

Broadening Our Approaches to Studying Dispersal in Raptors

Authors: Morrison, Joan L., and Wood, Petra Bohall

Source: Journal of Raptor Research, 43(2) : 81-89

Published By: Raptor Research Foundation

URL: <https://doi.org/10.3356/JRR-08-33.1>

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.

THE JOURNAL OF RAPTOR RESEARCH

A QUARTERLY PUBLICATION OF THE RAPTOR RESEARCH FOUNDATION, INC.

VOL. 43

JUNE 2009

No. 2

J. Raptor Res. 43(2):81–89

© 2009 The Raptor Research Foundation, Inc.

BROADENING OUR APPROACHES TO STUDYING DISPERSAL IN RAPTORS

JOAN L. MORRISON¹

Department of Biology, Trinity College, 300 Summit Street, Hartford, CT 06106 U.S.A.

PETRA BOHALL WOOD

U.S. Geological Survey, West Virginia Cooperative Fish and Wildlife Research Unit, Division of Forestry and Natural Resources, West Virginia University, P.O. Box 6125, Morgantown, WV 26506 U.S.A.

ABSTRACT.—Dispersal is a behavioral process having consequences for individual fitness and population dynamics. Recent advances in technology have spawned new theoretical examinations and empirical studies of the dispersal process in birds, providing opportunities for examining how this information may be applied to studies of the dispersal process in raptors. Many raptors are the focus of conservation efforts; thus, reliable data on all aspects of a species' population dynamics, including dispersal distances, movement rates, and mortality rates of dispersers, are required for population viability analyses that are increasingly used to inform management. Here, we address emerging issues and novel approaches used in the study of avian dispersal, and provide suggestions to consider when developing and implementing studies of dispersal in raptors. Clarifying study objectives is essential for selection of an appropriate methodology and sample size needed to obtain accurate estimates of movement distances and rates. Identifying an appropriate study-area size will allow investigators to avoid underestimating population connectivity and important population parameters. Because nomadic individuals of some species use temporary settling areas or home ranges before breeding, identification of these areas is critical for conservation efforts focusing on habitats other than breeding sites. Study designs for investigating raptor dispersal also should include analysis of environmental and social factors influencing dispersal, to improve our understanding of condition-dependent dispersal strategies. Finally, we propose a terminology for use in describing the variety of movements associated with dispersal behavior in raptors, and we suggest this terminology could be used consistently to facilitate comparisons among studies.

KEY WORDS: *behavior; dispersal; movements; natal area; natal dispersal; philopatry; raptors.*

AMPLIACIÓN DE LOS ENFOQUES PARA ESTUDIAR LA DISPERSIÓN EN LAS AVES RAPACES

RESUMEN.—La dispersión es un proceso de comportamiento que tiene consecuencias para la adecuación de los individuos y para la dinámica de las poblaciones. Avances tecnológicos recientes han conducido a nuevos exámenes teóricos y a estudios empíricos sobre la dispersión en las aves, lo que ha brindado oportunidades para examinar cómo puede aplicarse esta información al estudio de la dispersión en las aves rapaces. Debido a que muchas rapaces son el foco de esfuerzos de conservación, para poder realizar los análisis de viabilidad poblacional que son cada vez más usados como base para el manejo, es necesario contar con información confiable sobre todos los aspectos de la dinámica poblacional de las especies, incluyendo las distancias de dispersión, las tasas de movimiento y las tasas de mortalidad de los individuos que se dispersan. En este estudio, abordamos asuntos emergentes y enfoques novedosos utilizados para el estudio de la dispersión de las aves, y presentamos sugerencias para considerar al desarrollar e implementar estudios de la dispersión en las aves rapaces. Tener claros los objetivos de estudio es esencial para seleccionar

¹ Email address: joan.morrison@trincoll.edu

cionar una metodología adecuada y un tamaño de muestra suficiente para obtener estimados exactos de las distancias y tasas de movimiento. Identificar un área de estudio de tamaño adecuado permitirá que los investigadores no subestimen la conectividad de las poblaciones y algunos parámetros poblacionales importantes. Debido a que los individuos nómades de algunas especies se establecen en algunos sitios temporalmente antes de reproducirse, la identificación de esos sitios es crítica para los esfuerzos de conservación que se enfocan en hábitats distintos a los de cría. Los diseños experimentales para investigar la dispersión de las rapaces también deberían incluir análisis de los factores ambientales y sociales que afectan la dispersión para mejorar nuestro entendimiento de las estrategias de dispersión dependientes de la condición de los individuos. Finalmente, proponemos una terminología para describir la variedad de movimientos asociados con el comportamiento de dispersión en las rapaces y sugerimos que esta terminología podría ser empleada consistentemente para facilitar las comparaciones entre estudios.

[Traducción del equipo editorial]

Dispersal is a behavioral process that has profound consequences for both individuals and populations (Greenwood 1980, Johnson and Gaines 1990). As the primary mechanism by which individuals seek and acquire mates and breeding sites and colonize new areas, dispersal has consequences for the spacing of individuals, local patterns of age structure, survival and recruitment, the persistence of populations, and species' distributions. From an evolutionary perspective, dispersal determines the degree of gene flow within and among populations, and thus affects local patterns of relatedness and species' range expansions. Aspects of the dispersal process can be influenced by factors that have consequences for individual fitness, such as population density, habitat quality, mate quality, and intraspecific or interspecific interactions (Greenwood and Harvey 1982, Clobert et al. 2001). Dispersal behaviors and strategies can differ even among populations of the same species depending on environmental and social factors (Serrano et al. 2001). Accurate descriptions of dispersal patterns and potential influencing factors are essential for understanding these variations in behavior and the consequences of dispersal on individual fitness and population dynamics.

