of the ornithological literature, especially that on extrapair mating systems, portrays extraterritorial movements as raids, forays, or covert intrusions on the territories of neighboring conspecifics. However, individuals of most species make regular extraterritorial movements into a broader landscape for which they seemingly have detailed knowledge and a good cognitive map, and which they may exploit for a variety of reasons throughout the breeding season. Consequently, it seems more useful and accurate to view this area as an occupied, multipurpose home range rather than a hostile landscape to be covertly raided. This shifts the emphasis from a view of songbirds as living in isolation and defending territories from conspecifics to one in which conspecifics coexist in neighborhoods, have overlapping home ranges, and, while maintaining defended territories, have a detailed knowledge of their neighbors and regularly interact with them. They also have a keen awareness of the composition and distribution of resources across the broader landscape, covering an area that for some species may span several square kilometers.

This conceptual framework can serve as an omnibus for diverse topics related to the structure and interconnectedness of populations and distribution of individuals across landscapes. For example, it lends itself well to studies of resource selection and, in particular, landscape-scale habitat sensitivity (e.g., neighboring conspecifics can even be included as features in the landscape). It is also consistent with extrapair mating systems and the "hidden lek" hypothesis, which has been offered to explain aggregation of territories in some species of songbirds (Wagner 1998, Tarof et al. 2004). Finally, it contributes to a more comprehensive understanding of metapopulation processes (Hanski 1999) and informed dispersal (Clobert et al. 2009), whereby diverse types of information about the surrounding environment contribute to a bird's cognitive map and are used in future dispersal decisions.

Acknowledgments

This manuscript was greatly improved as a result of thoughtful feedback from M. Betts, M. Murphy, and G. Niemi.

Literature Cited

Anders, A. D., J. Faaborg, and F. R. Thompson III. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. Auk 115:349–358.

Anich, N. M. 2008. Home-range size and habitat use of Swainson's Warblers in eastern Arkansas. M.S. thesis, Arkansas State University, Jonesboro.

Anich, N. M., T. J. Benson, and J. C. Bednarz. 2009. Estimating territory and home-range sizes: Do singing locations alone provide an accurate estimate of space use? Auk 126:626–634.

Baker, M., N. Nur, and G. R. Geupel. 1995. Correcting biased estimates of dispersal and survival due to limited study area: Theory and an application using Wrentits. Condor 97:663–674.

Baker, R. R. 1993. The function of post-fledging exploration: A pilot study of three species of passerines ringed in Britain. Ornis Scandinavica 24:71–79.

Barg, J. J., J. Jones, and R. J. Robertson. 2005. Describing breeding territories of migratory passerines: Suggestions for sampling, choice of estimator, and delineation of core areas. Journal of Animal Ecology 74:139–149.

Bayne, E. M. 2000. Effects of forest fragmentation on the demography of Ovenbirds (*Seiurus aurocapillus*) in the boreal forest. Ph.D. dissertation, University of Saskatchewan, Saskatoon.

Bayne, E. M., and K. A. Hobson. 2001. Movement patterns of adult male Ovenbirds during the post-fledging period in fragmented and forested boreal landscapes. Condor 103:343–351.

Bayne, E. M., and K. A. Hobson. 2002. Apparent survival of male Ovenbirds in fragmented and forested boreal landscapes. Ecology 83:1307–1316.

Bayne, E. M., S. L. Van Wilgenburg, S. Boutin, and K. A. Hobson. 2005. Modeling and field-testing of Ovenbird (*Seiurus aurocapillus*) responses to boreal forest dissection by energy sector development at multiple spatial scales. Landscape Ecology 20:203–216.

Bélisle, M., A. Desrochers, and M.-J. Fortin. 2001. Influence of forest cover on the movements of forest birds: A homing experiment. Ecology 82:1893–1904.

Benson, A.-M., and K. Winker. 2001. Timing of breeding range occupancy among high-latitude passerine migrants. Auk 118:513–519.

Berkeley, L. I., J. P. McCarty, and L. L. Wolfenbarger. 2007. Postfledging survival and movement in Dickcissels (*Spiza americana*): Implications for habitat management and conservation. Auk 124:396–409.

Betts, M. G., G. J. Forbes, and A. W. Diamond. 2007. Thresholds in songbird occurrence in relation to landscape structure. Conservation Biology 21:1046–1058.

