ORNITOLOGIA NEOTROPICAL

Volume 9 1998 No. 2

ORNITOLOGIA NEOTROPICAL 9: 111–119, 1998

THE CONCEPT OF FLOATER

Kevin Winker

University of Alaska Museum, 907 Yukon Drive, Fairbanks, Alaska 99775-6960.
E-mail: ffksw@uaf.edu.

Abstract. The concept of "floater" is widely used in avian literature, yet lacks a definition fully encompassing its use. Formal definitions have tended to restrict its use to breeding systems. This is unwarranted, considering the widespread occurrence of territoriality in breeding and nonbreeding systems. A working definition of floater is: An individual member of a largely territorial population who is not defending a territory, and whose movements encompass an area substantially larger than those of the average territorial conspecific. Floating is apparently a widely occurring phenomenon, but remains one of the least-known aspects of territorial systems. A search is made for commonality in use among diverse studies, and suggestions are made for further research on this behavioral category. The presence of floaters in a population may be of use in gauging the density of a territorial population in relation to the defended resource base. The presence of this behavioral class has recently been proposed as a metric in assessing population limitation in relation to conservation concerns. Given the body of evidence from studies of territorial systems, demonstrating the existence of excluded individuals in territorial populations does constitute strong inference that resources are limiting. Nonbreeding Neotropical communities, where Nearctic-Neotropic migrants are frequently both common and territorial, and where habitat availabilities are undergoing alteration, are superb places to study this behavioral phenomenon, both as a behavior and as an indicator of population regulation in territorial systems. *Accepted 28 August 1998.*

Key words: Behavior, conservation, floating, habitat selection, territoriality, territorial systems.

INTRODUCTION

A concept needs a label, and a label is only as useful as the clarity of its definition. The term "floater" has been rather loosely applied in the literature, and has been given definitions (formally and through usage) that do not reflect the full extent of the existence of this behavioral category. This note discusses the concept of floater, examines usage of the term in the literature, and attempts to give some focus to the term and the behavioral class it describes. This is not intended as a review, but rather as a broad discussion of an interesting aspect of territoriality that is in need of further research. Although based in the avian literature, this discussion has wider applicability.

THE FLOATER

All individuals in territorial populations are not always territorial. Darwin (1871: 50, 103–8) noted both the presence of "wandering males" and in many cases rapid replacement of a lost mate when one of a pair was shot. Lack (1954: 272) and Deramond (1959: 193), among others, postulated the existence of nonterritorial individuals excluded from breeding by lack of suitable space. Individual birds whose behavior fits the concept of Lack's "wanderers" and Deramond's individuals "isolés errant çà et là" have been described in many territorial systems: Nonbreeding territorial systems (e.g., Rappole & Warner 1976, Kodric-Brown & Brown 1978, Myers *et al.* 1979, Rappole & Warner 1980, Davies & Houston 1981, Rappole *et al.* 1989, Winker *et al.* 1990, Stutchbury 1994); breeding territorial systems (e.g., Hickey 1940, Watson & Jenkins 1968, Manuwal 1974, Stutchbury & Robertson 1985, Szuba & Bendell 1988); and year-round territorial systems (e.g., Smith 1978, 1989). Although each of these studies described a similar class of individual, not all used the term floater as a descriptor. Nevertheless, this term has been used sufficiently through time that it serves well as a focus for discussion of this particular behavioral class (e.g., Morel & Bourlière 1962, Brown 1969, Smith 1978, Rappole & Warner 1980, Price 1981, Wilcove & Terborgh 1984, Stutchbury & Robertson 1985, Stamps 1988, Rappole & McDonald 1994).

