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POLYTERRITORIAL POLYGYNY IN NORTH AMERICAN PASSERINES

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Abstract.—Thirty-seven percent of the European passerines for which there are records of polygyny also practice polyterritoriality to varying degrees, and most of the polyterritorial species are also long-distance migrants that spend rather brief periods of time in the breeding area. As polygyny has been recorded for at least 71 species of North American (north of Mexico) passerines and, as many of these are long-distance migrants, it seems reasonable to assume that some of these species also practice polyterritoriality. A search of the literature revealed that there are records of polyterritorial polygyny for 11 species in North America, and there is circumstantial evidence for its occurrence in several additional species. In spite of considerable effort to understand the functional significance of polyterritoriality, especially for the Pied Flycatcher, *Ficedula hypoleuca,* it is still not clear exactly how this behavior might facilitate a mated male's acquisition of additional mates. Neither deception of females (i.e., males hiding their mated status) nor avoidance of female-female aggression appear to be wholly satisfactory explanations for polyterritoriality. Some instances of unmated males being polyterritorial for brief periods are also noted. It is likely that careful study of individually marked populations of passerines, as well as non-passerines, would discover additional species that at least occasionally practice polyterritoriality.

POLIGINIA POLITERRITORIAL EN PASERINOS DE NORTE AMÉRICA

Sinopsis.—El 37% de los paserinos europeos, en los cuales se ha encontrado la práctica de poliginia, practican algún tipo de politerritorialismo. La mayoría de las especies politerritoriales son a su vez migratorios de largas distancias que pasan muy poco tiempo en las áreas reproductivas. Como la poliginia ha sido informada en al menos 71 especies de paserinos de Norte América (al norte de México) y muchos de estos son migratorios de largas distancias, es razonable asumir que algunas de estas especies muestren politerritorialismo. Una búsqueda literaria reveló que hay informes de poliginia/politerritorialismo para 11 especies y que hay evidencia circunstancial para otras. A pesar del esfuerzo que se ha hecho para entender el significado de el politerritorialismo, en particular para *Ficedula hypoleuca,* no esta claro como esta conducta pueda facilitar la adquisición de parejas adicionales para un macho apareado. El engañar a hembras o el evitar agresiones entre hembras no parecen ser explicaciones satisfactorias para el politerritorialismo. Se han dado casos de machos que no están apareados y exhiben politerritorialismo. Es muy probable que estudios posteriores den lugar al descubrimiento de otras especies que practican el politerritorialismo.

Polyterritoriality, the concurrent holding of two or more disjunct territories in association with polygynous matings, has long been known to be of regular occurrence in several species of European passerines, most notably the Pied Flycatcher, *Ficedula hypoleuca* (von Haartman 1951, 1969). In a review of the mating systems of European passerines, Møller (1986) reported that polyterritoriality is actually rather widespread among species of this group; of 46 species for which there are both records of polygyny and adequate knowledge of territorial behavior, males of 17 species (37%) practice polyterritoriality at least to some extent. Møller's (1986) review also revealed that most of the species for which there are records of polyterritorial polygyny are long-distance migrants. Because at

TABLE 1. North American passerines for which there are records of polyterritorial polygyny.

Species	Reference
Acadian Flycatcher (*Empidonax virescens*)	Mumford 1964
American Dipper (*Cinclus mexicanus*)	Price and Bock 1973
Yellow Warbler (*Dendroica petechia*)	Spector 1991
Black-throated Blue Warbler (*D. caerulescens*)	Petit et al. 1988
Kirtland's Warbler (*D. kirtlandii*)	Walkinshaw 1983
Prairie Warbler (*D. discolor*)	Nolan 1978
American Redstart (*Setophaga ruticilla*)	Secunda and Sherry 1991
Common Yellowthroat[1] (*Geothlypis trichas*)	Stewart 1953
Brown-headed Cowbird (*Molothrus ater*)	Yokel 1986
Northern Oriole (*Icterus galbula bullockii*)	Williams 1982
Evening Grosbeak (*Coccothraustes vespertinus*)	Fee and Bekoff 1986

[1] Borderline between mono- and polyterritorial. Stewart (1953) asserted that the two females were probably unaware of each other.

least 71 species of North American (throughout this paper "North America" refers to the continental United States and Canada) passerines are known to practice polygyny to some extent (61 species in Ford 1983; at least 10 more species added since), many of them long-distance migrants, it is reasonable to expect that polyterritorial polygyny might also occur in this group of species. At present, only one paper has been published that deals explicitly with polyterritorial polygyny in a North American passerine (American Redstart, *Setophaga ruticilla,* Secunda and Sherry 1991). The purpose of this paper is to report records of polyterritorial polygyny for at least 10 more species of North American passerines (Table 1) and to point out that it is not clear exactly what role polyterritoriality might play in a male's acquisition of additional mates.