Betts, M. G., G. J. Forbes, A. W. Diamond, and P. D. Taylor. 2006. Independent effects of fragmentation on forest songbirds: An organism-based approach. Ecological Applications 16:1076–1089.

Betts, M. G., A. S. Hadley, and P. J. Doran. 2005. Avian mobbing response is restricted by territory boundaries: Experimental evidence from two species of forest warblers. Ethology 111:821–835.

Betts, M. G., A. S. Hadley, N. Rodenhouse, and J. J. Nocera. 2008a. Social information trumps vegetation structure in breeding-site selection by a migrant songbird. Proceedings of the Royal Society of London, Series B 275:2257–2263.

Betts, M. G., N. L. Rodenhouse, T. S. Sillett, P. J. Doran, and R. T. Holmes. 2008b. Dynamic occupancy models reveal within-breeding season movement up a habitat quality gradient by a migratory songbird. Ecography 31:592–600.

Bibby, C., N. Burgess, D. Hill, and S. Mustoe. 2000. Bird Census Techniques, 2nd ed. Academic Press, San Diego, California.

Birkhead, T. R., and A. P. Møller. 1992. Sperm Competition in Birds: Evolutionary Causes and Consequences. Academic Press, London.

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Brewer, R., and K. G. Harrison. 1975. The time of habitat selection by birds. Ibis 117:521–522.

Brooker, M., and I. Rowley. 1995. The significance of territory size and quality in the mating strategy of the Splendid Fairy-Wren. Journal of Animal Ecology 64:614–627.

Brown, D. R., and J. A. Long. 2007. What is a winter floater? Causes, consequences, and implications for habitat selection. Condor 109:548–565.

Brylawski, A. M. Z., and L. A. Whittingham. 2004. An experimental study of mate guarding and paternity in House Wrens. Animal Behaviour 68:1417–1424.

Cardinal, S. N. 2005. Conservation of Southwestern Willow Flycatchers: Home range and habitat use by an endangered passerine. M.S. thesis, Northern Arizona University, Flagstaff.

Cherry, J. D. 1985. Early autumn movements and prebasic molt of Swainson's Thrushes. Wilson Bulletin 97:368–370.

Chiver, I., B. J. M. Stutchbury, and E. S. Morton. 2008. Do male plumage and song characteristics influence female off-territory forays and paternity in the Hooded Warbler? Behavioral Ecology and Sociobiology 62:1981–1990.

Churchill, J. L., and S. J. Hannon. 2010. Off-territory movement of male American Redstarts (*Setophaga ruticilla*) in a fragmented agricultural landscape is related to song rate, mating status and access to females. Journal of Ornithology 151:33–44.

Clobert, J., J.-F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12:197–209.

Cody, M. L. 1981. Habitat selection in birds: The roles of vegetation structure, competitors, and productivity. BioScience 31:107–113.

Convery, K. M. 2002. Assessing habitat quality for the endangered Red-cockaded Woodpecker (*Picoides borealis*). M.S. thesis, Virginia Tech, Blacksburg.

Cooper, N. W., M. T. Murphy, and L. J. Redmond. 2009a. Age- and sex-dependent spring arrival dates of Eastern Kingbirds. Journal of Field Ornithology 80:35–41.

Cooper, N. W., M. T. Murphy, L. J. Redmond, and A. C. Dolan. 2009b. Density-dependent age at first reproduction in the Eastern Kingbird. Oikos 118:413–419.

Cornell, K. L., and T. M. Donovan. 2010a. Effects of spatial habitat heterogeneity on habitat selection and annual fecundity for a migratory forest songbird. Landscape Ecology 25:109–122.

Cornell, K. L., and T. M. Donovan. 2010b. Scale-dependent mechanisms of habitat selection for a migratory passerine: An experimental approach. Auk 127:in press.

Currie, D. R., T. Burke, R. L. Whitney, and D. B. A. Thompson. 1998. Male and female behaviour and extra-pair paternity in the wheatear. Animal Behaviour 55:689–703.

Dale, S., A. Lunde, and Ø. Steifetten. 2005. Longer breeding dispersal than natal breeding dispersal in the Ortolan Bunting. Behavioral Ecology 16:20–24.

Dall, S. R. X., L.-A. Giraldeau, O. Olsson, J. M. McNamara, and D. W. Stephens. 2005. Information and its use by animals in evolutionary ecology. Trends in Ecology and Evolution 20:187–193.

