

AVIAN REMOVAL EXPERIMENTS: DO THEY TEST FOR HABITAT SATURATION OR FEMALE AVAILABILITY?

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Abstract. The classical test for habitat saturation and the existence of floaters in birds involves removing territorial individuals and documenting whether replacement occurs. In most experiments with birds, only males are removed. An alternative explanation for the observed reoccupation of vacant territories by males is that they are attracted by the presence of unmated (widowed) females, and not necessarily by availability of habitat.

We performed experiments with a migratory passerine bird, the Black-throated Blue Warbler (*Dendroica caerulescens*), at the Hubbard Brook Experimental Forest, New Hampshire, in which we removed (1) only males, (2) only females, and (3) both males and females from breeding territories. In all cases when only males were removed, new or neighboring males colonized the vacant territory, whereas when both sexes were removed only one of nine territories was reoccupied; when females were removed, there was no replacement. Our results suggest the importance of considering female availability, in addition to habitat availability, in studies of habitat distributions and population dynamics of birds and other species.

Key words: *Dendroica caerulescens*; female limitation; floaters; habitat saturation; population regulation; removal experiments; surplus population; territorial behavior.

Territorial behavior during the breeding season has long been considered an important mechanism in determining the local distributions and abundances of many bird populations (Hinde 1956, Brown 1969, Fretwell and Lucas 1970, Watson and Moss 1970, Klomp 1972, Newton 1992). This assumes that habitats vary in quality and that, in years when bird density exceeds the carrying capacity of the more suitable habitats, some individuals are forced by already territorial individuals into suboptimal areas where reproductive success is compromised, or they become floaters and are prevented from breeding at all (Brown 1969). Territorial behavior has, therefore, been thought to act as a mechanism that limits local abundances (Fretwell and Lucas 1970, Newton 1992). Demonstrating habitat saturation, competitive exclusion, and the presence of a surplus population (i.e., floaters) has usually been attempted by experiments in which territorial individuals are removed and their vacated territories are monitored for replacements (see reviews by Klomp 1972, Newton 1992). In this paper, we present experimental results and theoretical arguments indicating that removal experiments, at least for species with particular life history and mating strategies, fail to demonstrate habitat saturation or even the existence of floaters. Alternative

hypotheses, such as how the availability of females influences male behavior, need to be given more consideration.

The classical test for habitat saturation and the existence of floaters in avian studies involves removing territorial individuals and documenting whether or not replacement occurs. If new individuals settle into experimentally vacated territories, it is concluded that a lack of suitable habitats, combined with territorial behavior, limits breeding opportunities (Klomp 1972, Newton 1992). Most experimental manipulations, however, especially those with passerine birds, have removed only males from territories, leaving females (e.g., see Hensley and Cope 1951, Stewart and Aldrich 1951, Thompson 1977, Arvidsson and Klaesson 1984, Hogstad 1989, Sherry and Holmes 1989; see Newton 1992 for additional references). Because females were left on the territories in these cases, an alternative explanation for the observed reoccupation by males is that they were attracted by the presence of these widowed females and not necessarily by the availability of habitat.

To test this hypothesis, we conducted removal experiments with Black-throated Blue Warblers (*Dendroica caerulescens*) breeding in a northern hardwoods forest, using three treatments: (1) removal of both the male and female, leaving the territory vacant; (2) re-

TABLE 1. Results of experimental removals of Black-throated Blue Warblers (*Dendroica caerulescens*) from breeding territories in northern hardwoods forest at Hubbard Brook Experimental Forest, West Thornton, New Hampshire.

Treatment	Number of territories treated				Number of territories with replacement ^{†,‡}			
	1990	1993	1994	Combined	1990	1993	1994	Combined
Male and female removed	2	6	1	9	0	0	1	1
Male removed	1	7	5	13	1	7	5	13
Female removed	0	0	5	5	0	0	0	0

[†] All replacements were males.