Previous definitions of the term floater have varied, but probably the most formal (e.g., Brown 1969, Smith 1978, Lincoln *et al.* 1985) have restricted its use to the breeding season. Brown (1969: 294) linked usage of the term in breeding territorial systems directly to the "population reserve" of Meunier (1960) as indicative of nonbreeding individuals (whose status as nonbreeders is not due to a physiological inability to reproduce). Smith (1978: 571) defined floaters as "sexually mature birds prevented from breeding by some factor (e.g., territorial behavior of others)". These definitions do not fully reflect usage in the literature. Morel & Bourlière (1962), Rappole & Warner (1980), and Price (1981) each used the term in connection with work done on the wintering grounds of long distance avian migrants, and Stamps (1988) used floater to describe nonterritorial juvenile *Anolis aenus* lizards, suggesting that a definition with a breeding ground bias is unwarranted. Interestingly, the term *territory* apparently went through a similar developmental phase, being first applied to breeding systems and later to nonbreeding (Nice 1941).

Because there appears to be abundant evidence that a similar type of individual exists in a variety of territorial systems, and no single term has been accurately and consistently used as a descriptor for this behavioral class, some focus can be given to discussion of this type of behavior by a comprehensive definition for it. Hence I offer a working definition of floater: An individual member of a largely territorial population who is not defending a territory, and whose movements encompass an area substantially larger than those of the average territorial conspecific. Implicit within this definition is that these movements are the result of a failure (thus far) to successfully compete for a sufficient quantity or quality of a required resource and the space it occupies. This definition seems consistent with the concepts that have led to the wide use of floater, but is not offered as a rigid definition; as our understanding of the underlying biology increases, the concept will surely continue to grow and change.

Floaters, whether encountered singly or in groups, constitute the floating portion of a population, or the proportion of the population lacking territories. Although this definition appears to restrict use of the term to intraspecific situations, interspecific territori-

ality may be found to create the same behavior class. I have purposely deviated from the usage of Morel & Bourlière (1962: 390) because of the broad scope at which they applied the term. These authors followed the earliest use I have seen: Burton (1860: 19) used the phrase "floating population" to describe non-native or non-permanent residents in a small town in Zanzibar. The "populations flottantes" of Morel & Bourlière (1962) were simply wintering migrant "species", compared with locally sedentary or resident "species" (emphases mine). The terms "wintering migrant, transient, resident, nonresident", and "sedentary" are sufficient descriptors at this level.

DISTINGUISHING A FLOATER

Not all nonterritorial birds are floaters. First, birds at very low densities relative to their resource base have no reason to defend resources, and are therefore nonterritorial. These birds are not floaters by definition, because they do not exist in a territorial system. Second, we must consider the causative factor of a floater's existence (lack of suitable unoccupied space) and other types of movement that might look very similar. Conceivably there are two types of movement that might be called floating: forced versus self-initiated. The term floater should be applicable only to the former, when an individual is forced to make relatively large-scale movements due to the actions of others. Environmental factors might function in conjunction with "actions of others" to cause individuals to float. Schwartz (1964) noted that some wintering first-year Northern Waterthrushes (*Seiurus noveboracensis*) in Venezuela "make major changes before finally settling" because the advancing dry season made their former areas "unsuitable."

Provided they are properly conducted, removal experiments constitute an excellent means of seeking out floaters by assessing the importance of vacant suitable space in a population. Experiments in which suitable vacancies have been created have shown that breeding season floaters (or presumed floaters) often quickly occupy vacancies (Stewart & Aldrich 1951, Hensley & Cope 1951, Watson & Jenkins 1968, Brown 1969, Klomp 1972, Manuwal 1974, Davies 1978, Smith 1978, Stutchbury & Robertson 1985; some of these references and others are discussed by Krebs 1971). Thus far, comparable experiments from the winter territorial systems of migrants are uncommon, but they suggest that the concept is equally applicable. Rappole & Warner (1980) reported seven removal experiments among four species resulting in the occupancy of the vacated area by presumed floaters. Morton *et al.* (1987) performed removal experiments in wintering Hooded Warblers (*Wilsonia citrina*), but were uncertain of the behavioral status of territorial replacements prior to the removal of the original territory holders. Similarly, three instances of replacement occurred in wintering Wood Thrushes (*Hylocichla mustelina*) after accidental removal (death) of territory holders, but the prior behavioral status of the replacement individuals was uncertain (Winker *et al.* 1990). Marra *et al.* (1993) conducted removal experiments in American Redstarts (*Setophaga ruticilla*) wintering in Jamaica, and Stutchbury (1994) conducted further removal experiments on Hooded Warblers wintering in Mexico. In both of these cases at least some of the replacing individuals were inferred to be floaters (unbanded birds entering a marked population).