Dalley, K. L., P. D. Taylor, and D. Shutler. 2009. Success of migratory songbirds breeding in harvested boreal forests of northwestern Newfoundland. Condor 111:314–325.

Desrochers, A., and S. J. Hannon. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. Conservation Biology 11:1204–1210.

Dolan, A. C., M. T. Murphy, L. J. Redmond, K. Sexton, and D. Duffield. 2007. Extrapair paternity and the opportunity for sexual selection in a socially monogamous passerine. Behavioural Ecology 18:985–993.

Double, M., and A. Cockburn. 2000. Pre-dawn infidelity: Females control extra-pair mating in Superb Fairy-Wrens. Proceedings of the Royal Society of London, Series B 267:465–470.

Evans, M. L., B. J. M. Stutchbury, and B. E. Woolfenden. 2008. Off-territory forays and genetic mating system of the Wood Thrush (*Hylocichla mustelina*). Auk 125:67–75.

Evans, M. L., B. E. Woolfenden, L. Friesen, and B. J. M. Stutchbury. 2009. Variation in the extra-pair mating systems of Acadian Flycatchers and Wood Thrushes in forest fragments in southern Ontario. Journal of Field Ornithology 80:146–153.

Evans, T. R., and L. C. Drickamer. 1994. Flight speeds of birds determined using Doppler radar. Wilson Bulletin 106:154–156.

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.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, Jr., P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, and others. 2010. Conserving migratory land birds in the New World: Do we know enough? Ecological Applications 20:398–418.

Fisher, R. J., and S. K. Davis. 2010. From Wiens to Robel: A review of grassland-bird habitat selection. Journal of Wildlife Management 74:265–273.

Francis, C. M., and F. Cooke. 1986. Differential timing of spring migration in wood warblers (Parulinae). Auk 103:548–556.

Fraser, G. S., and B. J. M. Stutchbury. 2004. Area sensitive forest birds move extensively among forest patches. Biological Conservation 118:377–387.

Gobeil, J.-F., and M.-A. Villard. 2002. Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. Oikos 98:447–458.

Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics 13:1–21.

Griffith, S. C., I. P. F. Owens, and K. A. Thuman. 2002. Extra pair paternity in birds: A review of interspecific variation and adaptive function. Molecular Ecology 11:2195–2212.

Hahn, B. A., and E. D. Silverman. 2006. Social cues facilitate habitat selection: American Redstarts establish breeding territories in response to song. Biological Letters 2:337–340.

Hahn, B. A., and E. D. Silverman. 2007. Managing breeding forest songbirds with conspecific song playbacks. Animal Conservation 10:436–441.

Hahn, T. P., K. W. Sockman, C. W. Breuner, and M. L. Morton. 2004. Facultative altitudinal movements by Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in the Sierra Nevada. Auk 121:1269–1281.

Haila, Y., A. O. Nicholls, I. K. Hanski, and S. Raivio. 1996. Stochasticity in bird habitat selection: Year-to-year changes in territory locations in a boreal forest bird assemblage. Oikos 76:536–552.

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Hanski, I. K. 1992. Territorial behaviour and mixed reproductive strategy in the chaffinch. Ornis Scandinavica 23:475–482.

Hanski, I. [K.] 1999. Metapopulation Ecology. Oxford University Press, London.

Hanski, I. K., and Y. Haila. 1988. Singing territories and home ranges of breeding chaffinches: Visual observation vs. radiotracking. Ornis Fennica 65:97–103.

Hinsley, S. A. 2000. The costs of multiple patch use by birds. Landscape Ecology 15:765–775.

Hinsley, S. A., P. E. Bellamy, I. Newton, and T. H. Sparks. 1995. Habitat and landscape factors influencing the presence of individual breeding bird species in woodland fragments. Journal of Avian Biology 26:94–104.

Holmes, R. T., P. P. Marra, and T. W. Sherry. 1996. Habitat-specific demography of breeding Black-throated Blue Warblers (*Dendroica caerulescens*): Implications for population dynamics. Journal of Animal Ecology 65:183–195.

Hoover, J. P. 2003. Decision rules for site fidelity in a migratory bird, the Prothonotary Warbler. Ecology 84:416–430.