[‡] Fisher's exact test comparing the proportion of combined removals to combined replacements for male-only treatments vs. male and female treatments ($\chi^2 = 22.562$, $df = 1$, $P < 0.000$).

removal of only the male, leaving the female; and (3) removal of only the female, leaving the male. We predicted that if there are male floaters present due to habitat saturation, then replacement should occur upon removal of both the male and female from the territory, i.e., in a completely vacated territory. Alternatively, if the presence of floaters is due to a shortage of females, then replacement should occur only when the male is removed, leaving the female. Finally, if nonbreeding (floating) females are present in the population, then they should settle in territories where resident females are removed. The latter finding would indicate a surplus of females, i.e., that females are not limiting.

Methods

This study was conducted in the Hubbard Brook Experimental Forest in the White Mountain National Forest, West Thornton, Grafton County, New Hampshire, USA. The forest is second-growth northern hardwoods, with the canopy dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula allegheniensis*), with some white ash (*Fraxinus americanus*) and red spruce (*Picea rubens*). The forest understory is composed primarily of the saplings of the canopy trees, along with hobblebush (*Viburnum alnifolium*), striped maple (*A. pensylvanicum*), and mountain maple (*A. spicatum*) (Bormann and Likens 1979, Holmes et al. 1986). Removals were conducted in areas with a dense shrub layer, the preferred habitat of Black-throated Blue Warblers (Holmes et al. 1992, 1996).

Black-throated Blue Warblers were removed from territories that were located ≥ 300 m, and often > 500 m, apart in an undisturbed section of forest in the west end of the Hubbard Brook valley. Neighbors of removed birds were not color-banded, which limited our ability to discriminate between true floaters and expansion by neighbors. However, falsification of our hypothesis only required us to determine that reoccupation did not occur when both males and females were removed. To aid in classifying replacement individuals as either territorial neighbors or floaters, we did a pre- and postremoval census of all singing males neigh-

boring the manipulated territory. These data, combined with territory maps of replacement birds (i.e., neighbors could often be followed back to their territories), provided some indication of the status of any new birds that appeared in the vacated territory. All territorial pairs were randomly assigned to one of three treatments: (1) removal of both the male and female, leaving the territory vacant; (2) removal of only the male, leaving the female; and (3) removal of only the female, leaving the territorial male. In total, we permanently removed individuals from 27 spatially separated territories (see Table 1 for details on number removed per treatment per year). Birds were collected with a 0.410-gauge shotgun, and specimens were deposited at Dartmouth College. Removals took place in early- to mid-June, during the incubation period and after spring migration was complete (Holmes et al. 1992, Holmes 1994). This timing of removals ensured that any birds reoccupying vacant areas were not late migrants, and that replacement birds would still have time to nest prior to late-summer departure.

On days 1, 3, 7, and 14 following removal, each territory was searched for 30–60 min for the presence of replacement Black-throated Blue Warblers. We considered a new male observed singing on an experimental territory or following a female, or the presence of a new female, on any of these days following a removal as constituting a replacement. To test for significance, a Fisher's exact test was used on data, combined across years, comparing the proportion of removals to replacements for the male-only treatment vs. the male and female treatment.

Results

In only one of nine cases in which both the male and the female were removed, leaving the territory vacant, did a new male reoccupy an experimentally vacated territory (Table 1). In this one case, the new bird was first seen on the vacant territory 1 d after removal of the original male and female, and was present on all but the last visit to the territory 2 wk later. This new male came from a direction where we had previously documented a neighboring male countersinging

with the male that was subsequently removed. After the removal, no countersinging male was recorded in that direction, suggesting that the new male was actually the neighbor who shifted his territory into the vacated territory, rather than an actual floater. On the other eight territories in which both members of the pair were removed, no Black-throated Blue Warbler of either sex was detected within the vacated territories on any subsequent visits.

