

THE INFLUENCE OF PERSONALITY ON DISPERSAL AND POPULATION DYNAMICS
IN A PASSERINE BIRD

by

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To my parents, Jose and Carrie, for their love and support and all of the sacrifices they have made to allow me to reach this milestone.

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ABSTRACT

Dispersal influences the genetic and social composition of populations, yet it has been difficult to understand the mechanisms underlying dispersal and this limits our ability to understand how dispersal may be influencing population dynamics. Behavioral traits, such as aggression, have been implicated as drivers of both dispersal and population dynamics. However, the influence on both has never been addressed in a single system. Western bluebirds (*Sialia mexicana*) provide an excellent opportunity to address this question, as their dispersal propensity is dependent upon aggressive phenotype and we have detailed observations over a period of more than a decade. I show that natal dispersal is influenced by an interaction between father and son aggressive phenotypes, in addition to available resources on the natal territory. Furthermore, population density is influenced by resource availability and an interaction between population aggression and recruitment of offspring as breeders. Males that breed for multiple seasons once the population has reached saturation recruit a higher proportion of offspring into the population, as do males that are nonaggressive. Males that are nonaggressive are more likely to breed for multiple seasons, which suggests an added cost to aggressive behavior in this species. Both aggressive behavior and the availability of resources are mechanisms influencing dispersal of individuals that manifest at the population scale.

CHAPTER I: INTRODUCTION

Dispersal is a fundamental component of life history and understanding the mechanisms underlying variation in dispersal is necessary to understand how it influences the genetic and social composition of populations (Hanski 1999; Clobert et al. 2001), as well as the overall dynamics of the population (Krebs 1996; McDevitt et al. 2013). Despite its importance, it has been difficult to understand the causes of dispersal (Greenwood and Harvey 1982; Clobert et al. 2001) and this limits our ability to understand how dispersal may be influencing population dynamics. It is incredibly difficult to address these questions in natural populations, as it requires the collection of data at both the individual and population level over a long period of time.

The influence of behavioral traits, such as aggression, boldness, and sociality, have been linked to dispersal (Fraser et al. 2001; Dingemanse et al. 2003; Cote and Clobert 2007; Duckworth and Badyaev 2007; Cote et al. 2010) and population dynamics (Gipps et al. 1980; Lambin and Krebs 1993; Mougeot et al. 2003) in a variety of species, which suggests that an individual's personality may be an important determinant of both. It is acknowledged that phenotype-dependent dispersal has important consequences for population dynamics and evolution (Clobert et al. 2009; Edelaar and Bolnick 2012; McDevitt et al. 2013), yet the mechanisms linking behavioral traits to dispersal and population dynamics are unknown. The influence of these behavioral traits on dispersal and population dynamics have previously been addressed separately, however a species that exhibits phenotype-dependent dispersal may have population dynamics that are influenced directly by personality traits or indirectly through the influence of behavior on dispersal.

This thesis examines the mechanisms underlying the influence of aggressive behavior on within-site spacing behavior and population dynamics in a nest box population of western bluebirds (*Sialia mexicana*), a secondary cavity nesting passerine bird with phenotype-dependent dispersal (Duckworth and Badyaev 2007) that has been intensely studied for over a decade (Duckworth 2006b, a; Duckworth and Badyaev 2007; Duckworth 2009; Duckworth and Sockman 2012). Here, I show that natal dispersal of first-year males is influenced by an interaction between father and son aggressive phenotypes, in addition to resource availability on parental territories (Appendix A). Aggressive sons, the sons of aggressive fathers, and sons with few resources on their natal territory dispersed farther distances from their natal nest (Appendix A). Because resource acquisition and personality type are interdependent in this species, these proximate influences on dispersal likely mediate changes in population density, behavior, and resource availability across years. I show that population density is influenced by resource availability and the interaction of population aggression and recruitment of offspring into the population (Appendix B). Further, the number of breeding seasons a male was present and his aggressive phenotype influence the number of offspring he recruits into the population (Appendix B). Additionally, nonaggressive males were more likely to breed for multiple seasons, which suggests aggression negatively influences survival in this species (Appendix B).