An important question to ask in any removal experiment is whether the relocating individual formerly occupied a different territory elsewhere. This is important in ascertaining whether floater is accurately applied, since a simple, direct movement from one territory

to another (probably perceived as better by the moving individual) would not constitute floating. For example, in a removal experiment involving Great Tits (*Parus major*), Krebs (1971) found that replacements were birds that had held territories in suboptimal habitat nearby. The occupancy of suboptimal habitat is another example of how population limitation can occur through territoriality (e.g., Brown 1969), but it need not involve floating individuals.

Given the generally rapid rate at which vacancies are filled, it is likely that some form of exploratory, or information-seeking movements are made by local individuals. These movements are probably made by territorial as well as nonterritorial members of the local population. I have seen a presumably territorial wintering Wood Thrush adopt a "subdued" demeanor when outside its territory while approaching to investigate a tape playback of two aggressive birds. I also found that unbanded (presumably nonterritorial) birds showed comparable behavior during similar playbacks (dubbed "cruising," Winker 1989). Schwartz (1964: 181) found that wintering Northern Waterthrushes became less aggressive when outside their territories. Nolan (1978: 341–343) gave a thorough description of exploration in male Prairie Warblers (*Dendroica discolor*). Only uniquely banded individuals enabled him to recognize these movements as being those of males holding territories elsewhere – quite distinct from the conception of floating movements. These observations caused Nolan to recognize the potential problem of mislabeling unidentified birds on others' territories. Additional records of extraterritorial forays and of "sneaking" behavior are sprinkled throughout the literature for breeding systems, but it remains to be determined what proportion of these are the movements of true floaters. Nevertheless, removal experiments can allow the investigator to learn something about the population under investigation, and the filling of vacancies suggests that floaters may be present.

In addition to exploration movements of territory holders, self-initiated dispersal and spacing movements (I follow Gauthreaux [1982: 127] in the use of these terms) might also appear to be the movements of a floater. Nolan (1978: 343) suggested that exploration might serve in part as a dispersal mechanism. Clearly, the true status of an individual can be difficult to ascertain, and the distinction between forced versus self-initiated movement would seem to require detailed knowledge of individual status. And individuals may not in some cases fit rigid categories. Staicer (1992) showed that individual behaviors in a wintering Nearctic-Neotropic migrant territorial system can be quite variable, with sedentary birds exhibiting behaviors along a continuum from aggressive defense to simply being a nonaggressive (seemingly nonterritorial) sedentary individual.

Further confusion might arise in a territorial system in which flocking also occurs. Floaters might very well join flocks, perhaps due to the well documented antipredation value of flocks, or perhaps to exploit dense, undefendable resources. Territorial members of a population might join flocks for the latter purpose as well, or passing migrants that are not true members of the population may flock. In other words, the simultaneous presence of these dual strategies in a population does not mean that floaters are present. Removal experiments to examine whether suitable space is limiting, with concurrent efforts to determine the prior behavior of replacing individuals, is the best way to determine whether floaters are present, regardless of the strategies they might adopt in lieu of territorial defense.

FLOATERS AND RESOURCES

Regardless of our knowledge of the former

status of an individual occupying a vacancy, we gain some information when vacancies are filled. When a vacancy in a territorial system becomes occupied, we know that: 1) The occupying individual is exercising an option not formerly available; and 2) By doing so it has abandoned a former course of action. The theory of natural selection suggests that in selecting a new course the individual has improved its lot in some fashion. Thus, regardless of whether the true status of an individual is known, the occupancy of freshly created vacancies suggests that territoriality is causing some individuals in the population to pursue a suboptimal course. Suboptimal courses are likely to include the occupancy of suboptimal habitat(s) (whether or not a territory is held there), and floating.