Hubalek, Z. 2001. Seasonal variation of forest habitat preferences by birds in a lowland riverine ecosystem. Folia Zoologica 50:281–289.

Humbird, S. K., and D. L. H. Neudorf. 2008. The effects of food supplementation on extraterritorial behavior in female Northern Cardinals. Condor 110:392–395.

Hung, S., S. A. Tarof, and B. J. M. Stutchbury. 2009. Extra-pair mating tactics and vocal behavior of female Acadian Flycatchers. Condor 111:653–661.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65–71.

Kempenaers, B., G. R. Verheyen, M. Van den Broeck, T. Burke, C. Van Broekhoven, and A. A. Dhondt. 1992. Extra-pair paternity results from female preference for high-quality males in the Blue Tit. Nature 357:494–496.

Kenward, R. E. 2001. A Manual for Wildlife Radio Tagging. Academic Press, New York.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125–166 *in* Radio Tracking and Animal Populations (J. J. Millspaugh and J. M. Marzluff, Eds.). Academic Press, NewYork.

Kershner, E. L., J. W. Walk, and R. E. Warner. 2004. Postfledging movements and survival of juvenile Eastern Meadowlarks (*Sturnella magna*) in Illinois. Auk 121:1146–1154.

King, D. I., R. M. DeGraaf, M.-L. Smith, and J. P. Buonaccorsi. 2006. Habitat selection and habitat-specific survival of fledgling Ovenbirds (*Seiurus aurocapilla*). Journal of Zoology (London) 269:414–421.

Koenig, W. D., D. Van Vuren, and P. N. Hooge. 1996. Detection, philopatry, and the distribution of dispersal distances in vertebrates. Trends in Ecology and Evolution 11:514–517.

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen, London.

Lang, J. D., L. A. Powell, D. G. Krementz, and M. J. Conroy. 2002. Wood Thrush movements and habitat use: Effects of forest management for Red-cockaded Woodpeckers. Auk 119:109–124.

Leonard, T. D. 2007. Songbird space use and movement in heterogeneous landscapes vary with landscape structure and spatial scale. M.Sc. thesis, Acadia University, Wolfville, Nova Scotia.

Leonard, T. D., P. D. Taylor, and I. G. Warkentin. 2008. Space use by songbirds in naturally patchy and harvested boreal forests. Condor 110:467–481.

Magrath, M. J. L., O. Vedder, M. van der Velde, and J. Komdeur. 2009. Maternal effects contribute to the superior performance of extra-pair offspring. Current Biology 19:792–797.

Marra, P. P., and R. T. Holmes. 1997. Avian removal experiments: Do they test for habitat saturation or female availability? Ecology 78:947–952.

Mays, H. L., and G. Ritchison. 2004. The effect of vegetation density on male mate guarding and extra-territorial forays in the Yellow-breasted Chat (*Icteria virens*). Naturwissenschaften 91:195–198.

Mazerolle, D. F., and K. A. Hobson. 2003. Do Ovenbirds (*Seiurus aurocapillus*) avoid boreal forest edges? A spatiotemporal analysis in an agricultural landscape. Auk 120:152–162.

Mitchell, G. W. 2007. Juvenile songbird movement and habitat use in a harvested boreal forest landscape of western Newfoundland. M.Sc. thesis, Acadia University, Wolfville, Nova Scotia.

Mitchell, G. W., P. D. Taylor, and I. G. Warkentin. 2010a. Assessing the function of broad-scale movements made by juvenile songbirds prior to migration. Condor 112:in press.

Mitchell, G. W., P. D. Taylor, and I. G. Warkentin. 2010b. Multiscale postfledging habitat associations of juvenile songbirds in a managed landscape. Auk 127:354–363.

Mitchell, G. W., I. G. Warkentin, and P. D. Taylor. 2009. Movement of juvenile songbirds in harvested boreal forest: Assessing residency time and landscape connectivity. Avian Conservation and Ecology 4(1):5. [Online.] Available at www.ace-eco.org/vol4/iss1/art5/.

Morse, D. H. 1989. American Warblers: An Ecological and Behavioral Perspective. Harvard University Press, Cambridge, Massachusetts.

Morton, M. L. 1991. Postfledging dispersal of Green-tailed Towhees to a subalpine meadow. Condor 93:466–468.

Morton, M. L. 2002. The Mountain White-crowned Sparrow: Migration and reproduction at high altitude. Studies in Avian Biology, no. 24.