Before recent advances in technology, dispersal represented a significant knowledge gap in our understanding of avian life histories (Walters 2000, Bennetts et al. 2001). These advances have spawned new theoretical examinations and empirical studies of the dispersal process in birds; many such examinations have been the focus of recent symposia and workshops (Clobert et al. 2001, Bullock et al. 2002, Pasinelli et al. 2003, Clark et al. 2004). Raptors were rarely included in these investigations, however, probably because dispersal data are particularly difficult to obtain for raptors and because the magnitude of movement distances can be very large, com-

plicating researchers' ability to address hypotheses (Clark et al. 2004).

Limited knowledge of the dispersal process and underlying influences is especially problematic for raptors because many species are the focus of conservation efforts (i.e., Morrison and Humphrey 2001, Buchanan 2004, Balbontín 2005, Catlin et al. 2005). Development of conservation strategies relies increasingly on models and population viability analyses for individual species. These models typically require extensive data on all aspects of an organism's population dynamics, and variability in parameters such as dispersal distances, movement rates, and mortality rates of dispersers can have profound consequences on model conclusions and thus influence a model's usefulness for management (Ruckelshaus et al. 1997, South 1999, Mooj and DeAngelis 2003). Appropriate parameterization of these models is particularly important in conservation planning for threatened and endangered species (Reed 1999) and for predicting recolonization of areas where populations have been extirpated (Kauffman et al. 2004, Seamans and Gutiérrez 2006, González et al. 2006).

The availability of improved techniques and methodologies for closing data gaps, combined with increasing conservation needs for reliable movement data, necessitate attention to advancement in our studies of the dispersal process in raptors. In this paper, we address some emerging issues in the study of avian dispersal and highlight novel approaches potentially useful in studies of raptor dispersal. We comment on current approaches used in studies of dispersal in raptors; however, our intent is neither to present a review of our current knowledge of raptor dispersal nor to provide an exhaustive list of the pertinent literature. Instead, we provide suggestions to consider when developing and implementing studies of dispersal in raptors and we

outline a standardized approach to dispersal terminology.

As originally defined by Greenwood (1980), the two events central to the dispersal process are natal dispersal and breeding dispersal. Natal dispersal is movement of an individual from its birthplace to place of first reproduction, whereas breeding dispersal is movement between breeding seasons from one breeding place to another. Both have consequences for gene flow and population structure. What happens during the time period between hatching and first breeding (natal dispersal) or between two breeding events (breeding dispersal) can encompass a wide variety of other movements and behaviors that are included under the general umbrella of “dispersal process” (Clobert et al. 2001). These movements and behaviors can affect local patterns of age structure, individual survival, and a species’ distribution, and can have implications for conservation and management decisions.

To date, studies of the dispersal process in raptors primarily have described patterns and timing of movements by individuals, usually juveniles, and have investigated a variety of factors that may explain variation in the timing and distances of particular movements associated with a specific period in the life history of the species under study. Relatively few studies have reported on actual natal and breeding dispersal events, and these events typically have been described as linear distances derived from band recoveries, resightings, and radiotelemetry. Numerous studies have investigated correlates of timing of permanent departure and distances moved; for example, hatching date (Korpimäki and Lagerström 1988, Mínguez et al. 2001), age (Soutullo et al. 2006), sex (Newton and Marquiss 1983), habitat or parent quality (Ferrer and Harte 1997, Miller et al. 1997), brood size (Wood et al. 1998), reproductive success (Korpimäki 1993), population density (Wiklund 1996, Negro et al. 1997), social factors (Ellsworth and Belthoff 1999, Serrano et al. 2003), environmental factors such as day length, temperature, or food availability (Sonerud et al. 1988, Coles et al. 2003, McIntyre and Collopy 2006) and physiological condition (Belthoff and Dufty 1998, Ferrer 1993a). Studies reporting on breeding dispersal have examined associations between timing and distances moved and territory quality (Korpimäki 1988, Forero et al. 1999, Blakesley et al. 2006), the role of conspecifics and prior breeding performance (Kenward et al. 2001, Serrano et al. 2001, Calabuig et al. 2008), and mate qual-

ity (Millsap and Bear 1997, Newton 2001). Experimental work focusing on raptor dispersal has been limited, although associations between food availability, potential predation risk, and movements out of the natal territory have been reported (Kenward et al. 1993, Hakkarainen et al. 2001, Kennedy and Ward 2003).

Even less is known about context or correlates of raptor movements made during the transition periods between permanent departure from the natal area and settlement at first breeding site or between successive breeding sites. Following permanent departure, some raptors undertake nomadic movements and periodically remain for varying lengths of time in locations called temporary settling areas (Ferrer 1993b, Balbontín 2005, Delgado and Penteriani 2005), temporary home ranges (Forsman et al. 2002), or communal roosts (Forero et al. 2002, J. Morrison unpubl. data). Examining observed patterns of dispersal in context of these settling areas would aid in understanding possible constraints on settlement (e.g., spatial distribution of appropriate habitat; Serrano et al. 2008), and in understanding behaviors occurring in the settlement areas including establishment of dominance hierarchies (Donazar and Fejoo 2002), finding mates (Krause and Ruxton 2002), information transfer (Marzluff and Heinrich 2001), and avoidance of territorial adults (Marzluff and Heinrich 1991). Knowing the fate of nomadic individuals or “floaters” occupying these settling areas is critical to understanding population stability (Delgado and Penteriani 2005), and identifying areas used by these nomadic individuals indicates the need for conservation efforts focusing on habitats other than just breeding sites (Penteriani et al. 2005, González et al. 2006).