This thesis demonstrates that aggressive behavior has both a direct and indirect effect on population dynamics in a well-studied population of western bluebirds. As it has been acknowledged that phenotype-dependent dispersal can have important consequences for the evolution and dynamics of populations (Clobert et al. 2009; Edelaar and Bolnick 2012; McDevitt et al. 2013), studies such as this thesis that work to identify the underlying mechanisms are increasingly necessary. This study addresses multiple scales of organization, from the individual

to the population, and shows that the importance of aggression spans these scales. At the population level, average aggression of the population directly influences population density across years. Further, aggression of individual males influences the number of offspring he recruits into the population as breeders and the subsequent spacing behavior of offspring when they breed. Future studies should continue to identify mechanisms that explain how behavior influences population dynamics directly and indirectly through phenotype-dependent dispersal.

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APPENDIX A: RESOURCE-MEDIATED BEHAVIORAL DYNAMICS AMONG KIN DRIVE
DISPERSAL IN A BIRD

ABSTRACT

Dispersal strongly influences population demographics and evolution. However, context-dependency of dispersal decisions, such as effects of social interactions and resource availability, are rarely disentangled from intrinsic factors, such as animal personality. Disentangling these factors can provide insight into intrinsic and extrinsic regulation of population dynamics. Here, we examine how interactions between personality, relatedness, and resource availability influence dispersal decisions in a passerine bird. We measured family dynamics and behavior over an eleven-year period enabling us to determine how distinct combinations of personality traits and resource availability affected dispersal decisions of offspring. We found that natal dispersal was driven by an interaction of father and son personalities in addition to resources on parental territories. Both aggressive sons and the sons of aggressive fathers dispersed longer distances, as did the offspring of parents who had fewer resources on their territories. Because resource acquisition and personality type are interdependent in this species, these proximate influences on dispersal likely mediate changes in population density, behavior, and resource availability across years. Thus, the frequency of behavioral types in a population can have important, but previously unappreciated, consequences for population dynamics.

Keywords: phenotype-dependent dispersal, personality, kin interactions, resource availability, aggression, *Sialia mexicana*.

INTRODUCTION

Dispersal is a fundamental component of life history and identifying the mechanisms underlying variation in dispersal is key to determining how it influences the overall genetic and social composition of populations (Hanski 1999; Clobert et al. 2001). Yet, despite its importance, determining the causes of dispersal has been difficult (Greenwood and Harvey 1982; Hanski 1999; Clobert et al. 2001). This is because the decision to disperse depends not only on an individual's phenotype (Fraser et al. 2001b; Fraser et al. 2001a; Dingemanse et al. 2003; Cote and Clobert 2007; Duckworth and Badyaev 2007), but also on environmental context, such as social interactions and resource availability (Cote and Clobert 2007; Clobert et al. 2009). Determining the relative importance of individual attributes versus environmental context is important because it can provide insight into the relative importance of intrinsic and extrinsic factors in population dynamics (Krebs 1996; McDevitt et al. 2013).

Behavioral traits, such as aggression, boldness, and sociality, have been linked to dispersal in a variety of species (Fraser et al. 2001b; Fraser et al. 2001a; Dingemanse et al. 2003; Cote and Clobert 2007; Duckworth and Badyaev 2007; Cote et al. 2010b), suggesting that an individual's propensity to disperse might be influenced by their personality (here, defined as consistent behavioral differences across time and/or contexts; Dall et al. 2004). While such phenotype-dependent dispersal is widely acknowledged to have important consequences for population dynamics and evolution (Clobert et al. 2009; Edelaar and Bolnick 2012; McDevitt et al. 2013), the mechanisms linking behavioral traits to dispersal are often unknown. Correlations between personality and dispersal are often assumed to reflect a functional link where the personality trait directly causes variation in dispersal behavior (Duckworth and Kruuk 2009; Cote et al. 2010a). For example, bolder individuals may be expected to move greater distances

because they are less fearful of novel environments and thus more apt to explore outside their natal environment. Yet, personality variation can also influence an individual's access to resources and social interactions, which in turn affect dispersal (Bowler and Benton 2005). Thus, correlations between dispersal and personality type may reflect a common dependence on environmental factors rather than a direct causal link between them.

