Natal dispersal in a social landscape: Considering individual behavioral phenotypes and social environment in dispersal ecology

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Abstract Natal dispersal, the movement of an organism from its birthplace to the site of first reproduction, is fundamental to many ecological and evolutionary processes. Mechanistically, individual dispersal decisions can depend on both individual phenotype and environmental cues. In particular, many established evolutionary theories of dispersal highlight the importance of the social environment. More recent research in behavioral ecology has focused on the importance of individual behavioral phenotypes. We reviewed the literature on individual behavioral phenotypes and dispersal and suggest that how individual behavioral phenotypes interact with the immediate social environment experienced by individuals in influencing dispersal is still poorly understood, despite growing interest. We found that very few studies had examined the interaction of individual behavioral phenotypes and social factors, and behavioral phenotypes related to social tendencies were less commonly measured than were behavioral phenotypes related to exploration or response to risk. Further, and unsurprisingly, studies on social behavioral phenotypes and dispersal behaviors during the transience stage of dispersal were underrepresented compared to the departure or settlement stages. Future studies in this area should aim to: a) make explicit links between behavioral traits and their proposed effects on dispersal decisions throughout multiple stages of dispersal, b) integrate more continuous dispersal variables, and c) consider the effects of the spatial distribution and phenotypes of conspecifics (i.e., the social landscape) encountered by individual dispersers.

Keywords Animal dispersal, Animal personality, Behavioral syndromes, Individual differences, Social landscape

1 Introduction

Natal dispersal, the movement of an organism from its birthplace to the site of first reproduction, is fundamental to a variety of ecological and evolutionary processes (Clobert et al., 2001, 2009, 2012; Bowler and Benton, 2005; Ronce, 2007). Studying natal dispersal in animals (hereafter, simply ‘dispersal’) is critical for understanding population dynamics (Gadgil, 1971; Pulliam, 1988; Hanski, 1999), gene flow (Wright, 1946; Slatkin, 1987; Bohonak, 1999), range expansions ( Kot et al., 1996; Sakai et al., 2001; Duckworth, 2008; Hudina et al., 2014), and population responses to changing environments (Le Gaillard et al., 2012; Baguette et al., 2012). At an ultimate level, the evolution of dispersal strategies is thought to be affected by forces such as competition avoidance and kin selection (Hamilton and May, 1977; Taylor, 1988; Ronce et al., 2000), inbreeding avoidance (Bengtsson, 1978; Greenwood, 1980; Pusey, 1987), and variation in habitat quality (Crespi and Taylor, 1990; McPeek and Holt, 1992). At a proximate level, an individual’s decision to disperse will depend on both the environmental cues that it detects and on its phenotype (these were referred to, respectively, as condition-dependent and phenotype-dependent dispersal by Clobert et al., 2009, where condition refers to the external environment, not body condition; they have alternatively been called “extrinsic” and “intrinsic” factors, Rémy et al., 2014). External cues include population density, habitat cues, sex ratio, and social interactions (reviewed in Bowler and Benton, 2005; Clobert et al., 2009; and Baguette et al., 2014), whereas intrinsic individual phenotypic traits include body condition (Ims and Hjermann, 2001), sex (Greenwood, 1980; Pusey, 1987), development and parental effects (Massot et al., 2002; Bernard and McCauley, 2008; Carere et al., 2010; Miller et al., 2012; Bitume et al., 2014), and behavioral phenotypes (Myers and Krebs, 1971; Cote et al., 2010). Despite recent progress, incorporating the effects of both individually variable characteristics and environ-
mental variation into more realistic models of dispersal remains particularly challenging (Bowler and Benton, 2005; Clobert et al., 2009).