Recent approaches to studies of avian dispersal behavior derive from a paradigm focusing on ecological and evolutionary aspects of the entire dispersal process (Clobert et al. 2001, Bullock et al. 2002, Clark et al. 2004, Bowler and Benton 2005), one we believe provides broad opportunity for expanding and improving our studies of the dispersal process in raptors. Of foremost importance in study design is a clear understanding of study objectives, which will allow selection of the most appropriate data collection and analysis methods. For example, capture-mark-recapture methods may be most appropriate for examining population connectivity within a raptor metapopulation, given that sample sizes are large enough to obtain accurate estimates of movement probabilities (Francis and Saurola

2004, Serrano et al. 2005, Zimmerman et al. 2007). However, if one is interested in knowing habitat selection or causes of juvenile mortality during the natal dispersal process, or understanding the influence of dispersal on range expansion, radio- or satellite telemetry is the recommended method (Walls et al. 1999, Martin et al. 2006, McIntyre and Collopy 2006).

In designing dispersal studies, researchers must avoid inadvertently making assumptions and assigning generalities regarding the dispersal process (e.g., that all habitat is the same and equally available, that movements at several scales can be collapsed into one parameter, or that a constant proportion of a population disperses each generation). Dispersal is a condition-dependent process with fitness gains dependent on changes over time in both environmental factors and individual state (Delgado and Penteriani 2008). Study designs for investigating raptor dispersal should address potential influencing factors, costs and benefits of dispersal, dispersal distances, and movement rates at a variety of spatial scales and in the context of the three temporal phases of dispersal: (1) departure from a natal site, (2) transition, searching for, or moving to a new site, and (3) settlement in a new site (Bennetts et al. 2001, Bowler and Benton 2005).

Recent advances in statistical methodology have improved the ability of researchers to integrate aspects of the dispersal process in birds. Data on movement rates and survival rates associated with various movements occurring throughout the lifespan of individuals, occupancy rates in settling areas, and variation associated with these parameters improve population viability models (Nichols and Kaiser 1999, Kendall and Nichols 2004). Estimation of these parameters is now more easily accomplished through the use of multistate models that successfully combine different types of encounter information, such as band recovery, telemetry, or mark-resighting data (Bennetts et al. 2001, Blums et al. 2003). To date, these methods have received only limited use for raptors (e.g., Serrano et al. 2005, Martin et al. 2007, Zimmerman et al. 2007).

Genetic approaches incorporating mitochondrial or microsatellite markers or using genetic fingerprinting techniques (i.e., genetic tagging or parentage analysis) have been used to infer patterns of dispersal (Raybould et al. 2002, Nathan et al. 2003). These methods may be most appropriate when used in combination with other methods for estimating demographic parameters such as mark-

recapture (Rousset 2001). F_{ST} methods that incorporate the distribution of alleles within and among populations and the frequency of inter-population movements may be useful for estimating numbers of migrants among populations but have serious limitations for estimating long-distance dispersal (LDD) events (Nathan et al. 2003). Alternative approaches utilizing patterns of differentiation among populations to estimate dispersal parameters are based on the observation that dispersal frequencies decline as distance increases (isolation by distance, Nathan et al. 2003). Relatively few studies of avian dispersal have incorporated genetic methods (e.g., Coulon et al. 2008, Ortego et al. 2008); others have used stable-isotope techniques in estimating dispersal rates (Hobson et al. 2004) and in making *a posteriori* estimations of an animal's location (Powell 2004). Extensive evaluation of approaches using these methods (e.g., reviews by Rousset 2001, Raybould et al. 2002, Nathan et al. 2003) and further studies are needed to identify their usefulness in studies of dispersal in raptors.

Essential to improving studies of the dispersal process in raptors is clarification and standardization of definitions. Although terminology has been proposed to describe broad groupings of avian movements (Kenward et al. 2002), we propose a more specific terminology for use in describing the variety of movements associated with breeding biology and dispersal behavior in raptors (Fig. 1). We suggest this terminology could be used consistently to facilitate comparisons among studies.

Natal-area movements include movements that occur within a defined natal area and before permanent departure from the natal area; these may be further divided into movements that occur during the pre- and post-fledging periods. Pre-fledging movements are often ascribed to owls (e.g., Short-eared Owl, *Asio flammeus*, Holt and Leasure 1993) as movements made away from the nest on foot by nestlings before they can fly (presumably to minimize risk of predation). Post-fledging movements occur within the natal area but may also include movements made by fledglings that travel outside the natal area but then typically return to the natal area within a time period specified by the investigator. Such post-fledging movements have been described as excursions (Walls and Kenward 1995) or exploratory movements (Ferrer 1993b).