Further, whereas focus is primarily placed on the behavior of the dispersing individual (reviewed in Cote et al. 2010a), natal dispersal is often the outcome of interactions among relatives. Social interactions between kin have been implicated as drivers of dispersal (reviewed in Lambin et al. 2001), where kin competition may promote dispersal (Strickland 1991; Ekman et al. 2002; Pasinelli and Walters 2002) and cooperation with or tolerance of kin may result in limited dispersal (Lambin and Krebs 1993; Eikenaar et al. 2007; Davis 2011). Most importantly, such social interactions may themselves depend on the personality type of the interacting kin (Bergmüller and Taborsky 2010; Aplin et al. 2013) as well as external factors, such as resource availability (Stacey and Ligon 1991; Brown and Brown 1993). When dispersal depends on both an individual's phenotype and the phenotypes of surrounding individuals, this should lead to distinct ecological dynamics compared to if dispersal depended on the focal individual's personality type alone (Clobert et al. 2009). Therefore, understanding the dispersal decision requires assessing the behavior of individuals likely to interact, in addition to resource availability.

Aggression, in particular, has been shown to be linked to dispersal (Myers and Krebs 1971; Duckworth and Badyaev 2007; Duckworth and Kruuk 2009) and aggressive individuals may have an innate propensity to disperse; yet, aggression also mediates social interactions and enables individuals to defend and acquire resources (Peiman and Robinson 2010). Moreover,

parental tolerance, which is known to be an important determinant of dispersal in many animals (Ekman and Griesser 2002; Eikenaar et al. 2007), might be mediated by the aggressive behavior of the parental generation. For example, more aggressive individuals can be less social (Ruzzante and Doyle 1991; Pruitt et al. 2008), such that higher aggression in the parental generation leads to lower tolerance of offspring and results in offspring dispersing greater distances (Figure 1b). Likewise, offspring that are more aggressive may also be less social and more likely to avoid kin. Alternatively, if parental tolerance for offspring is dependent on resource availability, then highly aggressive parents that are better at procuring resources may tolerate offspring settling closer to them than nonaggressive parents that are unable to procure excess resources for their offspring (Figure 1a). Thus, there are multiple ways that parent and offspring aggressive phenotypes can interact to produce an association between aggression and dispersal.

Investigating interactions between personality variation, resource acquisition, and dispersal decisions is difficult because it requires knowing the behavior, access to resources, and social relationships of all individuals in a population to understand how these factors interact. Western bluebirds (*Sialia mexicana*) provide a unique opportunity to determine the relative importance of personality variation, social context, and resource availability for dispersal because their main limiting resource is nest cavities (Brawn and Balda 1988; Guinan et al. 2000) – a resource that is discrete and easy to quantify – and variation in aggressive personality mediates competition for this resource. Aggressive behavior in this species shows consistent individual differences over time (within and between years: Duckworth 2006a; Duckworth and Badyaev 2007) and across contexts (across breeding stages and towards con- and heterospecifics: Duckworth 2006b), and thus classifies as an animal personality (Dall et al. 2004). Aggressive males outcompete nonaggressive males for territories that have more nest cavities (Duckworth

2006a). Moreover, western bluebirds are facultative cooperative breeders and can help both parents and brothers in offspring care (Dickinson and Akre 1998) and kin interactions play an important role in the dispersal decision – nonaggressive sons often gain a territory by budding off their parent’s territory and relatives often participate in joint territorial defense (Dickinson and Akre 1998; Duckworth 2008). As in other passerine bird species, dispersal in western bluebirds is sex-biased, with females tending to disperse farther distances (generally out of the natal population) and males being more variable in their dispersal strategy. Finally, aggression is both phenotypically and genetically correlated with dispersal, such that aggressive males generally disperse farther than nonaggressive males (Duckworth and Badyaev 2007; Duckworth and Kruuk 2009).

Although aggression, dispersal, kin interactions, and resource competition are all interlinked in this species (Duckworth 2006a; Duckworth and Badyaev 2007; Duckworth 2008), the role of kin’s personality type and access to resources in determining sons’ dispersal and settlement patterns have not been investigated. In this study, we combine a unique dataset in which aggression, dispersal, relatedness, and resource availability have been measured over an eleven-year period with behavioral observations of territorial interactions to investigate whether variation in aggression (of both sons and parents) influences kin interactions and resource acquisition to ultimately determine dispersal decisions. We predicted that, if parental access to resources drives offspring dispersal, the superior competitive ability of aggressive fathers should result in a negative relationship between son’s dispersal and father’s aggression, as these fathers will have more resources making it possible for their sons to acquire a territory nearby (Figure 1a). Alternatively, if aggression is linked to sociality in this species, we expected a positive relationship between son’s dispersal and father’s aggression because less aggressive fathers

would be more likely to tolerate their sons nearby and more aggressive fathers more likely to compete with their sons and drive them away (Figure 1b). However, if only the son's own aggressive phenotype causes personality-dependent dispersal, then we predicted that son's dispersal should not be correlated with their father's aggressive phenotype (Figure 1c). Finally, we use data from territorial interactions over six years to determine whether sharing territorial boundaries with kin provides a benefit of a neutral territory boundary that does not require defense.