I became interested in polyterritoriality during the course of an eight-year (1976–1983) study of Yellow Warblers, *Dendroica petechia,* in central Minnesota. In 1977 I discovered a male known to have a mate and nestlings on a territory in the central part of the study area 200 m northeast of that territory feeding the full-sized fledglings accompanying an unbanded female. It was late in the breeding season (13 July) and this "family" group had just appeared on the edge of the study area. The group remained in this vicinity for two more days, and I observed the male feeding the young on all 3 d. The last day I observed this male on his known territory was 12 July, but he may have returned there at times when I was not present. Because I observed males ignore begging fledglings that were not their own, I believe it likely that this male had earlier acquired a second territory and mate somewhere off my study area. In subsequent years I paid close attention to the extraterritorial activities of banded, mated males and observed a number of them behaving like territory holders for brief periods on disjunct areas 50–230 m from their primary territories. All sang frequently on the second sites, one was seen to chase another male from the area and one courted an unbanded female that appeared for part of a day. None of these males was successful

in acquiring a second mate and within 1–7 d all appeared to be limiting their territorial activities to their original site. (Subsequently, Spector [1991] reported that he found a male Yellow Warbler with mates on each of two non-adjacent territories on his study area in Massachusetts.)

During my study I observed three cases of bigamy in which the nests of the two females were separated from each other either by an expanse of open water or 30–40 m of unsuitable habitat (stands of tall forest). Based on my own sensory perception, however, the two nesting areas in all three cases were in visual and/or auditory range of each other. These could simply be viewed as elongate territories with some unsuitable habitat separating the nesting areas of two females. Such examples make it apparent that drawing an unambiguous line between monoterritoriality and polyterritoriality is not easy, and that some objective criteria should be stated in order to distinguish between the two types of territoriality. I consider a male to be polyterritorial if (1) there are territories of other males between the multiple territories of one male (e.g., Acadian Flycatcher), or (2) the expanse of unsuitable habitat between the two territories is such that they are out of sight and sound of each other (e.g., Prairie Warbler), or (3) a male behaves territorially in disjunct areas, but does not show such behavior as he passes through unoccupied, but suitable, habitat between the areas (e.g., American Redstart, Black-throated Blue Warbler) (scientific names and references in Table 1).

Based on these criteria there are 11 species of North American passerines listed in Table 1 for which I have found records of polyterritoriality. In addition to these 11 species, males of at least four other species have been observed to engage in behavior consistent with polyterritoriality. M. R. Lein (pers. comm.) has observed males of the Tennessee Warbler (*Vermivora peregrina*) and Yellow-rumped Warbler (*Dendroica coronata*) singing on areas 500–700 m from their known territories. Kendeigh (1945) reported that males of the Chestnut-sided Warbler (*D. pensylvanica*) and Black-throated Green Warbler (*D. virens*) wander over larger areas than their defended territories and sometimes sing while doing so. That this behavior might lead to polyterritoriality is suggested by the fact that Kendeigh also reported similar behavior for males of two species for which there are now records of polyterritorial polygyny, the Black-throated Blue Warbler and the American Redstart.

Even though it may seem obvious that a mated male becomes polyterritorial in order to enhance his chances of acquiring additional mates, it is still not clear exactly how a male benefits from such behavior. Møller (1986) observed that most species for which there are records of polyterritorial polygyny are long-distance migrants whose occupancy of the breeding area is rather brief. This information, together with Temrin's (1984) study of polyterritorial polygyny in the Wood Warbler (*Phylloscopus sibilatrix*) support the "deception" hypothesis of Alatalo et al. (1981) which proposed that spatially separated secondary territories permitted males to hide their mated status from potential second mates who, owing to the shortness of the breeding season, cannot afford to take a long time

to evaluate prospective mates prior to forming a pair bond. However, Stenmark et al. (1988) failed to support the deception hypothesis for the Pied Flycatcher, and Breiehagen and Slagsvold (1988) suggested that polyterritoriality in the Pied Flycatcher may function to prevent or reduce female-female aggression in polygynous matings. Experiments conducted by Rätti et al. (1994), however, lead them to believe that female-female aggression is too weak to prevent polygyny. Temrin's (1989) more recent study of the Wood Warbler and his (Temrin 1991) detailed evaluation of the deception hypothesis suggest that deception of females by mated males may not always be possible, or even necessary. His conclusions were recently given additional support by Slagsvold and Dale (1994) who reported that female Pied Flycatchers appear to be able to detect a male's mated status but may settle with a mated male rather than incur the cost of additional mate searching. Furthermore, females appear willing and able to resist the aggression of primary females if no alternative mating options are available. Thus, even though there has been considerable effort put into understanding the functional significance of polyterritoriality in the Pied Flycatcher, and to a lesser extent, the Wood Warbler, it is still not clear how this behavior facilitates a male's acquisition of additional mates. The conclusion that neither deception nor reduction of female-female aggression is a wholly satisfactory explanation for polyterritoriality in these two species, however, does not necessarily rule them out as having functional significance in other species. Future workers would probably be well advised to continue to consider them as possible explanations for polyterritorial behavior. A possible explanation for polyterritoriality that seems to have been overlooked is that a mated male becomes polyterritorial (when space is available) simply because advertising from multiple locations increases his chance of being discovered by an unmated female searching for a mate.

