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BROADENING OUR APPROACHES TO STUDYING DISPERSAL IN RAPTORS

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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 selec-

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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, complicating 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 quality (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 (Donázar and Feijoo 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

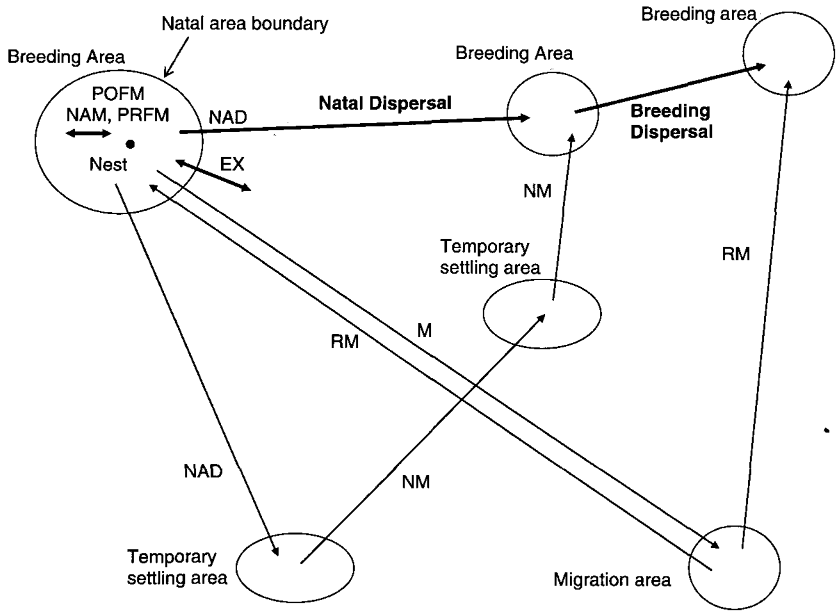

Figure 1. Proposed terminology to describe dispersal events and movements associated with dispersal behavior in raptors. Types of movements are designated by arrows, one- or two-way. Natal dispersal and breeding dispersal events are noted as bold arrows. Other movements are associated with the process 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 dispersal 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 linear 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.

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