MATERIALS AND METHODS

Study system and general methods

Data were collected for 11 breeding seasons (2002 – 2012) from a nest box population of western bluebirds in western Montana, USA (see Duckworth 2006a for a detailed description of the study site). GPS coordinates for all nest boxes were recorded each year to allow for accurate distance measurements and to account for any nest box additions or movement of nest boxes already present. The distribution of nest boxes on the site is semi-natural as many are placed on dead snags with natural nest cavities and thus it is also highly variable, which provides the opportunity for males to acquire more than one nest box on their territory. The distance between nearest neighbors ranges from a minimum of ~30 m to a maximum of ~300 m. Each year, nest boxes were visited at least twice weekly during the breeding season (April – August) to monitor nest progress, to determine the affiliation of breeding pairs with specific boxes, and to band offspring and adults. Adults were captured either at feeding trays baited with mealworms or in their nest box and banded with a USFWS metal band and a unique color combination of three plastic bands. Offspring were sexed on day 14 of the nestling period and females were banded

with a USFWS metal band and a year color, while males were banded with three unique colors in addition to the metal band. Female offspring were not banded with a unique color combination because they rarely remain in their natal population to breed.

Measurement of dispersal, conspecific density, and resource availability

We focused on the dispersal behavior of first-time breeding male offspring (born on the site and subsequently returned to breed) to avoid issues of autocorrelation due to dispersal decisions made in subsequent breeding seasons (e.g. the effect of prior residency). We identified a total of 97 first-time breeders between 2002 and 2012 and of these, 18 did not have kin present on the site during their first year of breeding (where “kin” indicates first-order relatives: fathers, mothers, and brothers). We focus here on social relationships only, under the assumption that individuals are unaware of any non-social kin that may arise due to extra-pair paternity or siblings that result from the parents’ prior breeding attempts. Dispersal distance was measured as the distance from natal nest to first breeding nest. We also measured the average distance from a focal individual’s breeding nest to all kin present on the study site. These two measures were highly correlated with each other (Mixed model: $F_{1,17} = 87.22$, $N = 79$, $P < 0.0001$). For males with kin absent from the site, only the first measurement was possible, and hence it is only possible to compare males with kin present to those with kin absent using this measure. However, the second measure is important for males with kin present, as the kin environment on the site during the first breeding attempt is incorporated in this measure. If a male was affiliated with multiple nest boxes during the breeding season (i.e. breeding or defending), the box in which he first initiated a nesting attempt was assigned as his breeding location for dispersal

measures. As any movement between boxes was typically between boxes a short distance apart, we do not expect choosing the box of first nest initiation to impact the analysis.

We measured local resource availability and conspecific density by creating a 350 m radius buffer around each focal male's natal nest box. Most territorial interactions of bluebirds occur within 150 m of the nest box (Duckworth 2006a), so using a 350 m buffer takes into account the area in which individuals on separate territories are likely to come into contact with each other over territorial interactions and also encompasses the distance a son may disperse if he is budding off a parent's territory. To assess local conspecific density, we measured the number of breeding adult western bluebirds within the buffer area during the focal male's natal year. Similarly for resource availability, we measured the number of empty nest boxes within the buffer area during the natal year. If a breeding pair was noted as defending or nesting in more than one nest box within the buffer area over the course of the breeding season, only one box was counted as occupied for the resource availability measurement. These measures are from the natal year because this is when fledglings are assessing the neighborhood around their natal box and beginning to form their dispersal decision.