Even though polyterritoriality is strongly associated with polygyny, short-term polyterritoriality might occasionally be advantageous in the seeking of a mate for a monogamous mating. Twice during the course of my study of Yellow Warblers I discovered unmated males from the study area singing in locations far from their known territories. In one case, a male had just arrived and re-occupied the same territory he had held the four previous seasons. Within a couple of days I discovered him singing not only on this territory but also on one 0.8 km away. A day later he acquired a mate on the new territory and even though he continued to return and sing on his original territory for five more days, he lost ground daily to an encroaching neighbor and eventually restricted his territorial defense to his new area. In the other case, also early in the season, a male returned to the study area for the fourth consecutive year and occupied a territory between two territories that he had held in previous years. Two days after his arrival I found him singing both on his study-area territory and an area approximately 1.2 km to the north. I do not know if he returned to this latter area on subsequent days. Three days after singing on both areas he acquired a mate on his first territory and later became a bigamist on

that territory. Unmated male Kirtland's (Mayfield 1960), Prairie (Nolan 1978), and Blackpoll, *Dendroica striata,* (B. Eliason, pers. comm.) Warblers have also been reported to sing on disjunct areas within the same day. Unmated males may benefit from intermittent polyterritoriality because it increases the area in which they might attract or encounter an unmated female. It may also enable males, either mated or unmated, to assess sites for possible later relocation. In fact, R. B. Payne (pers. comm.) has occasionally observed male Indigo Buntings (*Passerina cyanea*) singing several hundred meters from their territories and a few of these males have later made permanent shifts to the new area.

To date, fewer North American than European species of passerines have been detected practicing polyterritoriality, and no North American species appears to be as extensively polyterritorial as are several European species (e.g., Pied Flycatcher, Wood Warbler [Møller 1986]). Although this regional difference may prove to be real, it is also possible that it reflects a difference in the level of knowledge about the passerines of the two continents. For example, in 1969 von Haartmann reviewed the mating system of European passerines and found records of polygyny for 47 species. In that same year Verner and Willson (1969) reviewed the mating systems of North American passerines and reported that some polygyny or promiscuity occurs in 39 species. In 1986 the number of European passerines for which there were records of polygyny remained at 47 (Møller 1986). In 1983 when I reviewed the records of polygyny for North American passerines (Ford 1983) the number had increased to 61 species and currently that number is at least 71. A reasonable conclusion is that the breeding biology of a greater number and proportion of European passerines has been studied in comparison to North American passerines, and that as more color-banded populations of the latter are studied, more examples of polygyny (as well as polyandry) and polyterritoriality are being discovered. Currently, there are records of polygyny for 27.3% of European passerine species and approximately 26% of North American passerines. As it is likely that even now a smaller percentage of the latter group has been carefully studied compared to the former group, more cases of polygyny probably will be discovered. Polyterritoriality may prove to be an infrequent but fairly widespread phenomenon among North American passerines, especially when population densities are such that not all local suitable habitat is occupied early in the breeding season.

Field workers will have to make special efforts to detect polyterritoriality, however, because some males have been known to hold two territories that are more than a kilometer apart (e.g., Fee and Bekoff 1986, Mayfield 1960, Nolan 1978); the two nests of a bigamist male American Dipper were 3.2 km apart (Price and Bock 1973). As a further indication that additional records of polyterritoriality may be found for North American passerines, six of the 17 polyterritorial European species are members of genera that have species with sizeable breeding populations in North America (*Anthus, Cinclus, Oenanthe, Phyllosopus,* and *Carpodacus*), and only one of the current North American records is for a species of

one of these genera. In fact, all but two of the North American passerine species for which there are records of polyterritoriality are members of groups that do not occur in Europe (Tyrannidae, Parulinae and Icterinae). The only other group aside from *Cinclus* that is also represented by a species in Europe is the genus *Coccothraustes.*

The two groups with the greatest number of species known to practice polyterritoriality are the old world warblers (Sylviinae) in Europe and the new world warblers (Parulinae) in North America. Although these two groups are not thought to be closely related, the similar levels of polyterritoriality may reflect some similarity in behavioral and/or ecological adaptations that warrant further analysis. Many species of both groups are long-distance migrants, and both groups have a fairly large number of species practicing polygyny to various degrees. Approximately 30% (14 of 47) of European species for which there are records of polygyny are sylviines, the comparable figure for North American parulines is approximately 21% (15 of at least 71 species). It may also prove to be the case that marked populations of proportionally more species of these groups (especially the parulines) have been carefully studied than have species of other groups within their geographical areas.

Finally, even though the focus of this review is on passerines, students of non-passerine birds should also be alert to the possibility of polyterritoriality occurring in this group. A prime candidate in North America is the Boreal Owl (*Aegolius funereus*) which is regularly polyterritorial in Europe (Carlsson et al. 1987). In North America there is a report of a male Snowy Plover, *Charadrius alexandrius* (Warriner and Warriner 1978) simultaneously holding two non-adjacent territories, and at least two examples of bigamy in the Peregrine Falcon, *Falco peregrinus* (H. B. Tordoff, pers. comm.) in which the two nests of one male were 5 km apart and those of the other male over 6 km apart.

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