Individual dispersal is perhaps best understood as an integrated process with interdependencies among three stages—departure (or emigration), transience (or search), and settlement (or immigration)—rather than unrelated decisions to leave a natal habitat and settle in a new habitat (Bowler and Benton, 2005; Ronse, 2007; Clobert et al., 2009; Bonte et al., 2012). Generally, departure refers to the decision to leave the natal site, transience includes all movements between departure and settlement, and settlement refers to the decision to select and stay in a breeding site. Although advances have recently been made towards integrating this multi-stage perspective with individual behavioral phenotypes and their interaction with the environment (discussed in Cote et al., 2010), most studies typically do not follow individuals throughout the entire dispersal process, and thus much work is still needed to elucidate which aspects of the environment are most likely to interact with behavioral phenotypes during dispersal (Bowler and Benton, 2005).

There has long been interest in how consistent interindividual differences in behavior relate to dispersal and settlement patterns (e.g., Myers and Krebs, 1971; Svendsen, 1974; Bekoff, 1977). Bekoff (1977) was one of the first authors to explicitly discuss the importance of individual behavior on dispersal, emphasizing the need to study “the ontogeny of individual behavioral phenotypes [original author’s emphasis] and its relationship to later individual dispersal patterns”, especially in the context of social interactions. Broader frameworks explaining mechanisms for the evolution and maintenance of individual behavioral differences and their possible roles in ecological processes have recently been developed (Wilson, 1998; Gosling, 2001; Sih et al., 2004; Réale et al., 2007; Dingemanse et al., 2010), and interest in how such individual variation influences dispersal behavior has grown (Clobert et al., 2009; Cote et al., 2010). Several terms have been applied to individual behavioral variation (including “animal personality,” “behavioral types,” “behavioral syndromes,” “temperament,” and “coping styles”). Here, we will use the term “individual behavioral phenotypes” (sensu Bekoff, 1977), which encompasses these concepts without making explicit assumptions about behavioral correlations across either time or contexts.

The social environment features prominently in many theories of dispersal, and many dispersal studies docu-
potentially new environments.

Here, we explore the intersection between individual behavioral phenotypes and social context across the three stages of dispersal (Fig. 1). We first present results from a literature review of empirical studies of individual behavioral phenotypes and natal dispersal, specifically asking how many of these concurrently examine social effects. We next discuss some outstanding issues that emerge from the results of the review and develop the concept of a social landscape and its potential relevance to animal dispersal studies.

2 Literature Review

We searched the Web of Science database for studies examining the effect of individual behavioral phenotypes on natal dispersal in non-human animals. To search broadly and include potentially different terminologies used by different subfields for similar concepts, we initially included multiple terms that could refer to dispersal AND either individual behavioral differences OR behavioral traits of interest (see Appendix 1 for more details on search and selection procedure). We also checked two previous reviews (Clobert et al., 2009, and Cote et al., 2010) for additional references. Our criteria for inclusion in the formal review were relatively strict. We retained only studies that explicitly measured the relationship between individual behavioral phenotypes and natal dispersal, in which natal dispersal was measured at spatial and temporal scales likely to represent the process in nature (e.g., we excluded studies that only looked at short-term movements or used animals that might not be at the right life stage for natal dispersal). We also only considered individual behavioral phenotypes that were measured in at least two time points or two contexts in a standardized way, where individually differentiated behaviors were the measure of interest (e.g., either with an experimental assay or relative tendencies extracted from natural behaviors with statistical methods to control for other confounding factors; Bell, 2007). Our focus was on how many studies of individual behavioral phenotype and dispersal accounted for social factors, so we first filtered papers by the above criteria before asking which studies within this subset also examined social factors. After this thorough search, we narrowed the original list of 1,078 papers to a final set of only 17 empirical studies that met these criteria (full information in Appendix 2). Although our original intent was to conduct a meta-analysis examining the simultaneous effects of different individual behavioral phenotypes and sociality on dispersal outcomes, the small number of studies in the final list precluded this approach. Instead, we present numeric summaries of studies in the final list and qualitative analysis of results from the review.