Floaters seem to appear in populations when the preferred habitat or space is fully occupied by territorial individuals (Brown's [1969] critical density level 3). The appearance of floaters at population densities that are high relative to the resource base has been demonstrated for many breeding populations (e.g., Watson & Jenkins 1968, Manuwal 1974, Smith 1978, Stutchbury & Robertson 1985), and, given territorial theory and present evidence, seems a likely outcome in all territorial systems under high densities. This has yet to be demonstrated in relation to nonbreeding territories away from breeding areas, but such a demonstration will be difficult, given that in these situations survival is the coin by which optimality must be judged.

With the theoretical relationship between population density and the presence of floaters comes the implication that floaters are disadvantaged in relation to territorial conspecifics. The hypotheses that 1) floaters appear at high population densities, and 2) they are disadvantaged, are supported when it is shown A) that the option of territoriality is not present because preferred or suitable resources and the space they occupy are already defended, and B) that floaters are negatively affected in some way by the lack of suitable vacant space. These (A and B) must be shown (or at least strongly implicated) for a given population before the presence of floaters can be used as a criterion in assessing population densities. Note that here density refers to behavioral density (or density in relation to the resource base as exhibited through individual behavior), and not absolute density (number of individuals per square unit area). The latter has little meaning without a connection to the species' biology, except perhaps as a crude, indirect measure of resource availability, and then only under the assumption of relative resource homogeneity.

Although it is likely that in most breeding territorial systems an individual without a territory will be at a disadvantage, this is by no means assured (Gross & Charnov 1980). It is far less certain that a nonbreeding floater is at a disadvantage with respect to a nonbreeding territorial conspecific, particularly in migrant populations, where the wintering grounds are removed from the breeding area. In territorial systems of this type, where surviving in good condition until the advent of spring migration and the forthcoming breeding season is the only object, floaters are at a disadvantage only if they have a lower probability of survival. The very existence of territoriality in such situations suggests that this is the case, but unless nonbreeding mortality is very high, a disadvantage to floaters can be difficult to demonstrate, especially considering the necessity of an individually marked population and the potentially very dynamic nonbreeding territorial system (e.g., Myers *et al.* 1979, Staicer 1992). Nevertheless, it can be done: Rappole *et al.* (1989) showed that floating Wood Thrushes experienced higher mortality rates than territorial individuals in a wintering area in Mexico.

In examining the question of whether

declining Nearctic-Neotropic migrant species are limited on the breeding or wintering grounds, Rappole & McDonald (1994: 655) presented the following prediction: If populations were limited on the breeding grounds, a species would show little or no evidence of floaters in wintering populations. Given the body of evidence from studies of territorial systems, demonstrating the existence of excluded individuals in territorial populations does constitute strong inference that resources are limiting. Thus, comparisons of breeding and wintering tests for the presence of floaters in the same species and preferably during the same annual cycles across the same years (Rappole & McDonald 1998) could be illustrative in determining where population limitation occurs. Such tests would seem to be important in species of conservation concern, for to be effective conservation efforts must be directed toward the most limiting factor in the annual cycle.

Although the presence of floaters seems to indicate that the population under study fills available optimal habitat beyond capacity, demonstration of this behavioral category requires an intimate knowledge of individuals. Removal experiments showing relatively rapid filling of territory vacancies (regardless of whether we know the true behavioral status of the individuals filling the vacancies) suggest that optimal habitat is limiting in some manner. But the level of effort required to determine the behavioral status of marked individuals is rather high. Therefore, demonstrating the presence of floaters, or inferring their presence through removal experiments, may not be the best way to assess whether habitat availability limits a population. Instead, we might take advantage of the mobility of animals and their behavioral tendency to show occupancy times that are positively correlated with habitat quality. This reasoning caused Winker *et al.* (1995) to suggest that standard mark-recapture methods would serve to assess quality among habitats. By simple extension, significantly variable turnover rates among individuals occupying a variety of habitat types would suggest that habitats of variable suitabilities are occupied, and that optimal habitat is limiting. In this manner, both sample sizes and geographic coverage could be dramatically enhanced compared with what might be accomplished in a detailed behavioral study. Thus, if the question is solely one of population status in relation to resources, seeking floaters may not be the best approach, regardless of its utility in other contexts.