Behavioral Observations

Aggression for all breeding adults was measured by simulating a territorial intrusion by a live tree swallow (*Tachycineta bicolor*), a heterospecific nest competitor (Robertson et al. 1992; Meek and Robertson 1994), during the incubation stage. See Duckworth (2006b) for a detailed description of aggression trials. Briefly, a tree swallow in a wire cage was placed on top of a bluebird pair's nest box for 2-min trials. The number of times an individual bluebird attacked, flew by, or hovered near the cage was counted and a score of 1 – 6 was assigned, with 1

indicating a nonaggressive response and 6 indicating the most aggressive response. To avoid pseudoreplication, different tree swallows were used each day trials were performed. We assessed aggression toward this heterospecific competitor because this measure is positively correlated with conspecific aggression and measuring aggression towards a conspecific can result in infanticide. Moreover, using a heterospecific allows us to standardize aggressive responses of males and females, as responses to conspecifics are sex-specific (Gowaty and Wagner 1988; Duckworth 2006a). Finally, measuring the response to tree swallows is not only related to resource acquisition (Duckworth 2006b), but is also repeatable across nest stages, across contexts, and over a bird's life (Duckworth 2006a, 2008; Duckworth and Kruuk 2009).

To determine whether kin with adjacent territories had fewer territorial disputes compared to unrelated individuals sharing territorial boundaries, we observed aggressive interactions between conspecifics during the 2004-2009 breeding seasons. Each day, during the pre-breeding period from mid-March through April, we randomly selected a region of the study site consisting of 6-8 bluebird territories for intensive observation. Aggressive interactions (such as chases and fights), the individuals or pairs that were involved, and the locations in which they occurred were noted. We spent at least 30-mins observing the focal pair in each territory. In addition to these systematic observations, we also noted, throughout the breeding season, any aggressive interactions observed when trapping adults for banding and during scheduled nest checks. We used this information to compare the frequency of aggressive interactions over territory boundaries between related and unrelated individuals.

Statistical Analyses

All statistical analyses were performed using SAS version 9.2 (SAS Institute 2008). To assess if first-time breeding males settle randomly with respect to the natal nest, the group of males with kin absent from the site were used. In these males, the influence of the natal site is not confounded with the influence of kin, so it is possible to determine if males are attracted to or repelled from the natal site, or if they settle independent of it. We used this as a comparison to better understand where males wanted to breed in the absence of parental influences. We compared the distances between each male's breeding nest and natal nest to an expected distance under the null hypothesis of random settlement using a Wilcoxon signed-rank test. We calculated the expected distance as the average of all potential distances to the focal male's natal nest (e.g. the average distance to a male's natal nest from all potential breeding nests he could have chosen).

We compared the frequency of aggressive interactions over territory boundaries between related and unrelated individuals using a χ^2 test to determine if aggressive interactions occur more frequently between unrelated individuals sharing a territory boundary. We calculated the expected frequencies of aggressive interactions for this test using the proportions of territory boundaries out of the total that were between related or unrelated individuals, respectively.

Throughout the subsequent analyses, we took a mixed model approach to avoid reducing our sample size. This allowed us to account for the dependence of observations when brothers from the same clutch returned to breed, while still including all observations in our analyses. We included birth nest as a random effect in each of the mixed models to account for this dependence and take into account any variability that is a result of it. We included year in all initial analyses, but determined it was non-significant and have not included it in the analyses presented here. We determine the importance of kin presence, box availability, conspecific

density, and parental and offspring aggression, as well as their interaction, on the distance dispersed by the offspring using this mixed model approach. Important interactions between offspring and parents occur during the time after hatching and before winter migration – some offspring become completely independent of parents at this time, whereas others remain in their family group. Thus, we focus on the parent's aggression during the hatch year and the son's aggression during the first year of breeding (this is the son's first possible measurement because aggression is only measured in adults). If more than one measurement is available for that year, we preferentially use the measurement taken during the incubation stage or the average of measurements taken during the incubation stage. If no trials were available during the appropriate year (hatch year for parents and first year of breeding for sons), we used the next available measurement. This is justified given the high repeatability of aggressive behavior across years in this species (Duckworth and Sockman 2012). When kin are absent from the site, a mixed model was not necessary or appropriate because we have independent observations, so general linear models (GLMs) were used when we were analyzing the importance of resource availability and conspecific density on dispersal in these males. All data were standardized before analyses were conducted and we normalized the distance measurements with a square root transformation to keep zero distance measurements.

RESULTS

How does kin presence influence dispersal?