Departure from the natal area is the first step in the dispersal process (Phase I; Bennetts et al. 2001) and occurs when an individual moves out of the

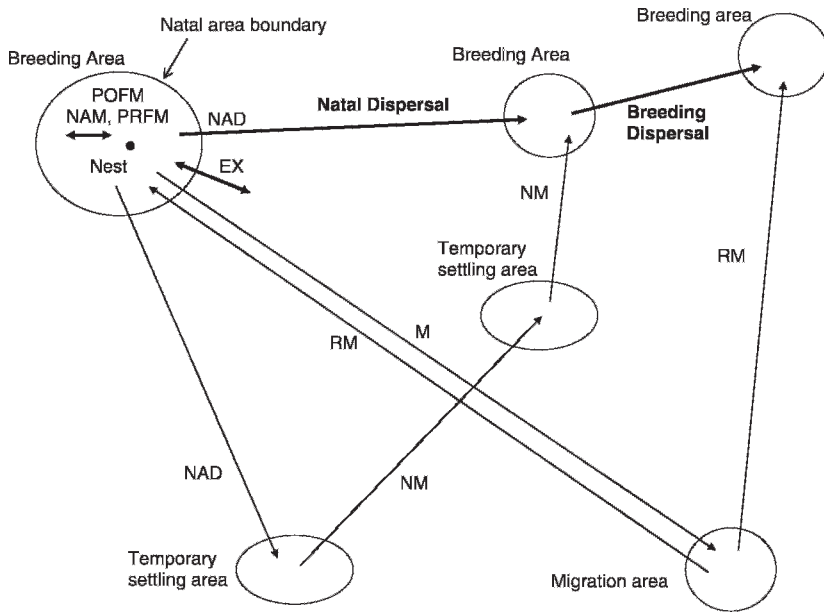


Figure 1. Proposed terminology to describe dispersal events and movements associated with dispersal behavior in raptors. Types of movements are designated by arrows, one- or two-way. Natal dispersal and breeding dispersal events are noted as bold arrows. Other movements are associated with the process that occurs before or between dispersal events. NAM = natal area movement, PRFM = pre-fledging movement, POFM = post-fledging movement but before natal area departure, EX = excursion, NAD = natal area departure, NM = nomadic movements, M = migration, RM = return migration.

natal area and/or home range and does not return. For raptors, natal area departure is usually recorded as time or age post-fledging, but it may also be associated with brood or habitat characteristics (Ellsworth and Belthoff 1999, Kenward et al. 2001, Martin et al. 2007). Density-dependent factors also may influence natal-area departure (Sutherland et al. 2002), but these have been rarely examined for raptors (but see Burgess et al. 2008).

Nomadic movements occur after permanent departure from the natal area and during the transitional phase (Phase II; Bennetts et al. 2001), when an individual, often of a species exhibiting delayed breeding, moves throughout its range presumably seeking territorial openings, conspecifics, food, or safety. These movements have also been described in the context of prospecting (Reed et al. 1999) and exploration (Baker 1993). Nomadic movements also include movements between areas in which individuals remain for varying periods but do not breed (temporary settling areas, Fig. 1; i.e., Greenwood 1980, Ferrer 1993b). For these species, information about movements made during the extended nonbreeding period provides more insight about dis-

persal behavior within a population than simply reporting linear dispersal distances. Nomadic movements also can provide information about search behaviors (Doerr and Doerr 2005), conspecific attraction (Seamans and Gutiérrez 2006), and the frequency, type, and context of social interactions that occur during the nonbreeding period (Forero et al. 2002, Serrano et al. 2004, Sergio and Penteriani 2005). Movements made within the transitional phase can include migration to and from a wintering or other nonbreeding season area. Migration in raptors has been treated separately and extensively (e.g., Bildstein 2006); thus, we do not address migratory movements.

More challenging is defining “settlement” and “philopatry”; important consequences of the dispersal process. As noted above, nomadic individuals may temporarily settle in areas essential for foraging or roosting. Breeding settlement (Phase III; Bennetts et al. 2001) occurs when an individual attains a breeding site and attempts reproduction. For raptors, philopatry has been identified by some investigators as individuals returning to breed within their natal area or natal colony, or, alternatively, as a lin-

ear distance or number of home ranges between the natal area and the breeding site (Ferrer 1993b, Walls and Kenward 1995, Negro et al. 1997). Ideally, researchers should include *a priori* definitions of the natal area, home range, post-fledging area (Kennedy et al. 1994, McClaren et al. 2005) and study population as required by specific research questions and to facilitate interpretation (e.g., Martin et al. 2007). If this information is not available *a priori*, we encourage researchers to develop such information from populations they study, for future reference. Boundary identification and consistent use of area and specific distances or numbers of territories traversed in defining settlement and philopatry, respectively (e.g., Walls and Kenward 1995, González et al. 2006) will help clarify the types and context of particular movements being investigated, facilitate comparisons among studies, and avoid erroneous conclusions for conservation and management.

Finally, and essential to consider in studies of raptor dispersal is study-area size, which is well known to influence conclusions about dispersal behavior and distances, particularly conclusions based on capture reencounter data (Franzén and Nilsson 2007). Typically, frequency distributions of dispersal distances are truncated because the study area is not large enough with respect to dispersal capabilities of the target species (Koenig et al. 1996, Zimmerman et al. 2007). Size of the study area required for adequate assessment of dispersal patterns can be influenced by degree of fragmentation, population sizes, and even weather conditions (Paradis et al. 1998, Walls et al. 2005). Moreover, undetected emigration from the study area can lead to underestimates of survival probabilities and population growth rates (Cilimburg et al. 2002, Zimmerman et al. 2007). LDD events are particularly critical to identify because of their disproportionate importance for population connectivity and because they can directly affect the evolutionary trajectory of species. Such events determine the rate of range expansions, enable gene flow between distant populations, and may be crucially important in the face of climate change (Watkinson and Gill 2002).