We scored each paper to determine what combination of behavioral traits, stages of dispersal during which individuals were followed, specific dispersal variables measured, social factors (if any), and their interactions with behavioral phenotypes were examined in each study (Table 1). We categorized behavioral traits according to five ecologically relevant groupings suggested by Réale et al. (2007): boldness (response to risk), exploration (reaction to a new situation, including novel objects), activity (in absence of risk or novelty), aggressiveness (towards conspecifics), and sociability (response to conspecifics other than aggression). Behavioral traits that did not clearly fall into one of these categories were counted as “other”. We categorized the stages of dispersal examined as departure (focusing on a decision to leave a natal habitat), settlement (focusing on choice of an initial breeding habitat), and transience (focusing on movements between departure and settlement, including prospecting). We categorized several common dispersal variables measured in animal studies: dispersed or not, final dispersal distance, immigrant or resident, dispersal morph, and dispersal delay. Dispersal measures that did not clearly fall into one of these categories were counted as “other”. We also noted if any aspect of the social environmental was measured, and
whether any interaction between social factors and behavioral phenotype was considered.

### 2.1 Results from literature review

Several points emerge from this literature review. First, despite the large literature on animal dispersal behavior overall, the number of studies that formally measured both individual behavioral phenotypes and natal dispersal is very small, and the number of studies that concurrently include the effects of social factors on dispersal is smaller still. Second, dispersal stages and dispersal outcome variables were not evenly represented in these studies. Although many studies examined more than one stage of dispersal, the transience stage is still under-studied compared to the departure and settlement stages. In terms of the dispersal outcomes measured, the most common was the binary variable "dispersed or not," followed by a binary classification of individuals within a population as immigrants or residents. Interestingly, these are very similar variables, distinguished by whether the researchers are focusing on individual movement decisions at the beginning of the three-stage dispersal process or on population-level outcomes at the end (immigrant or resident). Relatively few studies that satisfied our specific criteria considered other dispersal variables, such as dispersal distance or the timing of dispersal. Finally, behavioral traits were not evenly represented in these studies; exploration was by far the most common trait examined (Table 1).

Notwithstanding the small absolute number of studies in Table 1, the number of studies on individual behavioral phenotypes and dispersal has increased rapidly in recent years (Table A1, Appendix 2). Most of the studies were published after 2003, and half (9/17) have been published since Cote et al.'s (2010) review of dispersal and animal personality. The final papers included in Table 1 were necessarily somewhat biased towards the behavioral organism literature, with many earlier studies did not publish specific behavioral variables measured. In light of this, it is perhaps unsurprising that only a handful of studies to date have looked at the interaction between individual behavioral phenotype and social environment on dispersal decisions. However, the importance of social factors on dispersal is still understudied compared to the departure and settlement stages. In terms of the dispersal outcomes measured, the most common was the binary variable "dispersed or resident," followed by a binary classification of individuals within a population as immigrants or residents. Interestingly, these are very similar variables, distinguished by whether the researchers are focusing on individual movement decisions or population-level outcomes at the end (immigrant or resident). Relatively few studies that satisfied our specific criteria considered other dispersal variables, such as dispersal distance or the timing of dispersal. Finally, behavioral traits were not evenly represented in these studies; exploration was by far the most common trait examined (Table 1). Notwithstanding the small absolute number of studies in Table 1, the number of studies on individual behavioral phenotypes and dispersal has increased rapidly in recent years (Table A1, Appendix 2). Most of the studies were published after 2003, and half (9/17) have been published since Cote et al.'s (2010) review of dispersal and animal personality. The final papers included in Table 1 were necessarily somewhat biased towards the behavioral organism literature, with many earlier studies did not publish specific behavioral variables measured. In light of this, it is perhaps unsurprising that only a handful of studies to date have looked at the interaction between individual behavioral phenotype and social environment on dispersal decisions. However, the importance of social factors on dispersal is still understudied compared to the departure and settlement stages. In terms of the dispersal outcomes measured, the most common was the binary variable "dispersed or resident," followed by a binary classification of individuals within a population as immigrants or residents. Interestingly, these are very similar variables, distinguished by whether the researchers are focusing on individual movement decisions or population-level outcomes at the end (immigrant or resident). Relatively few studies that satisfied our specific criteria considered other dispersal variables, such as dispersal distance or the timing of dispersal. Finally, behavioral traits were not evenly represented in these studies; exploration was by far the most common trait examined (Table 1).
tors in well-established theories of dispersal, as well as Bekoff’s (1977) very specific hypotheses about individual behavioral phenotypes and social interactions, indicate that this gap in dispersal ecology research has long been recognized. In particular, we emphasize that studies addressing the social effects at a very fine and individualized scale (which is arguably the most relevant to individual dispersal decisions) are rare.