In conjunction with other information (particularly in nonbreeding systems), the presence of floaters in a territorial system would seem to be informative about a population's status in relation to its resources. Demonstrating the nature and degree of disadvantage suffered by floaters in not having a territory may be difficult in some territorial systems.

WHERE TO LOOK FOR FLOATERS?

The creation of suitable vacant space and the responses of local individuals are of fundamental importance when assessing the status of a territorial population and when seeking floaters. Although I use the concept of territory as the space that defended resources occupy, floaters should not appear with equal likelihood in any type of territorial system. By what is currently known or hypothesized, floating should be more common at high densities under conditions when space becomes limiting: when floating becomes a forced alternative. Floating behavior has been described in territorial systems corresponding to Nice's (1941) territorial types A (mating, nesting, and feeding ground for young), B (mating and nesting but not feeding ground), D (restricted to narrow surroundings of nest), and E (winter territories). Floaters might

appear in systems of types C (mating station only) and F (roosting territories) under space-limiting conditions, such as when roosting territories are holes. Use in the literature suggests that the term does not apply to situations such as a communal roost, or a lek, in which an unsettled individual might engage in periphery-searching for a space of its own. Thus far, usage implies rather large-scale spatial movements on the part of floaters (i.e., greater than the periphery of a grouse lek or a starling roost).

By occupying vacancies, individuals are attempting to improve their situation in a socially competitive environment. Following this line of thought, it seems likely that differences might be found between territory holders and replacements. Potential differences would probably occur along lines that commonly determine the outcome of contests: age (and the accompanying experience), body mass or size, and sex, for example. Predicting that such differences might appear prior to a removal experiment would constitute a valid null hypothesis. Pedersen (1988) successfully followed this course in conducting removal experiments on male Willow Ptarmigan (*Lagopus l. lagopus*) on their breeding grounds in Norway, although he had background information on his study population that facilitated his success. The timing of his removals was particularly important. Krebs (1971) also discussed the importance of timing in conducting removals. Briefly, the most credible results are likely to be obtained from a relatively stable population (e.g., after settling and the passage of migrants) that has not yet undergone an annual or semi-annual episode of mortality or emigration. Marra *et al.* (1993) and Stutchbury (1994) found evidence for differences in sex (American Redstarts) and age (Hooded Warblers) when comparing former winter territory holders with their replacements.

It should be remembered that one cannot determine that floaters are not present if one does not properly look for them. For example, a selective, nonrandom individual marking program, such as using tape playback to capture responding individuals (e.g., Holmes *et al.* 1989, Wunderle 1992), has a likelihood of excluding or under-representing entire categories of individuals (e.g., females, young, floaters). Such methods may be appropriate for other questions, however.

Although I have discussed the term floater largely in an avian context, the concept has wider applicability. For example, in mammalian literature individuals showing floating behavior have been called "runners" (Beer & Meyer 1951), "homeless" (Errington 1963), "transients" (Andelt 1985), and nomads. It is probable that most territorial systems, regardless of taxon, will occasionally contain relatively mobile individuals in search of suitable vacant space. Territoriality occurs when there is competition for space, suggesting that there is not equally suitable space for all who need it, and that, as a consequence, some will occasionally be excluded. Floater as defined here should continue to be a useful label for the excluded and wandering individual. Neotropical ecosystems, many of which are undergoing high levels of anthropogenic habitat alteration, are ideal places to study floaters. Habitat destruction can be viewed as an ongoing experiment in which resource levels are steadily diminished, leaving individuals facing correspondingly increased levels of competition for what remains.