In all 13 cases in which only the male was removed, leaving the female to continue nesting, new males reoccupied the vacated territories (Table 1), often 1 d after the removal. This represents a significantly greater proportion of replacements relative to treatments in which both male and female were removed (Fisher's exact test; $\chi^2 = 22.562$, $df = 1$, $P < 0.000$). Although neighbors were not color-banded, we were able to determine that in five of the 13 removals (38%), the replacement male was indeed a neighbor enlarging its territory to encompass the newly available female (determined by following these males back to their primary territories). The origins of the remaining replacement males could not be determined; they could have been territorial males from more distant territories, or they could have been true floaters. In all of the male-only removals, new males appeared usually within the first 1–3 d, and were seen on all subsequent visits to the territory, unless a nest had been depredated (which happened in five of the 13 cases after new males had already appeared). In the latter situations, neither the male nor the female could be found after the predation event, and those territories remained vacant for the remainder of the season. A replacement male present on a removal territory usually sang above the nest while the female incubated, or followed her while she foraged. None of these replacement males fed young at the nest or fledglings of the removed male, similar to the findings of Power (1975) with Mountain Bluebirds (*Sialis currucoides*). We also found no evidence of infanticide by the new males, as reported for Tropical House Wrens (*Troglodytes aedon*) by Freed (1987).

In the final treatment, in which only the female was removed ($n = 5$), none of the males acquired a new female. Soon after removal of their female, these males shifted their singing locations from the subcanopy to the canopy, and their song rates increased dramatically (P. P. Marra, *personal observation*). These widowed males were often absent from their territories, suggesting that they were wandering, possibly looking for available females or extra-pair mating opportunities.

Discussion

Our results challenge the validity of conventional removal experiments as tests for habitat saturation and the presence of floaters in the breeding season. The

presence of female Black-throated Blue Warblers on territories where males had been removed clearly attracted new males, whereas removing both sexes and leaving the territories vacant resulted in no replacement. In only one out of 10 cases in which both the male and female warbler were removed did a new male reoccupy the empty territory. We conclude that removal experiments in which only males are removed may not adequately test whether or not the habitat is saturated. In the following discussion, we consider the efficacy of avian removal experiments and argue that another factor, specifically female availability, needs to be considered as an influence on male behavior and distribution during the breeding season, at least for species with certain life history strategies.

Can removal experiments ever be appropriate tests of habitat saturation? The few unambiguous demonstrations of habitat saturation involving the removal of both the male and female from a territory have been conducted with cavity-nesting passerines (e.g., Krebs 1971, 1977, Power 1975, Ekman et al. 1981, Bowman and Bird 1986, Wesolowski et al. 1987), resident non-passerines (e.g., Watson 1965, Hannon 1983, Mossop 1985), and resident passerines (Knapton and Krebs 1974). Our study appears to be the first to remove both the male and the female from the territory of a migratory, open-cup nesting passerine species. We will argue that excluded males in such species may wander more in search of females than of territory vacancies. As a result, even experiments removing both the male and the female, creating a complete territory vacancy, may not provide an adequate test of habitat saturation.

Different life history strategies may complicate predictions of why replacements might or might not occur, depending on what factor(s) most limits a particular species. For example, in the case of cavity-nesting species, nest sites seem to be most limiting (e.g., Balda and Brawn 1988, Gustafsson 1988), and often new pairs move into a territory following removal of the resident pair (Krebs 1971). With resident bird species, territories are more critical for adult survival during the non-breeding season (McCleery and Perrins 1985), so adult males defend territories year-round, and will occupy territories made vacant by the removal of both male and female (Knapton and Krebs 1974). For open-cup nesting migratory passerines, the availability of suitable habitat may be a limiting factor as males arrive and settle into breeding habitats each season; saturation of these habitats may be determined in part by territorial behavior and male density (Fretwell and Lucas 1970). Another important factor is the number of males relative to the number of females (i.e., operational sex ratio, Emlen and Oring 1977), which determines the ratio of mated to unmated males. We propose that this latter ratio, in particular, influences the results of re-

removal experiments for migratory, open-cup nesting passerines.