Studies included in Table 1 were not evenly spread over taxonomic groups (see also Appendix 2, Table A1). The most detailed information comes from a few well-studied vertebrate systems (e.g., great tits *Parus major*; common lizards *Lacerta vivipara*). Mammals, particularly rodents, are the most widely represented taxon. Invertebrates were represented by a single study, in which the outcome was dispersal morph (i.e., potential for dispersal), rather than actual dispersal. The uneven emphasis across taxa is likely due to a traditional focus on individual behavioral variation and social factors in certain groups (e.g., birds and mammals) and to very few study systems having the breadth of data to cover these topics. While we cannot rule out terminological biases (e.g., in the invertebrate literature, “migration” is often used interchangeably with “dispersal”, Holyoak et al., 2008; Dingle, 2014), we suggest that our results indeed reflect the relatively low number of invertebrate movement studies that focus on individuals (Holyoak et al., 2008) or that consider behavioral phenotypes separately from dispersal morphs (Ducatez et al., 2012). Thus, invertebrates are a relatively understudied group for examining questions about the interaction between individual behavioral phenotypes and social context on dispersal. However, invertebrates are likely to be more tractable study systems than most vertebrates at the spatial and temporal scales amenable to studying natal dispersal, especially in laboratory and experimental settings. While tracking individually identified individuals in the field remains a major challenge due to their small size, methodological advancements continue to make this an exciting time to tackle this challenge (e.g., Hagner et al., 2001; Wikelski et al., 2007; Ovaskainen et al., 2008).

### 2.2 Measurement of dispersal outcomes

It is not surprising that the most common dispersal variables measured by researchers were binary (e.g., “dispersed or not”, “immigrant or resident”). Relatively few studies looked at other potential outcomes, such as dispersal distance or timing (delay in departure). Empirical studies of individual animal dispersal in general have largely focused on either the decision to depart from a site, or to settle in a new site (Bowler and Benton, 2005). Far fewer studies have followed individuals during the transience stage connecting departure and settlement (Wiens, 2001), likely due to the logistical difficulty of studying individually marked animals continuously throughout the entire dispersal process (Koening et al., 1996). Further, even studies that followed individuals during transience did not necessarily measure a variable specific to that stage, such as search patterns; instead, final dispersal distance was typically measured. Although recent dispersal studies have begun to focus on the transience stage or exploratory movements (Haughland and Larsen, 2004; Doerr and Doerr, 2005; Selonen and Hanski, 2006; Mabry and Stamps, 2008 a, b; Debeffe et al., 2013, 2014), such studies remain relatively rare. However, technological advances, including the development of more tractable automated tracking tools, should continue to make the study of the transience stage of dispersal more feasible (e.g., Bridge et al., 2011; Krause et al., 2013). The transience stage, during which many costs of dispersal are hypothesized to be incurred, is of fundamental biological importance, and our understanding of the dispersal process will remain incomplete without more empirical work on this stage.