We recognize the inevitability of constraints in time and funding, and the difficulties in identifying a study area large enough to reduce biases, yet small enough to be logistically practical in the execution of studies of raptor dispersal. To avoid drawing erroneous conclusions from predictive models and misinforming management, however, we must refine parameter estimates associated with all aspects

of the dispersal process, including behaviors, survival and movement rates, areas used, and distances traversed. Ultimately, our best approach will be to identify the estimators and study-area size most appropriate for the spatial scale of study, necessary sample sizes, and the combination of technology, genetic techniques, and other data collection and analysis methods most appropriate for minimizing bias associated with obtaining and reporting data required by the research questions (Anderson 2001, Buchanan 2004). In addition, efforts should be made to carry out long-term studies whenever possible, which will facilitate a more comprehensive understanding of movements and behaviors associated with the dispersal process in raptors, their consequences for demography, and their application for conservation.

ACKNOWLEDGMENTS

We thank members of the Raptor Research Foundation for input and feedback on the ideas we originally presented on this topic at the 1999 annual meeting in La Paz, Mexico. We also thank P. Kennedy and J. Belthoff for stimulating discussions about terminology, and D. Andersen, J. Belthoff, J. Edwards, D. Serrano, B. Smith, D. Tinkler, J. Walters, and two anonymous reviewers for their comments on earlier drafts of this manuscript.

LITERATURE CITED

- ANDERSON, D.R. 2001. The need to get the basics right in wildlife field studies. *Wildl. Soc. Bull.* 29:1294–1297.
- BAKER, R.R. 1993. The function of post-fledging exploration: a pilot study of three species of passerines ringed in Britain. *Ornis. Scand.* 24:71–79.
- BALBONTÍN, J. 2005. Identifying suitable habitat for dispersal in Bonelli's Eagle: an important issue in halting its decline in Europe. *Biol. Conserv.* 126:74–83.
- BELTHOFF, J.R. AND A.M. DUFTY, JR. 1998. Corticosterone, body condition, and locomotor activity: a model for dispersal in screech owls. *Anim. Behav.* 55:405–415.
- BENNETTS, R.E., J.D. NICHOLS, J.D. LEBRETON, R. PRADEL, J.E. HINES, AND W.M. KITCHENS. 2001. Methods for estimating dispersal probabilities and related parameters using marked animals. Pages 3–17 in J. Clobert, E. Danchin, A.A. Dhondt, AND J.D. Nichols [Eds.], *Dispersal*. Oxford Univ. Press, New York, NY U.S.A.
- BILDSTEIN, K. 2006. *Migrating raptors of the world: their ecology and conservation*. Comstock Publishing, Sacramento, CA U.S.A.
- BLAKESLEY, J.A., D.R. ANDERSON, AND B.R. NOON. 2006. Breeding dispersal in the California Spotted Owl. *Condor* 108:71–81.
- BLUMS, P., J.D. NICHOLS, J.E. HINES, M.S. LINDBERG, AND A. MEDNIS. 2003. Estimating natal dispersal movement rates of female European ducks with multistate modeling. *J. Anim. Ecol.* 72:1027–1042.