Our results with Black-throated Blue Warblers suggest that males respond to female availability, not to habitat vacancies, consistent with other recent observations on the life history and mating systems of this species and other migratory passerine birds. The classical view for such species is that late-arriving males will fail to acquire a territory and will become "floaters," spending their time wandering inconspicuously among territory holders, presumably continuing to look for territory vacancies (e.g., Delius 1965, Brown 1969, Krebs 1971, Welsh 1975, Smith 1978, Arcese 1987, Breitwisch 1989, Hogstad 1989). Our results suggest that this presumption that "floaters" search for habitat vacancies may, in fact, be flawed. Searching for a territory vacancy after initial settlement assumes that there is some probability of attracting an unmated female on that territory; this appears to be unlikely in many, if not most, migratory open-cup nesting passerines (Breitwisch 1989, and this study). For females, being a floater would be a poor strategy, since a female can often pair with an already-mated male and experience some reproductive success, albeit lower, as a secondary mate (see Slagsvold and Lifjeld 1994), but higher than if she remains unmated for an entire breeding season. Therefore, if a male is still unmated when migration is complete, searching for available females, either to sire a second brood (Meek and Robertson 1992) or to obtain extra-pair copulations, may result in higher fitness than acquiring a territory and trying to attract a floater female. This scenario is consistent with recent DNA fingerprinting data that indicate high levels of extra-pair copulations in some passerine species (e.g., Brooker et al. 1990, Westneat 1990, Westneat et al. 1990, Mulder et al. 1994, Stutchbury et al. 1994, Birkhead and Møller 1995). Although most studies find that the cuckolding males are predominantly the territorial neighbors, a small percentage of nestlings usually cannot be assigned paternity (e.g., Gibbs et al. 1990, Westneat 1990, Mulder et al. 1994), possibly because they were sired by floater males. Therefore, the best strategy for males, especially if they are unmated, would be to seek out a female, rather than a territory, so as to experience some reproductive success.

Pruett-Jones and Lewis (1990) conducted an experiment, similar to ours, with the Superb Fairy Wren (*Malurus cyaneus*), a cooperative breeder, to determine whether offspring delayed dispersing from their natal territory because of limited availability of habitat or of females. Their results demonstrated that nonbreeding males did not disperse onto vacant, but previously occupied, territories in the absence of females, but did so when females were reintroduced onto those terri-

ories. They concluded that young males in this species delay dispersal and remain cooperative in response to a limited number of females, and only secondarily in response to habitat limitation. This system is similar to that of Black-throated Blue Warblers, in that female availability appears to determine the behavioral strategies of unmated males.

Female availability may be significant because male-biased sex ratios are thought to be widespread among socially monogamous birds (Breitwisch 1989). For Black-throated Blue Warblers in undisturbed northern hardwoods forest, the percentage of unmated males ranges from 0 to 26% (Holmes et al. 1992), suggesting a strong male bias in at least some years. This percentage may be appreciably higher in disturbed or fragmented habitats. The factors creating male-biased sex ratios in birds are poorly understood (Breitwisch 1989). The sex ratio of zygotes in birds is assumed to be 1:1 (Clutton-Brock 1986, Slagsvold et al. 1986), so a deficiency of females must be due to higher female mortality. Differential mortality could result from higher levels of parental investment and predation risk for breeding females (Trivers 1972; see Breitwisch 1989) or from events in the nonbreeding period, such as the exclusion of females into less suitable habitats by dominant males (Marra et al. 1993), resulting in higher mortality (Sherry and Holmes 1996; P. P. Marra, *personal observation*). More information on male, and especially on female, mortality schedules during the breeding and nonbreeding periods is necessary to better understand the factors that control female availability in bird populations.

In summary, male removal experiments do not provide an adequate test for habitat saturation or for the presence of floaters, at least for migratory, open-cup nesting passerine birds. Furthermore, female availability may play an important role in determining mating strategies and spatial dynamics of males. Differentiating between the relative effects of habitat availability vs. female availability will be challenging. Replacement following experimental removal of both the male and female from a territory may provide the best evidence of habitat limitation (Newton 1992), although, as we discussed, this may not be appropriate for all avian taxa. Another approach would be to examine the territorial dispersion of color-banded individuals across habitats and years to determine how variations in population size influence the spacing patterns (territorial vs. floating) and behavior (mated vs. unmated) of males and females. Such data would also provide much-needed information on the demographic structure of bird populations and would contribute to our understanding of how populations are regulated.

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