THE CONDOR

AN INTERNATIONAL JOURNAL OF AVIAN BIOLOGY

Volume 102 Number 3 August 2000

The Condor 102:479–481

SPECIAL SECTION
DISPERSAL BEHAVIOR

DISPERSAL BEHAVIOR: AN ORNITHOLOGICAL FRONTIER

JEFFREY R. WALTERS

Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061-0406, e-mail: jrwalt@vt.edu

Dispersal behavior is one of the fundamental features of an organism, and is a major determinant of many of the most basic patterns and processes characterizing organisms. For example, it plays a critical role in geographical distribution, population structure, and population dynamics. Despite its importance, our knowledge of avian dispersal remains limited. Its characterization remains in many ways theoretical, in contrast to the other life history features of equal rank, fecundity and mortality, which have been well described empirically. In the past, a theoretical characterization of dispersal has been sufficient in developing basic theories of biogeography, population genetics, and population dynamics. Recently, however, lack of information about dispersal has begun to limit progress on several biological fronts. In research on population dynamics and structure, to the traditional closed population models have been added various types of metapopulation models (Harrison 1991, Stith et al. 1996) in which dispersal between subunits is critical. In conservation, where theory must be applied, inadequate knowledge of dispersal has been especially problematic. Effects of habitat fragmentation and other changes to the landscape on population dynamics can not be predicted without a thorough knowledge of dispersal behavior (Kareiva 1990, Walters 1998). Complex spatially-explicit population models have been developed to investigate population dynamics in complex landscapes, but estimation of the dispersal parameters that these models contain has been a contentious issue (Ruckelshaus et al. 1997, 1999, South 1999), largely because there is little empirical basis for estimation. The need for information about dispersal behavior has never been greater.

This was the incentive that compelled Peter Stacey and I to organize a symposium on avian dispersal behavior for the 115th meeting of the American Ornithologists' Union held in Minneapolis in August, 1997. The intent of the symposium was to increase awareness about the critical need for and stimulate interest in studies of dispersal. The four papers that follow were developed from presentations included in that symposium. Each addresses a different facet of dispersal studies. Daniels and Walters examine the classic problem of the relationship between natal dispersal and inbreeding, and in the process present a data set including more than 600 natal dispersal records for female Red-cockaded Woodpeckers (*Picoides borealis*). There is a

critical need for empirical information about dispersal like these data, and two of the five papers presented at the symposium that are not published here also provided such data. John Fitzpatrick, Glen Woolfenden, and Reed Bowman described the frequency of dispersal within and between habitat patches by Florida Scrub-Jays (*Aphelocoma coerulescens*) throughout the range of the species (Fitzpatrick et al. 1999). Emmanuelle Cam, Thierry Boulinier, and Etienne Danchin described breeding dispersal between colonies and between cliffs within colonies in Black-legged Kittiwakes (*Rissa tridactyla*) (Cam et al. 1998, Danchin et al. 1998).

The data presented in these studies were obtained through long-term monitoring of large numbers of color-marked birds. Such data are valuable, but in most cases it is difficult to obtain representative samples of dispersal by this method. The woodpeckers and jays are relatively sedentary, endangered, cooperative breeders whose limited distributions are accurately known. Kittiwakes are seabirds that are highly concentrated within a few small areas when nesting. For other avian species in which individuals can not be located so conveniently, resighting of color-marked birds produces biased assessments of dispersal. Here, Koenig, Hooge, Stanback, and Haydock discuss this problem, and offer some solutions, drawing upon data from their long-term studies of yet another relatively sedentary cooperative breeder, the Acorn Woodpecker (*Melanerpes formicivorus*). In another presentation not published here, Charles Francis discussed the use of an additional technique, analysis of band recoveries, for investigating dispersal patterns.

Martin, Stacey, and Braun employ some of the methodologies suggested by Koenig et al. to measure natal recruitment within, and natal and breeding dispersal between, populations of White-tailed Ptarmigan (*Lagopus leucurus*) inhabiting discrete patches of alpine tundra in Colorado. Specifically they studied multiple populations and surveyed additional populations for marked birds, and employed radio-telemetry to track dispersing individuals. Here, Martin et al. show that the majority of new recruits to populations are not natal birds, or even birds from nearby populations, but instead are individuals from distant populations, especially in the case of females. They argue that individual populations are dependent on other populations for demographic rescue, and thus interact as a metapopulation. They further argue that this situation may be common in birds. In another presentation not published here, Peter Stacey discussed the appropriateness of metapopulation models of population dynamics for birds, emphasizing applications in conservation and the critical need for empirical data on dispersal.

In the final paper, Arguedas and Parker use genetic markers to examine gene flow between populations in migratory and sedentary forms of the House Wren (*Troglodytes aedon* and *T. musculus*). They report that in this case migratory behavior is associated with greater gene flow. This paper exemplifies the development of increasingly variable genetic markers that enable increasingly fine resolution of population structure, and thereby characterization of dispersal between populations.