Morton, M. L., M. W. Wakamatsu, M. E. Pereyra, and G. A. Morton. 1991. Postfledging dispersal, habitat imprinting, and philopatry in a montane, migratory sparrow. Ornis Scandinavica 22:98–106.

Naguib, M., R. Altenkamp, and B. Griessmann. 2001. Nightingales in space: Song and extra-territorial forays of radio-tagged songbirds. Journal für Ornithologie 142:306–312.

Neudorf, D. L., B. J. M. Stutchbury, and W. H. Piper. 1997. Covert extraterritorial behavior of female Hooded Warblers. Behavioral Ecology 8:595–600.

Neudorf, D. L., D. J. Ziolkowski, Jr., V. Nolan, Jr., and E. D. Ketterson. 2002. Testosterone manipulation of male attractiveness has no detectable effect on female home-range size and behavior during the fertile period. Ethology 108:713–726.

Nice, M. M. 1941. The role of territory in bird life. American Midland Naturalist 26:441–487.

Nocera, J. J., G. J. Forbes, and L.-A. Giraldeau. 2009. Aggregations from using inadvertent social information: A form of ideal habitat selection. Ecography 32:143–152.

Norris, D. R., and B. J. M. Stutchbury. 2001. Extraterritorial movements of a forest songbird in a fragmented landscape. Conservation Biology 15:729–736.

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Norris, D. R., and B. J. M. Stutchbury. 2002. Sexual differences in gap-crossing ability of a forest songbird in a fragmented landscape revealed through radiotracking. Auk 119:528–532.

Nudds, R. L., and D. M. Bryant. 2000. The energetic cost of short flights in birds. Journal of Experimental Biology 203:1561–1572.

Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory. 1998. Patterns of natal and breeding dispersal in birds. Journal of Animal Ecology 67:518–536.

Pedersen, M. C., P. O. Dunn, and L. A. Whittingham. 2006. Extraterritorial forays are related to a male ornamental trait in the Common Yellowthroat. Animal Behaviour 72:479–486.

Pitcher, T. E., and B. J. M. Stutchbury. 2000. Extraterritorial forays and male parental care in Hooded Warblers. Animal Behaviour 59:1261–1269.

Poole, A., Ed. 2005. The Birds of North America Online. Cornell Laboratory of Ornithology, Ithaca, New York. [Online.] Available at bna.birds.cornell.edu/BNA/.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pages 65–110 *in* Research Techniques in Animal Ecology (L. Boitani and T. K. Fuller, Eds.). Columbia University Press, New York.

Ralph, C. J., J. R. Sauer, and S. Droege, Eds. 1995. Monitoring Bird Populations by Point Counts. U.S. Department of Agriculture, Forest Service General Technical Report PSW-GTR-149.

Rappole, J. H., and K. Ballard. 1987. Postbreeding movements of selected species of birds in Athens, Georgia. Wilson Bulletin 99:475–480.

Reed, J. M., T. Boulinier, E. Danchin, and L. W. Oring. 1999. Informed dispersal: Prospecting by birds for breeding sites. Pages 189–259 in Current Ornithology, vol. 15 (V. Nolan, Jr., E. D. Ketterson, and C. F. Thompson, Eds.). Plenum Press, New York.

Reed, J. M., and L. W. Oring. 1992. Reconnaissance for future breeding sites by Spotted Sandpipers. Behavioral Ecology 3:310–317.

Robinson, R. A., R. E. Green, S. R. Baillie, W. J. Peach, and D. L. Thomson. 2004. Demographic mechanisms of the population decline of the Song Thrush *Turdus philomelos* in Britain. Journal of Animal Ecology 73:670–682.

Rodenhouse, N. L., T. S. Sillett, P. J. Doran, and R. T. Holmes. 2003. Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season. Proceedings of the Royal Society of London, Series B 270:2105–2110.

Rodríguez, A., H. Andrén, and G. Jansson. 2001. Habitat-mediated predation risk and decision making of small birds at forest edges. Oikos 95:383–396.

Roth, R. R., M. S. Johnson, and T. J. Underwood. 1996. Wood Thrush (*Hylocichla mustelina*). *In* The Birds of North America, no. 246 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Rush, S. A., and B. J. M. Stutchbury. 2008. Survival of fledgling Hooded Warblers (*Wilsonia citrina*) in small and large forest fragments. Auk 125:183–191.