ACKNOWLEDGMENTS

I thank B. C. Eliason, J. Klicka, G. Lefebvre, F. McKinney, D. W. Warner, M. Ward, and J. Wiley for helpful comments on earlier drafts.

REFERENCES

Andelt, W. F. 1985. Behavioral ecology of coyotes

in south Texas. Wildl. Monogr. 94: 1–45.
Beer, J. R., & R. K. Meyer 1951. Seasonal changes in the endocrine organs and behavior patterns of the muskrat. J. Mammal. 32: 173–191.
Brown, J. L. 1969. Territorial behavior and population regulation in birds: a review and re-evaluation. Wilson Bull. 81: 239–329.
Burton, R. F. 1860. The lake regions of Central Africa: a picture of exploration, Vol. 1. Longman, Green, Longman, & Roberts, London.
Darwin, C. 1871. The descent of man and selection in relation to sex, Vol. 2. John Murray, London.
Davies, N. B. 1978. Ecological questions about territorial behaviour. Pp. 317–350 *in* Krebs, J. R., & N. B. Davies (eds.). Behavioural ecology: an evolutionary approach. Blackwell, Oxford.
Davies, N. B., & A. I. Houston. 1981. Owners and satellites: the economics of territory defense in the Pied Wagtail, *Motacilla alba*. J. Anim. Ecol. 50: 157–180.
Deramond, M. 1959. La dynamique des populations d'oiseaux à la lumière des travaux récents. Alauda 27: 193.
Errington, P. L. 1963. Muskrat populations. Iowa State Univ. Press, Ames, Iowa.
Gauthreaux, S. A., Jr. 1982. The ecology and evolution of avian migration systems. Pp. 93–168 *in* Farner, D. S., J. R. King, & K. C. Parkes (eds.). Avian Biology, Vol. 6. Academic Press, New York.
Gross, M. R., & E. L. Charnov 1980. Alternative male life history strategies in bluegill sunfish. Proc. Natl. Acad. Sci. (USA) 77: 6937–6940.
Hensley, M. M., & J. B. Cope. 1951. Further data on removal and repopulation of the breeding birds in a spruce-fir forest community. Auk 68: 483–493.
Hickey, J. L. 1940. Territorial aspects of the American Redstart. Auk 57: 255–256.
Holmes, R. T., T. W. Sherry, & L. Reitsma. 1989. Population structure, territoriality and overwinter survival of two migrant warbler species in Jamaica. Condor 91: 545–561.
Klomp, H. 1972. Regulation of the size of bird populations by means of territorial behavior. Neth. J. Zool. 22: 456–488.
Kodric-Brown, A., & J. H. Brown. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. Ecology 59: 285–296.
Krebs, J. R. 1971. Territory and breeding density in the Great Tit, *Parus major*, L. Ecology 52: 2–22.
Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.
Lincoln, R.J., G. A. Boxshall & P. F. Clark. 1985. A dictionary of ecology, evolution, and systematics. Cambridge Univ. Press, New York.
Manuwal, D. A. 1974. Effects of territoriality on breeding in a population of Cassin's Auklet. Ecology 55: 1399–1406.
Marra, P. P., T. W. Sherry, & R. T. Holmes. 1994. Territorial exclusion by a long-distance migrant warbler in Jamaica: a removal experiment with American Redstarts (*Setophaga ruticilla*). Auk 110: 565–572.
Meunier, K. 1960. Grundsätzliches zur Populationsdynamik der Vögel. Z. Wiss. Zool. 163: 397–445.
Morel, G. & F., Bourlière 1962. Relations écologiques des avifaunes sédentaire et migratrice dans une savane sahélienne du bas Sénégal. Terre Vie 16: 371–393.
Morton, E. S., J. F. Lynch, K. Young, & P. Melhop. 1987. Do male Hooded Warblers exclude females from nonbreeding territories in tropical forest? Auk 104: 133–135.
Myers, J. P., P. G. Connors, & F. A. Pitelka. 1979. Territory size in wintering Sanderlings: the effects of prey abundance and intruder density. Auk 95: 551–561.
Nice, M. M. 1941. The role of territory in bird life. Am. Midl. Nat. 26: 441–487.
Nolan, V. Jr. 1978. The ecology and behavior of the Prairie Warbler (*Dendroica discolor*). Ornithol. Monogr. 26: 1–595.
Pedersen, H. C. 1988. Territorial behavior and breeding numbers in Norwegian Willow Ptarmigan: a removal experiment. Ornis Scand. 19: 81–87.
Price, T. 1981. The ecology of the Greenish Warbler *Phylloscopus trochiloides* in its winter quarters. Ibis 123: 131–144.
Rappole, J. H., & D. W. Warner. 1976. Relationships between behavior, physiology, and weather in avian transients at a nonbreeding stopover site. Oecologia 26: 193–212.
Rappole, J. H., & D. W. Warner. 1980. Ecological aspects of migrant bird behavior in Veracruz,