Another neglected aspect of dispersal behavior is its proximate control. In another presentation included in the symposium but published elsewhere, Alfred Dufty and James Belthoff reported on the hormonal changes associated with natal dispersal in Eastern and Western Screech-Owls (*Otus asio* and *O. kennicottii*) (Dufty and Belthoff 2000). With the development of field techniques in behavioral endocrinology, the proximate control of dispersal promises to receive increasing attention.

Several themes indicative of critical needs in dispersal research emerged from the symposium. First, as discussed by Koenig et al., progress depends on improved methodologies. Radio-telemetry, field endocrinology, and genetic markers are technologies that are especially critical. Second, more dispersal data are needed. Three of the papers provide data on dispersal events, one indirectly through genetic markers and two directly through observations of marked individuals. Only one, however, provides data on dispersal behavior. We know even less about how individuals move and interact with the landscape than we know about where they end up. Advances in radio-telemetry technology remain the best hope for improving the quality and quantity of data on dispersal behavior, as the study by Martin et al. demonstrates. The third theme, addressed in two of the papers, is use of dispersal data in evaluating alternative models of avian population structure. This work may well revolutionize views of avian populations. The fourth theme is the importance of dispersal information

to conservation, and here knowledge of behavior during dispersal is especially critical. Dispersal behavior is relevant to general problems in conservation. For example, relative sensitivity to habitat fragmentation may well depend on differences in dispersal behavior among species (Walters 1998). It is also relevant to specific problems. For example, dispersal behavior has been perhaps the most critical issue in preservation of populations of the Northern Spotted Owl (*Strix occidentalis*) (McKelvey et al. 1992).

Dispersal behavior represents one of the remaining frontiers of avian population biology. Those who participated in the symposium hope that their efforts might inspire others to contribute to this important area of research. There is much work to be done, and it requires a wide variety of expertise. We hope that in the future ornithologists will focus their energy and intellect on dispersal just as they focused it on other parameters such as clutch size in the past. We look forward to the day when dispersal behavior pattern can be indicated along with clutch size in species accounts for birds of all sorts.

ACKNOWLEDGMENTS

I thank Peter Stacey for his efforts in organizing and presenting the symposium. I also thank the American Ornithologists' Union for allowing Peter and I to include the symposium in their program.

LITERATURE CITED

CAM, E., J. E. HINES, J. Y. MONNAT, J. D. NICHOLS, AND E. DANCHIN. 1998. Are adult nonbreeders prudent parents? The kittiwake model. Ecology 79:2917–2930.

DANCHIN, E., T. BOULINIER, AND M. MASSOT. 1998. Breeding habitat selection based on conspecific reproductive success: implications for the evolution of coloniality. Ecology 79:2415–2428.

DUFTY, A. M., JR., AND J. R. BELTHOFF. 2000. Proximate mechanisms of dispersal: the role of hormones and body condition. *In* J. Clobert, J. D. Nichols, E. Danchin, and A. Dhondt [EDS.], Causes, consequences and mechanisms of dispersal at the individual, population and community level. Oxford Univ. Press, London. In press.

FITZPATRICK, J. W., G. E. WOOLFENDEN, AND R. BOWMAN. 1999. Dispersal distance and its demographic consequences in the Florida Scrub-Jay. Proc. Int. Ornithol. Congr. 22:2465–2479.

HARRISON, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biol. J. Linnean Soc. 42:73–88.

KAREIVA, P. 1990. Population dynamics in spatially complex environments: theory and data. Phil. Trans. Soc. Lond. B 330:175–190.

MCKELVEY, K., B. R. NOON, AND R. H. LAMBERSON. 1992. Conservation planning for species occupying fragmented landscapes: the case of the Northern Spotted Owl, p. 424–450. *In* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey [EDS.], Biotic interactions and global change. Sinauer, Sunderland, MA.

RUCKELSHAUS, M., C. HARTWAY, AND P. KAREIVA. 1997. Assessing the data requirements of spatially explicit dispersal models. Conserv. Biol. 11:1298–1306.

RUCKELSHAUS, M., C. HARTWAY, AND P. KAREIVA. 1999. Dispersal and landscape errors in spatially explicit population models: a reply. Conserv. Biol. 13:1223–1224.

SOUTH, A. 1999. Dispersal in spatially explicit population models. Conserv. Biol. 13:1039–1046.

STITH, B. M., J. W. FITZPATRICK, G. E. WOOLFENDEN, AND B. PRANTY. 1996. Classification and conservation of metapopulations: a case study of the Florida Scrub Jay, p. 187–215. *In* D. R. McCullough [ED.], Metapopulations and wildlife conservation. Island Press, Washington, DC.

WALTERS, J. R. 1998. The ecological basis of avian sensitivity to habitat fragmentation, p. 181–192. *In* J. M. Marzluff and R. Sallabanks [EDS.], Avian conservation. Island Press, Washington, DC.