Schmiegelow, F. K. A., C. S. Machtans, and S. J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology 78:1914–1932.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

Sergio, F., J. Blas, and F. Hiraldo. 2009. Predictors of floater status in a long-lived bird: A cross-sectional and longitudinal test of hypotheses. Journal of Animal Ecology 78:109–118.

Shuster, S. M., and M. J. Wade. 2003. Mating Systems and Strategies. Princeton University Press, Princeton, New Jersey.

Smiseth, P. T., and T. Amundsen. 1995. Female Bluethroats (*Luscinia s. svecica*) regularly visit territories of extrapair males before egg laying. Auk 112:1049–1053.

Smith, S. M. 1984. Flock switching in chickadees: Why be a winter floater? American Naturalist 123:81–98.

Smith, S. M. 1988. Extra-pair copulations in Black-capped Chickadees: The role of the female. Behaviour 107:15–23.

Smith, T. M., and H. H. Shugart. 1987. Territory size variation in the Ovenbird: The role of habitat structure. Ecology 68:695–704.

Stamps, J. A. 2006. The silver spoon effect and habitat selection by natal dispersers. Ecology Letters 9:1179–1185.

St. Clair, C. C. 2003. Comparative permeability of roads, rivers, and meadows to songbirds in Banff National Park. Conservation Biology 17:1151–1160.

Stutchbury, B. J. M. 1998. Extra-pair mating effort of male Hooded Warblers, *Wilsonia citrina*. Animal Behaviour 55:553–561.

Stutchbury, B. J. M., T. E. Pitcher, D. R. Norris, E. M. Tuttle, and R. A. Gonser. 2005. Does male extra-territory foray effort affect fertilization success in Hooded Warblers *Wilsonia citrina*? Journal of Avian Biology 36:471–477.

Stutchbury, B. J. M., S. A. Tarof, T. Done, E. Gow, P. M. Kramer, J. Tautin, J. W. Fox, and V. Afanasyev. 2009. Tracking long-distance songbird migration by using geolocators. Science 323:896.

Tarof, S. A., L. M. Ratcliffe, M. Kasumovic, and P. T. Boag. 2004. Are Least Flycatcher (*Empidonax minimus*) clusters hidden leks? Behavioral Ecology 16:207–217.

Tarof, S. A., B. J. M. Stutchbury, W. H. Piper, and R. C. Fleischer. 1998. Does breeding density covary with extra-pair fertilizations in Hooded Warblers? Journal of Avian Biology 29:145–154.

Tarwater, C. E., and J. D. Brawn. 2008. Patterns of brood division and an absence of behavioral plasticity in a Neotropical passerine. Behavioral Ecology and Sociobiology 62:1441–1452.

Taylor, P. D., and M. A. Krawchuk. 2005. Scale and sensitivity of songbird occurrence to landscape structure in a harvested boreal forest. Avian Conservation and Ecology 1(1):5. [Online.] Available at www.ace-eco.org/vol1/iss1/art5/.

Townsend, A. K., A. B. Clark, and K. J. McGowan. 2010. Direct benefits and genetic costs of extrapair paternity for female American Crows (*Corvus brachyrhynchos*). American Naturalist 175:E1–E9.

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.

Vega Rivera, J. H., W. J. McShea, and J. H. Rappole. 2003. Comparison of breeding and postbreeding movements and habitat requirements for the Scarlet Tanager (*Piranga olivacea*) in Virginia. Auk 120:632–644.

Vega Rivera, J. H., W. J. McShea, J. H. Rappole, and C. A. Haas. 1999. Postbreeding movements and habitat use of adult Wood Thrushes in northern Virginia. Auk 116:458–466.

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Vega Rivera, J. H., J. H. Rappole, W. J. McShea, and C. A. Haas. 1998. Wood Thrush postfledging movements and habitat use in northern Virginia. Condor 100:69–77.

Vitz, A. C., and A. D. Rodewald. 2006. Can regenerating clearcuts benefit mature-forest songbirds? An examination of post-breeding ecology. Biological Conservation 127:477–486.

Vitz, A. C., and A. D. Rodewald. 2007. Vegetative and fruit resources as determinants of habitat use by mature-forest birds during the postbreeding period. Auk 124:494–507.