Another pattern that emerged is the opportunity for wider explicit study of continuous dispersal traits, which is critical for capturing continuous variation in ecological and evolutionary outcomes and understanding dispersal behavior in natural populations. Many dispersal measures are inherently continuous (e.g., dispersal distance or duration of search), and this variation is lost or artificially truncated when individuals are artificially binned into the categories of “dispersed” or “did not disperse.” Furthermore, it can often be difficult to categorize an individual as a disperser or non-disperser; for example, if natal and adult ranges overlap imperfectly, if there are not clear boundaries between "natal" and "other" habitat, or if individuals leave but return to the natal habitat (e.g., Conradt et al., 2003; Spiegel et al., 2015). Utilization of continuous measures should allow for more flexible discussion of dispersal behavior and of the three stages of dispersal. In particular, the study of behavior during the search or transience stage of dispersal should benefit, as disperser/resident designations explicitly omit this stage. For example, individuals that might eventually be classified as residents because they came back to a natal area could still engage in search behavior. In terms of the behavioral mechanisms underlying dispersal patterns and genetic consequences for
dispersal evolution, it may be most informative to consider multiple dispersal variables where possible. For instance, if an individual settles in its natal area after a prolonged search phase, that individual would experience similar movement costs as an individual that dispersed farther, but might have the same effect on gene flow as an individual that settled without a prolonged search period.

2.3 Linking behavioral traits to each stage of dispersal

The most common behavioral trait measured was exploration in a novel environment (11/17 studies). The focus on exploration is likely due to intuitive links between exploratory behavior and all stages of dispersal; e.g., if an individual will decide to leave a familiar habitat, and how it will search for and settle in a novel habitat. Given the focus on the role of social interactions in dispersal theory, it is interesting that fewer studies measured either individual aggressiveness (8/17) or sociability (5/17), which are potentially the most relevant behavioral traits in the context of interactions with the social environment. Notably, we found no studies focusing on aggressiveness or sociability during the transience stage, showing another major empirical gap. Parsing out the (average) effects of social environment and effects of individual social tendencies on dispersal behaviors thus remains, in our opinion, one of the most exciting directions for research.

Theoretically, differential responses to social interactions during transience by individuals varying in aggressiveness or sociability could be extremely important for the dispersal process and outcomes. Developing models that will simultaneously account for heterogeneity in environmental conditions encountered en route and the heterogeneity in phenotype dependent response to these conditions remains a conceptual challenge to the field. Currently, although we can make some basic predictions about how individuals with different social behavioral phenotypes might respond to social interactions or cues during transience, this is empirically an unanswered question. Another major challenge is testing the absolute and relative importance of different behavioral dimensions at different stages. For example, variation in response to predators might be more important than aggression during transience, but does this trade off with social traits during departure and settlement? In general, more discussion of the ecological links between behavioral phenotypes and a priori expectations for measured behaviors to the dispersal process would be useful. Logistically, it is extremely difficult to collect detailed data on social cues and other environmental parameters encountered during transience, but increasingly accurate and tractable automated tracking equipment (Wikelski et al., 2007; Bridge et al., 2011) provides exciting possibilities for adding to our knowledge about individual movements and social factors during search phases.

3 Dispersal in a Social Landscape

3.1 What is a social landscape?

In studying the interplay between individual behavioral phenotypes and the social environment, it should be important to consider the detailed social landscape, i.e., where resident conspecifics of known phenotype are located spatially and how they interact with each other and with dispersers. The environment through which potential or active dispersers gather information and make decisions about whether/when to leave and where to settle will contain information about both the physical and social environment. Ecologists are familiar with considering how the physical landscape and the spatial distribution of resources might influence animal dispersal and movement decisions. Similarly, the distribution of conspecifics in space, the social cues they provide, and the potential barriers they represent could all influence individual dispersal decisions. Social landscape variables can be thought of as analogous to, but distinct from, physical landscape variables or non-spatially explicit social variables and thus quantified using similar methods. We distinguish social landscape effects from density effects more generally in that the particular distribution and use of the physical landscape by nearby conspecifics are more specific aspects of the social environment. Even individuals within the same density treatment could have different social landscape covariates (i.e., social landscape variables would be nested within population/local density). In practice, social landscapes might vary the most when potential dispersers are prospecting or otherwise moving through the physical landscape and encountering new social environments.