First-time breeding males with kin absent from the study site dispersed shorter distances from the natal nest than expected under a random dispersal strategy (Wilcoxon signed-rank test: $N = 18$, $W = 13$, $P < 0.001$). Males that had kin present dispersed farther from the natal nest (mean \pm SE

= 767.69 ± 57.44 m, $N = 79$) compared to males that did not have kin present (mean \pm SE = 433.29 ± 113.26 m, $N = 18$; $N = 97$, $F_{1,18} = 11.54$, $P = 0.003$, Figure 2). Finally, father's presence at the natal nest did not influence the distance son's dispersed ($N = 54$, $F_{1,10} = 1.15$, $P = 0.308$; son's dispersal distance with father at natal nest: mean \pm SE = 644.62 ± 77.58 m, $N = 30$ versus son's dispersal distance when father moved from the natal nest: mean \pm SE = 806.28 ± 102.67 , $N = 24$).

How does parental and offspring aggression influence dispersal?

There was a significant interaction between father and son personality types on son's dispersal from kin such that sons only remained close to kin when both they and their fathers were nonaggressive (Table 1, Figure 3a). A similar pattern was found for the distance son's dispersed from their natal site, but the interaction was not significant (Table 1). There was no influence of mother's aggression on son's dispersal from either kin or from the natal site, even when accounting for son's own aggression (Table 1).

Do territorial interactions differ between related and unrelated individuals?

There were no observed disputes over territory boundaries between relatives during any of the observation periods despite frequent observations of disputes between unrelated individuals sharing territory boundaries ($N = 90$) resulting in a highly significant difference in frequency of territorial disputes between kin versus non-kin ($\chi^2 = 25.71$, $P < 0.0001$). Even if territorial interactions between an individual with relatives at adjacent territories and an unknown conspecific are assumed to be an interaction between relatives, territorial interactions still occurred significantly more often between non-relatives than relatives ($\chi^2 = 4.85$, $P = 0.028$).

How does conspecific density and resource availability influence dispersal?

Local resource availability during the hatch year and distance dispersed from the natal nest were negatively related for males with kin present ($N = 79$, $F_{1,18} = 4.93$, $P = 0.039$, Figure 3b), while no relationship was found for males with kin absent (GLM: $N = 18$, $F_{1,17} = 0.02$, $P = 0.890$, Figure 3b). However, local conspecific density during the hatch year was not related to distance dispersed from the natal nest for males with kin present ($N = 79$, $F_{1,18} = 0.47$, $P = 0.500$) or with kin absent (GLM: $N = 18$, $F_{1,17} = 0.02$, $P = 0.897$).

DISCUSSION

Determining the causal factors behind individual dispersal decisions has been difficult (Clobert et al. 2001). The influence of behavioral traits, such as aggression, boldness, and sociality, on dispersal has added a new dimension to understanding its causes. Yet, thus far, the focus has been placed primarily on the influence of personality variation of the dispersing individual alone (Fraser et al. 2001b; Dingemanse et al. 2003; Cote and Clobert 2007; Duckworth and Badyaev 2007; Cote et al. 2010b), even though interactions between differing personalities under a variety of social and ecological contexts can lead to distinct dispersal outcomes (Cote et al. 2011). Yet, the mechanism by which these population level patterns are generated is unclear. Here, we used a long-term dataset in a species with personality-dependent dispersal to show that interactions of family group members can influence the dispersal decision.

Specifically, we found that offspring dispersal was strongly influenced by an interaction between father and son aggressive phenotypes. Sons dispersed farther when their fathers were highly aggressive, irrespective of the son's own aggressive phenotype (Table 1, Figure 3a). This

pattern suggests that aggressive fathers are less likely to tolerate their sons nearby compared to nonaggressive fathers, even when their sons are nonaggressive. This suggests that aggression is linked to sociality in this species, as has been shown in other taxa (Ruzzante and Doyle 1991; Pruitt et al. 2008; Clark and Fewell 2013). Western bluebirds historically depended on successional habitat and aggressive males are most likely to colonize new areas that have a low density of conspecifics (Duckworth 2008, 2012). Thus, if more aggressive males are also less social this might explain why aggressive fathers are less tolerant of offspring breeding close to them and also why aggressive offspring tend to be more dispersive in general. Moreover, if nonaggressive fathers are more social, they may be more likely to cooperate with their offspring, accounting for a greater tolerance of sons breeding nearby when fathers are nonaggressive. Intense behavioral observations across years supports this interpretation – we observed no instances of aggression between related individuals sharing territory boundaries despite frequent observations of aggression at territory boundaries between unrelated individuals. However, the interaction between father and son personality type indicates that, if even one member of the father-son pair is aggressive, such tolerance breaks down.