Vitz, A. C., and A. D. Rodewald. 2010. Movements of fledgling Ovenbirds (*Seiurus aurocapilla*) and Worm-eating Warblers (*Helmitheros vermivorum*) within and beyond the natal home range. Auk 127:364–371.

Wagner, R. H. 1998. Hidden leks: Sexual selection and the clustering of avian territories. Pages 123–146 *in* Avian Reproductive Tactics: Female and Male Perspectives (P. G. Parker and N. T. Burley, Eds.). Ornithological Monographs, no. 49.

Walters, J. R. 1998. The ecological basis of avian sensitivity to habitat fragmentation. Pages 181–192 *in* Avian Conservation: Research and Management (J. M. Marzluff and R. Sallabanks, Eds.). Island Press, Washington, D.C.

Walters, J. R. 2000. Dispersal behavior: An ornithological frontier. Condor 102:479–481.

Weathers, W. W., and K. A. Sullivan. 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. Ecological Monographs 59:223–246.

Webster, M. S., K. A. Tarvin, E. M. Tuttle, and S. Pruett-Jones. 2007. Promiscuity drives sexual selection in a socially monogamous bird. Evolution 61:2205–2211.

Westneat, D. F. 1988. Male parental care and extrapair copulations in the Indigo Bunting. Auk 105:149–160.

Westneat, D. F., and I. R. K. Stewart. 2003. Extra-pair paternity in birds: Causes, correlates, and conflict. Annual Review of Ecology, Evolution, and Systematics 34:365–396.

Whitaker, D. M., and W. A. Montevecchi. 1999. Breeding bird assemblages inhabiting riparian buffer strips in Newfoundland, Canada. Journal of Wildlife Management 63:167–179.

Whitaker, D. M., D. F. Stauffer, G. W. Norman, P. K. Devers, J. Edwards, W. M. Giuliano, C. Harper, W. Igo, J. Sole, H. Spiker, and B. Tefft. 2007. Factors associated with variation in home-range size of Appalachian Ruffed Grouse (*Bonasa umbellus*). Auk 124:1407–1424.

Whitaker, D. M., P. D. Taylor, and I. G. Warkentin. 2008. Survival of adult songbirds in boreal forest landscapes fragmented by clearcuts and natural openings. Avian Conservation and Ecology 3(1):5. [Online.] Available at www.ace-eco.org/vol3/iss1/art5/.

White, G. C., and R. A. Garrott. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, New York.

White, J. D., and J. Faaborg. 2008. Post-fledging movement and spatial habitat-use patterns of juvenile Swainson's Thrushes. Wilson Journal of Ornithology 120:62–73.

Williams, P. L. 1990. Use of radiotracking to study foraging in small terrestrial birds. Pages 181–186 *in* Avian Foraging: Theory, Methodology, and Applications to Saline Lakes (M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr., Eds.). Studies in Avian Biology, no. 13.

Wiltschko, W., and R. Wiltschko. 1978. A theoretical model for migratory orientation and homing in birds. Oikos 30:177–187.

Winker, K., J. H. Rappole, and M. A. Ramos. 1995. The use of movement data as an assay of habitat quality. Oecologia 101:211–216.

Winkler, D. W., P. H. Wrege, P. E. Allen, T. L. Kast, P. Senesac, M. F. Wasson, and P. J. Sullivan. 2005. The natal dispersal of Tree Swallows in a continuous mainland environment. Journal of Animal Ecology 74:1080–1090.

Woolfenden, B. E., B. J. M. Stutchbury, and E. S. Morton. 2005. Male Acadian Flycatchers, *Empidonax virescens*, obtain extrapair fertilizations with distant females. Animal Behaviour 69:921–929.

Yezerinac, S. M., and P. J. Weatherhead. 1997. Reproductive synchrony and extra-pair mating strategy in a socially monogamous bird, *Dendroica petechia*. Animal Behaviour 54:1393–1403.

Zach, R., and J. B. Falls. 1979. Foraging and territoriality of male Ovenbirds (Aves: Parulidae) in a heterogeneous habitat. Journal of Animal Ecology 48:33–52.

Zack, S., and B. J. Stutchbury. 1992. Delayed breeding in avian social systems: The role of territory quality and "floater" tactics. Behaviour 123:194–219.

Received 12 May 2010, accepted 14 June 2010

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use