Although the term “social landscape” has been used generally to refer to the idea of the combined social and spatial environment, we particularly reference two sources that define and demonstrate useful applications of more formal social landscape variables that are distinct from population or even local density, as commonly defined. Formica and Tuttle (2009) suggested using spatially explicit social landscape models to quantify social heterogeneity, focusing on modeling how local densities
corresponded to social niche partitioning and cuckoldry risk in white-throated sparrows *Zonotrichia albicollis*. They specifically suggested quantifying social environments by approaching them “as landscapes by measuring social and behavioural variables across a spatial coordinate system” and describe their measure of the actual conspecific density experienced by each individual as a “social-landscape variable” (page 2,397). Zamudio and Sinervo (2003) suggested another type of social landscape variable, predicting that the “grain” (scale) of social heterogeneity could select for and maintain different levels of within-population polymorphism, analogous to the role of environmental heterogeneity in general. They tested these ideas using the number and stability of neighboring territories as social landscape characteristics across species of small territorial lizards, and suggested that the ideas could easily be extended to other species. Both these examples illustrate how sociospatial characteristics other than the average population or local density can influence individual experience.

3.2 Connecting social landscape variables to individual behavioral phenotypes and dispersal

Further consideration of the interactions between individual behavioral phenotypes and social landscape variables will be informative for how individuals use social experience in making dispersal decisions. Recent studies suggest some likely future directions for advancement in this area. For example, Blumstein et al. (2009) tested the “social cohesion hypothesis” (suggested by Bekoff, 1977) in yellow-bellied marmots *Marmota flaviventris* by quantifying the number, strength, and patterning of social interactions of young marmots, and asking if these measures were associated with dispersal in yearling marmots. This study indeed found evidence that the structure of the local social network influenced the probability of departure in female, but not male, marmots. Specifically, more affiliative females that were better connected to others in the social network were less likely to disperse. However, Blumstein et al. (2009) did not put social interactions into a landscape context, and so did not examine to what extent the spatial distribution of conspecifics influenced the social interactions that eventually influenced dispersal.

In contrast, Wojan et al. (2015) used a spatially-explicit capture-recapture model to estimate population density across space and show that individual juvenile brush mice *Peromyscus boylii* tended to disperse from areas of lower conspecific density into areas of higher population density, while accounting for overall temporal changes in population density across the landscape. Interestingly, here the cue is the relative population density in natal and settlement areas, rather than one or the other in isolation. This study does include one landscape variable (local density in the areas used by dispersers) but did not have individual-level information on social interactions experienced by dispersers, nor on individual behavioral phenotypes. It would also be interesting to explore if individuals that differ in their sociability or aggressiveness also differ in their decision thresholds on where to settle, compared to their natal habitat.

In other study systems, different behavioral phenotypes are characteristically found in different group sizes or densities (e.g., Duckworth and Badyaev, 2007; Riechert and Jones 2008; Vercken et al., 2012). Dispersal has been suggested as a central mechanism to explain the link between population density and frequency of particular behavioral phenotypes (Chitty, 1967; Duckworth and Badyaev, 2007; Fogarty et al., 2011; Vercken et al., 2012), but the generality of this mechanism remains to be tested. Studies combining the socially-explicit aspects of Blumstein et al. (2009) with the spatially-explicit aspects of Wojan et al. (2015) would advance our understanding of dispersal in a social landscape context tremendously. These examples illustrate how both actual interactions and social proxies such as number of territories moved through could give a sense of the amount of social information and variation in social experience dispersers have.