Sociality and aggression are linked in other systems, such as spiders in the *Anelosimus* genus (Pruitt et al. 2008), social insects (Clark and Fewell 2013), and fish (Ruzzante and Doyle 1991) suggesting a correlation between these behaviors is a common phenomenon. In these systems, asocial individuals tend to be more aggressive and social individuals tend to be less aggressive. One explanation for such a general link between sociality and aggression is that asocial behavior is the outcome of individuals having a higher propensity toward aggressive competition, whereas social behavior is the outcome of individuals having a higher propensity toward nonaggressive, cooperative behavior.

Interestingly, while father's aggression was a significant predictor of the average distance dispersed from kin on the study site, mother's aggression was not (Table 1), which suggests father-son interactions are more important than mother-son interactions in the dispersal and settlement of this species. Similarly, in Siberian jays (*Perisoreus infaustus*) the experimental removal of fathers and subsequent replacement with an unrelated male resulted in the dispersal of retained offspring (Ekman and Griesser 2002). Thus, fathers seem to generally play a key role in the dispersal decision of offspring.

We found a negative relationship between resource availability and distance dispersed from the natal nest (Figure 3b), but only when males had kin present on the site. One explanation for this pattern is that when kin are absent, sons must compete for resources without any benefit or hindrance from kin. Yet, when kin are present, the relationship between resource availability and dispersal could arise due to a tradeoff between direct and indirect fitness benefits in the parents. When resources are not readily available, parents may have no incentive to allow kin to settle nearby, as this will result in a decrease of their own access to the resource and offspring dispersal should be promoted as a way to avoid negative fitness costs (Strickland 1991; Ronce et al. 1998; Cote and Clobert 2010). However, when resources are abundant, benefits to both the offspring and parents can be gained when the parents tolerate offspring remaining nearby (Lambin and Krebs 1993; Eikenaar et al. 2007; Davis 2011).

Males with kin absent from the site dispersed non-randomly and settled closer to the natal nest than expected under a random dispersal pattern. This suggests that natal site familiarity is likely to be an additional driver of dispersal in this species, as has been shown in other species (Schjørring 2001) as well as theoretical models (Stamps et al. 2009). Yet, when kin are present, males disperse farther from the natal nest compared to when kin are absent (Figure 2). Because

parents often return to breed in the same or nearby nest box in subsequent years, their offspring can be prevented from occupying the natal site. However, our results suggest that sons are not only prevented from occupying the natal nest itself, but also from settling too close to the natal site, as if a buffer exists within which sons will not be tolerated by parents. Familiarity with the breeding territory can provide many benefits to a first-time breeder, including knowledge of foraging locations and potential competitors in the area, and familiarity with a location has been shown to increase the success of territory acquisition (Stamps 1987). In red-winged blackbirds (*Agelaius phoeniceus*) (Beletsky and Orians 1989) and great tits (*Parus major*) (Grabowska-Zhang et al. 2011), individuals with familiar neighbors had increased reproductive success compared to those with unfamiliar neighbors. Moreover, breeding near the natal nest is likely to ensure that a male breeds near his parents, if they return, and may provide opportunities for joint territorial defense (Dickinson and Akre 1998) or neutral territories boundaries (this study). Thus, the finding that presence of parents on the study site deters most offspring from breeding close to the natal site provides further support to the idea that competition among kin is at least as, if not more, important than cooperation in this species. Overall, dispersal of offspring that remain in their natal population appears to be driven by a balance between compatibility of father and son personality types as well as resource availability near the natal site.

Our study emphasizes the importance of interactions between personality types to understand dispersal dynamics and suggests that the frequency of distinct personality types within a population can have profound consequences for population dynamics (see also Cote et al. 2011). Population density, aggression, and resource availability fluctuate over time in western bluebird populations (Duckworth 2008, 2012), yet the mechanisms linking these fluctuations is currently not known. This study suggests that aggressive interactions among kin over resources

may play an important role in mediating these population-level changes in behavior and ecology as the interdependence of dispersal, competitive behavior, resource availability, and social environment has the potential to produce intercorrelated changes in each of these components over time. Thus, our results suggest that measuring personalities of individuals known to interact is essential to both understanding the causal links underlying personality-dependent dispersal and understanding the larger scale consequences of dispersal decisions.

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Table 1. Influence of parental aggression on the distance dispersed from kin in western bluebirds.