- BOWLER, D.E. AND T.G. BENTON. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Cambridge Phil. Soc. Biol. Rev.* 80:205–225.
- BUCHANAN, J.B. 2004. Managing habitat for dispersing Northern Spotted Owls - are the current management strategies adequate? *Wildl. Soc. Bull.* 32:1333–1345.
- BULLOCK, J.M., R.E. KENWARD, AND R.S. HAILS. [EDS.]. 2002. Dispersal ecology. Blackwell, Malden, MA U.S.A.
- BURGESS, M.D., M.A. NICOLL, C.G. JONES, AND K. NORRIS. 2008. Restricted dispersal reduces the strength of spatial density dependence in a tropical bird population. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 275:1209–1216.
- CALABUIG, G., J. ORTEGO, P.J. CORDERO, AND J.M. APARICIO. 2008. Causes, consequences and mechanisms of breeding dispersal in the colonial Lesser Kestrel, *Falco naumanni*. *Anim. Behav.* 76:1989–1996.
- CATLIN, D.H., D.K. ROSENBERG, AND K.L. HALEY. 2005. The effects of nesting success and mate fidelity on breeding dispersal in Burrowing Owls. *Can. J. Zool.* 83:1574–1580.
- CILIMBURG, A.B., M.S. LINDBERG, J.J. TEWKSBURY, AND S.J. HEJL. 2002. Effects of dispersal on survival probability of adult Yellow Warblers (*Dendroica petechia*). *Auk* 119:778–789.
- CLARK, R.G., K.A. HOBSON, J.D. NICHOLS, AND S. BEARHOP. 2004. Avian dispersal and demography: scaling up to the landscape and beyond. *Condor* 106:717–719.
- CLOBERT, J., E. DANCHIN, A.A. DHONDT, AND J.D. NICHOLS. [EDS.]. 2001. Dispersal. Oxford Univ. Press, New York, NY U.S.A.
- COLES, C.F., S.J. PETTY, J.L. MACKINNON, AND C.J. THOMAS. 2003. The role of food supply in the dispersal behaviour of juvenile Tawny Owls *Strix aluco*. *Ibis* 145:E59–E68.
- COULON, A., J.W. FITZPATRICK, R. BOWMAN, B.M. STITH, C.A. MAKAREWICH, L.M. STENZLER, AND I.J. LOVETTE. 2008. Congruent population structure inferred from dispersal behaviour and intensive genetic surveys of the threatened Florida Scrub-Jay (*Aphelocoma coerulescens*). *Mol. Ecol.* 17:1685–1701.
- DELGADO, M.M. AND V. PENTERIANI. 2008. Behavioral states help translate dispersal movements into spatial distribution patterns of floaters. *Am. Nat.* 172:475–485.
- AND ———. 2005. Eagle Owl *Bubo bubo* dispersal patterns and the importance of floaters for the stability of breeding populations. *Ornithol. Anz.* 44:153–158.
- DOERR, E.D. AND V.A. DOERR. 2005. Dispersal range analysis: quantifying individual variation in dispersal behavior. *Oecologia* 142:1–10.
- DONÁZAR, J.A. AND J.E. FEJOO. 2002. Social structure of Andean Condor roosts: influence of sex, age, and season. *Condor* 104:832–837.
- ELLSWORTH, E.A. AND J.R. BELTHOFF. 1999. Effects of social status on the dispersal behavior of Western Screech Owls. *Anim. Behav.* 57:883–892.
- FERRER, M. 1993a. Ontogeny of dispersal distances in young Spanish Imperial Eagles. *Behav. Ecol. Sociobiol.* 32:259–263.
- . 1993b. Juvenile dispersal behaviour and natal philopatry of a long-lived raptor, the Spanish Imperial Eagle *Aquila adalberti*. *Ibis* 135:132–138.
- AND M. HARTE. 1997. Habitat selection by immature Spanish Imperial Eagles during the dispersal period. *J. Anim. Ecol.* 34:1359–1364.
- FORERO, M.G., J.A. DONÁZAR, J. BLAS, AND F. HIRALDO. 1999. Causes and consequences of territory change and breeding dispersal distance in the Black Kite. *Ecology* 80:1298–1310.
- , ———, AND F. HIRALDO. 2002. Causes and fitness consequences of natal dispersal in a population of Black Kites. *Ecology* 83:858–872.
- FORSMAN, E.D., R.G. ANTHONY, J.A. REID, P.J. LOSCHL, S.G. SOVERN, M. TAYLOR, B.L. BISWELL, A. ELLINGSON, E.C. MESLOW, G.S. MILLER, K.A. SWINDLE, J.A. THRAILKILL, F.F. WAGNER, D.E. SEAMAN, J.G. REID, AND K.A. THRAILKILL. 2002. Natal and breeding dispersal of Northern Spotted Owls. *Wildl. Monogr.* 149:1–35.
- FRANCIS, C.M. AND P. SAUROLA. 2004. Estimating population dynamics and dispersal distances of owls from nationally coordinated ringing data in Finland. *Anim. Biodiv. Conserv.* 27:403–415.
- FRANZÉN, M. AND S.G. NILSSON. 2007. What is the required minimum landscape size for dispersal studies? *J. Anim. Ecol.* 76:1224–1230.
- GONZÁLEZ, L.M., B.E. ARROYO, A. MARGALIDA, R. SÁNCHEZ, AND J. ORIA. 2006. Effect of human activities on the behaviour of breeding Spanish Imperial Eagles (*Aquila adalberti*): management implications for the conservation of a threatened species. *Anim. Conserv.* 9:85–93.
- GREENWOOD, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28:1140–1162.
- AND P.H. HARVEY. 1982. The natal and breeding dispersal of birds. *Ann. Rev. Ecol. Syst.* 13:1–21.
- HAKKARAINEN, H., P. ILMONEN, V. KOIVUNEN, AND E. KORPI-MÄKI. 2001. Experimental increase of predation risk induces breeding dispersal of Tengmalm's Owl. *Oecologia* 126:355–359.
- HOBSON, K.A., L.I. WASSENAAR, AND E. BAYNE. 2004. Using isotopic variance to detect long-distance dispersal and philopatry in birds: an example with Ovenbirds and American Redstarts. *Condor* 106:732–743.
- HOLT, D.W. AND S.M. LEASURE. 1993. Short-eared Owl (*Asio flammeus*). In A. Poole and F. Gill [EDS.], The birds of North America, No. 62. The Academy of Natural Sciences, Philadelphia, PA and The American Ornithologists' Union, Washington, DC U.S.A.
- JOHNSON, M.L. AND M.S. GAINES. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Ann. Rev. Ecol. Syst.* 21:449–480.
- KAUFFMAN, M.J., J.F. POLLOCK, AND B. WALTON. 2004. Spatial structure, dispersal, and management of a recovering raptor population. *Am. Nat.* 164:582–597.
- KENDALL, W.L. AND J.D. NICHOLS. 2004. On the estimation of dispersal and movement of birds. *Condor* 106:720–731.