In general, the interaction between social landscape variables and individual behavioral phenotypes may be key to linking decisions at different stages of dispersal. For example, during the transience stage, dispersers are thought to gather information about suitable habitats as they move through the environment (i.e., search or prospect for a new home; Chaine et al., 2013; Delgado et al., 2014). Individuals that travel greater distances should encounter more conspecifics by chance alone, so more active or exploratory individuals might receive more social cues than would individuals with other behavioral phenotypes. Different personality types might also move through the landscape differently. For example, bolder individuals might be more willing to use risky habitat than shyer individuals, and if more conspecifics are found in safe habitats, then shyer individuals would encounter more conspecifics during transience. The specific cues than any disperser will receive will also depend on the phenotype of conspecifics in the local social landscape. A potential disperser surrounded by aggressive individuals, and that is more likely to
experience aggression during initial forays, might be less likely to continue exploring than an individual who encounters less aggressive individuals early on in transience. Additionally, these responses could interact with the potential disperser’s behavioral phenotype (Cote and Clobert, 2007). A social individual that encounters many conspecifics during transience would be predicted to use this experience very differently from an asocial individual with the same experience; a social individual should be more likely to settle near these conspecifics whereas an asocial individual should be more likely to move on. The local social landscape should then also influence how much time a disperser spends searching and how much space the disperser will cover, in a phenotype-dependent way.

Another general question is to what extent temporal and spatial stability (or heterogeneity) might affect the relationship between behavioral phenotypes and dispersal decisions. The hypothesis presented by Zamudio and Sinervo (2003) about social environmental heterogeneity influencing phenotypic specialization presents some intriguing testable predictions. Specifically, more stable social environments might select for more highly differentiated behavioral phenotypes (Laskowski and Pruitt, 2014; but see Laskowski and Bell, 2013, Modlmeier et al., 2014). The consequences of individual specialization for dispersal behavior and fitness are exciting areas of study, and it generally remains to be seen whether stable social environments do select for behavioral specialists or for behavioral plasticity (Montiglio et al., 2013). This expectation also extends to discussions of how environmental variation, beyond the social context, might influence the evolution of individual behavioral consistency or plasticity (e.g., Sih et al., 2004; Snell-Rood, 2013). In the context of dispersal, we might predict that less heterogeneous, more stable social environments should result in more highly behaviorally differentiated dispersal strategies. Conversely, more heterogeneous, less stable social environments should select for less differentiated dispersal strategies. It will be interesting to test these expectations in behavioral traits, which can be quite labile, as opposed to relatively fixed morphological traits (as in Zamudio and Sinervo, 2003).

4 Conclusion

Bekoff (1977) explicitly argued the importance of and developed hypotheses for studying the development of individual behavioral phenotypes, particularly in the context of social interactions, and their effect on later dispersal decisions. Almost 40 years later, in a rapidly changing world, the relevance of dispersal ecology and the role of individual behavioral phenotypes and social environment in this process has only grown (Sih et al., 2010). Despite many advances, the number of empirical papers addressing the combination of individual behavioral phenotypes, social factors, and natal dispersal is still strikingly small. Based on our review of the literature, we highlighted the need for more continuous measures of dispersal variables and making more explicit links between behavioral traits and their proposed effects on dispersal decisions. We also suggest that studying the effects of social landscapes is especially promising for future research.

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References


Appendix 1  Details on literature search

1  Search Terms

(dispers* OR immigration OR emigration) AND
((personalit* OR temperament OR “behavioral syndrome” OR “behavioral type” OR “coping style”) OR (boldness OR explorat* OR aggress* OR sociability OR neoph* OR fearfulness))

We did not include the term “migration” because this typically refers to movements that differ from our intended focus on natal dispersal (Clobert et al., 2012). While noting that “migration” is often used interchangeably with “dispersal” in the invertebrate literature (Holyoak et al., 2008; Dingle, 2014), the relevant studies should have been captured by the search terms “immigration” and “emigration”.