México. Pp. 353–393 *in* Keast, A., & E. S. Morton (eds.). Migrant birds in the Neotropics. Smithsonian Inst. Press, Washington, D.C.

Rappole, J. H., M. A. Ramos, & K. Winker. 1989. Movements and mortality in wintering Wood Thrushes. Auk 106: 402–410.

Rappole, J. H., & M. V. McDonald. 1994. Cause and effect in population declines of migratory birds. Auk 111: 652–660.

Rappole, J. H., & M. V. McDonald. 1998. Response to Latta and Baltz (1997). Auk 115: 246–251.

Schwartz, P. 1964. The Northern Waterthrush in Venezuela. Living Bird 3: 179–184.

Smith, S. M. 1978. The "underworld" in a territorial sparrow: adaptive strategy for floaters. Am. Nat. 112: 571–582.

Smith, S. M. 1989. Black-capped Chickadee summer floaters. Wilson Bull. 101: 344–349.

Staicer, C. A. 1992. Social behavior of the Northern Parula, Cape May Warbler, and Prairie Warbler wintering in second-growth forest in southwestern Puerto Rico. Pp. 308–320 *in* Hagan III, J. M., & D. W. Johnston (eds.). Ecology and conservation of Neotropical migrant landbirds. Smithsonian Inst. Press, Washington, D.C.

Stamps, J. A. 1988. Conspecific attraction and aggregation in territorial species. Am. Nat. 131: 329–347.

Stewart, R. E., & Aldrich, J. W. 1951. Removal and repopulation of breeding birds in a spruce-fir forest community. Auk 68: 471–482.

Stutchbury, B. J. 1994. Competition for winter territories in a Neotropical migrant: the role of age, sex and color. Auk 111: 63–69.

Stutchbury, B. J., & R. J. Robertson. 1985. Floating populations of female Tree Swallows. Auk 102: 651–654.

Szuba, K. J., & J. F. Bendell. 1988. Nonterritorial males in populations of Spruce Grouse. Condor 90: 492–496.

Watson, A., & D. Jenkins. 1968. Experiments on population control by territorial behaviour in Red Grouse. J. Anim. Ecol. 37: 595–614.

Wilcove, D. S., & J. W. Terborgh. 1984. Patterns of population decline in birds. Amer. Birds 38: 10–13.

Winker, K. 1989. The Wood Thrush (*Catharus mustelinus*) on its wintering grounds in southern Veracruz, Mxico. M. Sc. thesis, Univ. Minnesota, Minneapolis.

Winker, K., J. H. Rappole, & M. A. Ramos. 1990. Population dynamics of the Wood Thrush (*Hylocichla mustelina*) in southern Veracruz, México. Condor 92: 444–460.

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

Wunderle, J. M., Jr. 1992. Sexual habitat segregation in wintering Black-throated Blue Warblers in Puerto Rico. Pp. 299–307 *in* Hagan III, J. M., & D. W. Johnston (eds.). Ecology and conservation of Neotropical migrant landbirds. Smithsonian Inst. Press, Washington, D.C.