- KENNEDY, P.L. AND J.M. WARD. 2003. Effects of experimental food supplementation on movements of juvenile Northern Goshawks (*Accipiter gentilis atricapillus*). *Oecologia* 134:284–291.
- , ———, G.A. RINKER, AND J.A. GESSAMAN. 1994. Post-fledging areas in Northern Goshawk home ranges. *Stud. Avian Biol.* 16:75–82.
- KENWARD, R.E., V. MARCSTRÖM, AND M. KARLBOM. 1993. Post-nesting behaviour in goshawks, *Accipiter gentilis*: I: The causes of dispersal. *Anim. Behav.* 46:365–370.
- , S.P. RUSHTON, C.M. PERRINS, D.W. MACDONALD, AND A.B. SOUTH. 2002. From marking to modeling: dispersal study techniques for land vertebrates. Pages 50–71 in J.M. Bullock, R.E. Kenward, AND R.S. Hails [Eds.], *Dispersal ecology*. Blackwell Publishing, Oxford, U.K.
- , S.S. WALLS, AND K.H. HODDER. 2001. Life path analysis: scaling indicates priming effects of social and habitat factors on dispersal distances. *J. Anim. Ecol.* 70:1–13.
- KOENIG, W.D., D. VAN VUREN, AND P.N. HOOGE. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends Ecol. Evol.* 11:514–517.
- KORPIMÄKI, E. 1988. Effects of territory quality on occupancy, breeding performance, and breeding dispersal in Tengmalm's Owl. *J. Anim. Ecol.* 57:97–108.
- . 1993. Does nest-hole quality, poor breeding success or food depletion drive the breeding dispersal of Tengmalm's Owls? *J. Anim. Ecol.* 62:606–613.
- AND M. LAGERSTRÖM. 1988. Survival and natal dispersal of fledglings of Tengmalm's Owl in relation to fluctuating food conditions and hatching date. *J. Anim. Ecol.* 57:433–441.
- KRAUSE, J. AND G.D. RUXTON. 2002. *Living in groups*. Oxford series in ecology and evolution. Oxford University Press, Inc., New York, NY U.S.A.
- MARTIN, J., W.M. KITCHENS, AND J.E. HINES. 2007. Natal location influences movement and survival of a spatially structured population of Snail Kites. *Oecologia* 153:291–301.
- , J.D. NICHOLS, W.M. KITCHENS, AND J.E. HINES. 2006. Multiscale patterns of movement in fragmented landscapes and consequences on demography of the Snail Kite in Florida. *J. Anim. Ecol.* 75:527–539.
- MARZLUFF, J.M. AND B. HEINRICH. 2001. Raven roosts are still information centers. *Anim. Behav.* 61:F14–F15.
- AND ———. 1991. Foraging by Common Ravens in the presence and absence of territory holders: and experimental analysis of social foraging. *Anim. Behav.* 42:755–770.
- MCCLAREN, E.L., P.L. KENNEDY, AND D.D. DOYLE. 2005. Northern Goshawk (*Accipiter gentilis laingi*) post-fledging areas on Vancouver Island, British Columbia. *J. Raptor Res.* 39:253–263.
- MCINTYRE, C.L. AND M.W. COLLOPY. 2006. Postfledging dependence period of migratory Golden Eagles (*Aquila chrysaetos*) in Denali National Park and Preserve, Alaska. *Auk* 123:877–884.
- MILLER, G.S., R.J. SMALL, AND E.C. MESLOW. 1997. Habitat selection by Spotted Owls during natal dispersal in western Oregon. *J. Wildl. Manage.* 61:140–150.
- MILLSAP, B.A. AND C. BEAR. 1997. Territory fidelity, mate fidelity, and dispersal in an urban-nesting population of Florida Burrowing Owls. *Raptor Res. Rep.* 9:91–98.
- MÍNGUEZ, E., E. ANGULO, AND V. SIEBERING. 2001. Factors influencing length of the post-fledging period and timing of dispersal in Bonelli's Eagle (*Hieraetus fasciatus*) in southwestern Spain. *J. Raptor Res.* 35:228–234.
- MOOJ, W.M. AND D.L. DEANGELIS. 2003. Uncertainty in spatially explicit animal dispersal models. *Ecol. Appl.* 13:794–805.
- MORRISON, J.L. AND S.R. HUMPHREY. 2001. Conservation value of private lands for Crested Caracaras in Florida. *Conserv. Biol.* 15:675–684.
- NATHAN, R., G. PERRY, J.T. CRONIN, A.E. STRAND, AND M.L. CAIN. 2003. Methods for estimating long-distance dispersal. *Oikos* 103:261–273.
- NEGRO, J.J., F. HIRALDO, AND J.A. DONÁZAR. 1997. Causes of natal dispersal in the Lesser Kestrel: inbreeding avoidance or resource competition. *J. Anim. Ecol.* 66:640–648.
- NEWTON, I. 2001. Causes and consequences of breeding dispersal in the sparrowhawk *Accipiter nisus*. *Ardea* 89:144–154.
- AND M. MARQUISS. 1983. Dispersal of sparrowhawks between birthplace and breeding place. *J. Anim. Ecol.* 52:463–477.
- NICHOLS, J.D. AND A. KAISER. 1999. Quantitative studies of bird movement: a methodological review. *Bird Study* 46(Suppl.): S289–S298.
- ORTEGO, J., J.M. APARICIO, P.J. CORDERO, AND G. CALABUIG. 2008. Individual genetic diversity correlates with the size and spatial isolation of natal colonies in a bird metapopulation. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 275:2039–2047.
- PARADIS, E., S.R. BAILLIE, W.J. SUTHERLAND, AND R.D. GREGORY. 1998. Patterns of natal and breeding dispersal in birds. *J. Anim. Ecol.* 67:518–536.
- PASINELLI, G., K. SCHIEGG, AND E. MATTHYSEN. 2003. Measuring natal dispersal: current approaches and future challenges. *Alauda* 73:261–263.
- PENTERIANI, V., F. OTALORA, F. SERGIO, AND M. FERRER. 2005. Environmental stochasticity in dispersal areas can explain the “mysterious” disappearance of breeding populations. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 272:1265–1269.
- POWELL, L.A. 2004. A multistate capture-recapture model using a *posteriori* classification to enhance estimation of movement rates. *Condor* 106:761–767.
- RAYBOULD, A.F., R.T. CLARKE, J.M. BOND, R.E. WELTERS, AND C.J. GLIDDON. 2002. Inferring patterns of dispersal from allele frequency data. Pages 89–110 in J.M. Bullock, R.E. Kenward, AND R.S. Hails [Eds.], *Dispersal ecology*. Blackwell Publishing, Oxford, U.K.
- REED, J.M. 1999. The role of behavior in recent avian extinctions and endangerments. *Conserv. Biol.* 13:232–241.