We also did not include the term “habitat selection” in the initial search because this typically referred to shorter-term behavior. However, a separate search with the terms (habitat selection) AND (juvenile OR natal) and all possible behavioral search terms resulted in 29 studies, all of which were either captured by our original search or were not relevant for inclusion.

2  Number of Studies

Our initial search (conducted on September 23, 2014) turned up 1,078 studies. After limiting our search to topics in behavior and ecology, sorting the initial list, and excluding journals outside the field of behavioral ecology, we had 769 studies. We then excluded titles clearly outside of our area of interest (e.g., on plant dispersal or marine larval dispersal). We then read abstracts and filtered out papers that did not potentially address animal dispersal and individual-level variation in behavior, leaving 111 papers. We divided these papers randomly between all authors to read for inclusion criteria and score in more detail for variables of interest.

Two relevant studies were published during the writing and revision process of our review, and they were included in the final version of Table 1. These studies were picked up by rerunning our original search for the years 2014–2015 only, which resulted in 81 studies after restricting the search to relevant research areas. These 81 studies included some overlap with our original search and were reviewed and scored by one of us (TWW). The list is complete to our knowledge as of May 24, 2015.

3  Exclusion of Studies

We did not include studies that focused on interspecific behavioral differences (that did not also look at within-species behavioral variation) nor studies that focused on human behavior and movements. While difficult to draw a line, we also excluded studies that explored relevant topics if they did not measure dispersal or behavioral phenotype variables that matched our criteria. For example, several studies measured differences in aggression or affiliation rates, or patterns of social interactions, without explicitly developing the individually variable component, and thus were not included in Table 1 counts. We also excluded studies that focused on adult breeding dispersal or shorter-term movements that did not seem representative of natal dispersal. Although broader definitions of ecologically relevant dispersal and behavioral phenotype measures might include a few more studies in our summary, we are confident that these would not qualitatively change the observed patterns and that our final counts are representative of the literature available. The same results from a dataset were only included once (e.g., if they were cited in another paper). However, different studies (i.e., different individual animals studied) from the same system/lab were included.
## Appendix 2 Additional metadata, discussion, and full citations for the 16 papers included in Table 1.

### Table A1 Descriptive metadata for papers included in Table 1. Papers are sorted by year of publication.

<table>
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<tr>
<th>Authors</th>
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<th>Journal</th>
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<th>Scientific name</th>
<th>Other variables** studied</th>
<th>Conducted in field or semi-natural conditions?</th>
<th>Experimental manipulation?</th>
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<td><em>Proceedings of the Royal Society B: Ecological Sciences</em></td>
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* Each species counted separately for Table 1; ** Denotes whether the effects of other types of variables on dispersal behaviors were considered. Most studies included research done in field or semi-natural conditions, with only three done entirely in lab conditions, which is a benefit for representing more naturalistic behaviors. On the other hand, less than half of the studies included any experimental manipulation, which makes it potentially difficult to distinguish the effects of behavioral phenotypes from effects of other factors. Most studies in our sample had also measured body mass as a covariate, and most had considered individuals of both sexes. Some had even measured age at dispersal, suggesting that individual variation in timing of dispersal could be important in these cases. As discussed in the main text, taxonomic groups were unevenly represented in this list, and the work in birds and reptiles largely represents work from one species from each taxa.
Table A2  Alternate presentation of in-text Table 1, showing which studies examine particular combinations of variables. Formatted following Cote et al. 2010 Phil. Trans. B., Table 1. Numbers correspond to the assigned paper number under “Papers cited”, below.

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<th>Behavioral trait</th>
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<th>Dispersal variable measured</th>
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<td>Transience</td>
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<td>Exploration</td>
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<td>Boldness</td>
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<td>Activity</td>
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<td>Aggressiveness</td>
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<td>Sociability</td>
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<tr>
<td>Other</td>
<td>3,6,10,14,16</td>
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Papers cited (in alphabetical order)