- , T. BOULINIER, E. DANCHIN, AND L.W. ORING. 1999. Informed dispersal: prospecting by birds for breeding sites. *Curr. Ornithol.* 15:189–259.
- ROUSSET, F. 2001. Genetic approaches to the estimation of dispersal rates. Pages 18–28 in J. Clobert, E. Danchin, A.A. Dhondt, AND J.D. Nichols [Eds.], *Dispersal*. Oxford Univ. Press, New York, NY U.S.A.
- RUCKELSHAUS, M., C. HARTWAY, AND P. KAREIVA. 1997. Assessing the data requirements of spatially explicit dispersal models. *Conserv. Biol.* 11:1298–1306.
- SEAMANS, M.E. AND R.J. GUTIÉRREZ. 2006. Spatial dispersion of Spotted Owl sites and the role of conspecific attraction on settlement patterns. *Ethol. Ecol. Evol.* 18:99–111.
- SERGIO, F. AND V. PENTERIANI. 2005. Public information and territory establishment in a loosely colonial raptor. *Ecology* 86:340–346.
- SERRANO, D., M. CARRETE, AND J. TELLA. 2008. Describing dispersal under habitat constraints: a randomization approach in Lesser Kestrels. *Basic Appl. Ecol.* 9:771–778.
- , M.G. FORERO, J.A. DONÁZAR, AND J.L. TELLA. 2004. Dispersal and social attraction affect colony selection and dynamics of Lesser Kestrels. *Ecology* 85:3438–3447.
- , D. ORO, E. URSÚA, J. TELLA, D.E. PROMISLOW, AND J.B. LOSOS. 2005. Colony size selection determines adult survival and dispersal preferences: allee effects in a colonial bird. *Am. Nat.* 166:E22–E31.
- , J.L. TELLA, J.A. DONÁZAR, AND M. POMAROL. 2003. Social and individual features affecting natal dispersal in the colonial Lesser Kestrel. *Ecology* 84:3044–3054.
- , ———, M.G. FORERO, AND J.A. DONÁZAR. 2001. Factors affecting breeding dispersal in the facultatively colonial Lesser Kestrel: individual experience vs. conspecific cues. *J. Anim. Ecol.* 70:568–578.
- SONERUD, G.A., R. SOLHEIM, AND K. PRESTRUD. 1988. Dispersal of Tengmalm's Owl *Aegolius funereus* in relation to prey availability and nesting success. *Ornis Scand.* 19:175–181.
- SOUTH, A. 1999. Dispersal and landscape errors in spatially explicit population models. *Conserv. Biol.* 13:1039–1046.
- SOUTULLO, A., V. URIOS, M. FERRER, AND S.G. PEÑARRUBIA. 2006. Post-fledging behaviour in Golden Eagles *Aquila chrysaetos*: onset of juvenile dispersal and progressive distancing from the nest. *Ibis* 148:307–312.
- SUTHERLAND, W.J., J.A. GILL, AND K. NORRIS. 2002. Density-dependent dispersal in animals: concepts, evidence, mechanisms, and consequences. Pages 134–151 in J.M. Bullock, R.E. Kenward, AND R.S. Hails [Eds.], *Dispersal ecology*. Blackwell Publishing, Oxford, U.K.
- WALLS, S.S. 1998. Movements of radiotagged buzzards *Buteo buteo* in early life. *Ibis* 140:561–568.
- AND R.E. KENWARD. 1995. Movements of radio-tagged Common Buzzards *Buteo buteo* in their first year. *Ibis* 137:177–182.
- , ———, G.J. HOLLOWAY, AND J. GRAHAM. 2005. Weather to disperse? Evidence that climatic conditions influence vertebrate dispersal. *J. Anim. Ecol.* 74:190–197.
- , S. MAÑOSA, R.M. FULLER, K.H. HODDER, AND R.E. KENWARD. 1999. Is early dispersal enterprise or exile? Evidence from radio-tagged buzzards. *J. Avian Biol.* 30:407–415.
- WALTERS, J.R. 2000. Dispersal behavior: an ornithological frontier. *Condor* 102:479–481.
- WATKINSON, A.R. AND J.A. GILL. 2002. Climate change and dispersal. Pages 410–428 in J.M. Bullock, R.E. Kenward, AND R.S. Hails [Eds.], *Dispersal ecology*. Blackwell Publishing, Oxford, U.K.
- WIKLUND, C.G. 1996. Determinants of dispersal in breeding Merlins (*Falco columbarius*). *Ecology* 77:1920–1927.
- WOOD, P.B., M.W. COLLOPY, AND C.M. SEKERAK. 1998. Post-fledging nest dependence period for Bald Eagles in Florida. *J. Wildl. Manage.* 62:333–339.
- ZIMMERMAN, G.S., R.J. GUTIÉRREZ, AND W.S. LAHAYE. 2007. Finite study areas and vital rates: sampling effects on estimates of spotted owl survival and population trends. *J. Appl. Ecol.* 44:963–971.

Received 12 May 2008; accepted 4 December 2008