Effect	Average distance to all kin			Natal dispersal distance		
	$\beta \pm \text{SE}$	<i>F</i>	<i>P</i> -value	$\beta \pm \text{SE}$	<i>F</i>	<i>P</i> -value
Influence of father (<i>N</i> = 45)						
Son aggression	0.037 ± 0.084	0.20	0.671	0.113 ± 0.122	0.85	0.387
Father aggression	0.119 ± 0.177	0.46	0.522	-0.064 ± 0.128	0.25	0.634
Son aggression × father aggression	-0.332 ± 0.106	9.93	0.016	-0.198 ± 0.130	2.32	0.172
Influence of mother (<i>N</i> = 29)						
Son aggression	0.449 ± 0.173	6.71	0.122	0.368 ± 0.188	3.82	0.146
Mother aggression	0.177 ± 0.196	0.81	0.463	-0.043 ± 0.169	0.06	0.815
Son aggression × mother aggression	-0.329 ± 0.147	5.01	0.155	-0.123 ± 0.169	0.53	0.518

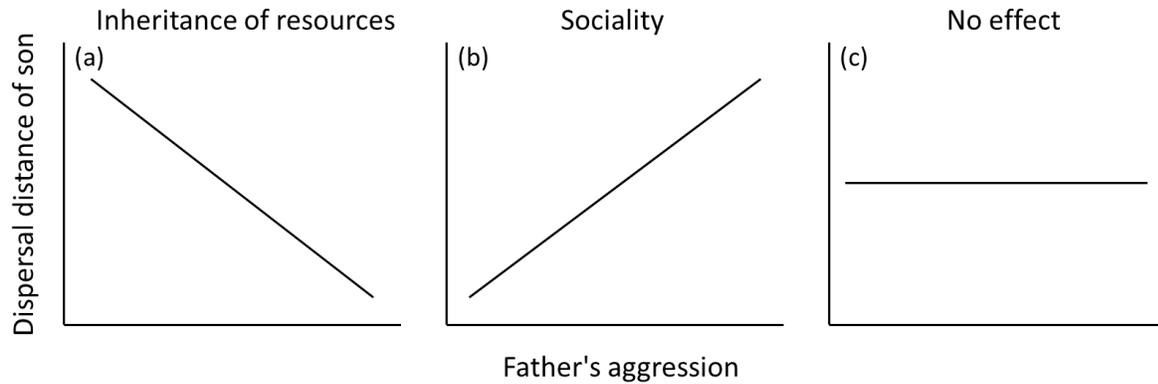


Figure 1 Predictions for three alternative hypotheses explaining how fathers' aggression can influence sons' dispersal distance. (a) Because more aggressive fathers acquire more resources, they may be more likely to tolerate a son breeding close to them, producing a negative relationship between sons' dispersal distance and fathers' aggressive personality type. (b) If aggression is correlated with sociality, as has been shown in other species, then more aggressive fathers will be less tolerant of sons breeding nearby and this would produce a positive association between sons' dispersal and fathers' aggression. (c) Fathers may have no influence on their sons' dispersal behavior because dispersal is primarily determined by sons' own personality type and/or other factors such as resource availability.

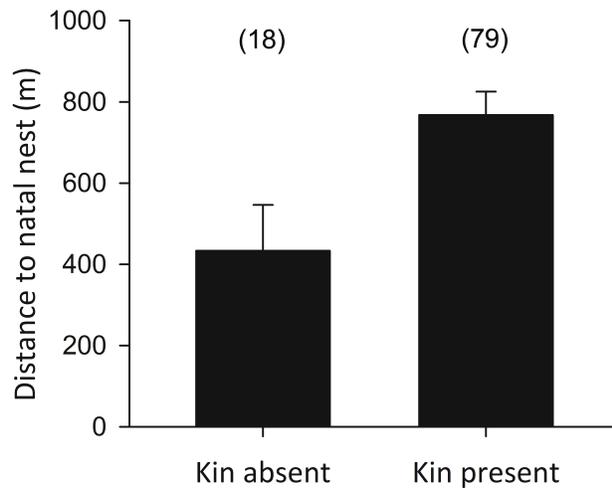


Figure 2 Male western bluebirds with kin absent dispersed significantly shorter distances from the natal nest compared to males with kin present on the study site. Bars indicate mean \pm SE and the numbers above the bars indicate sample size. The analysis was conducted as a mixed model, but the results presented are raw data.

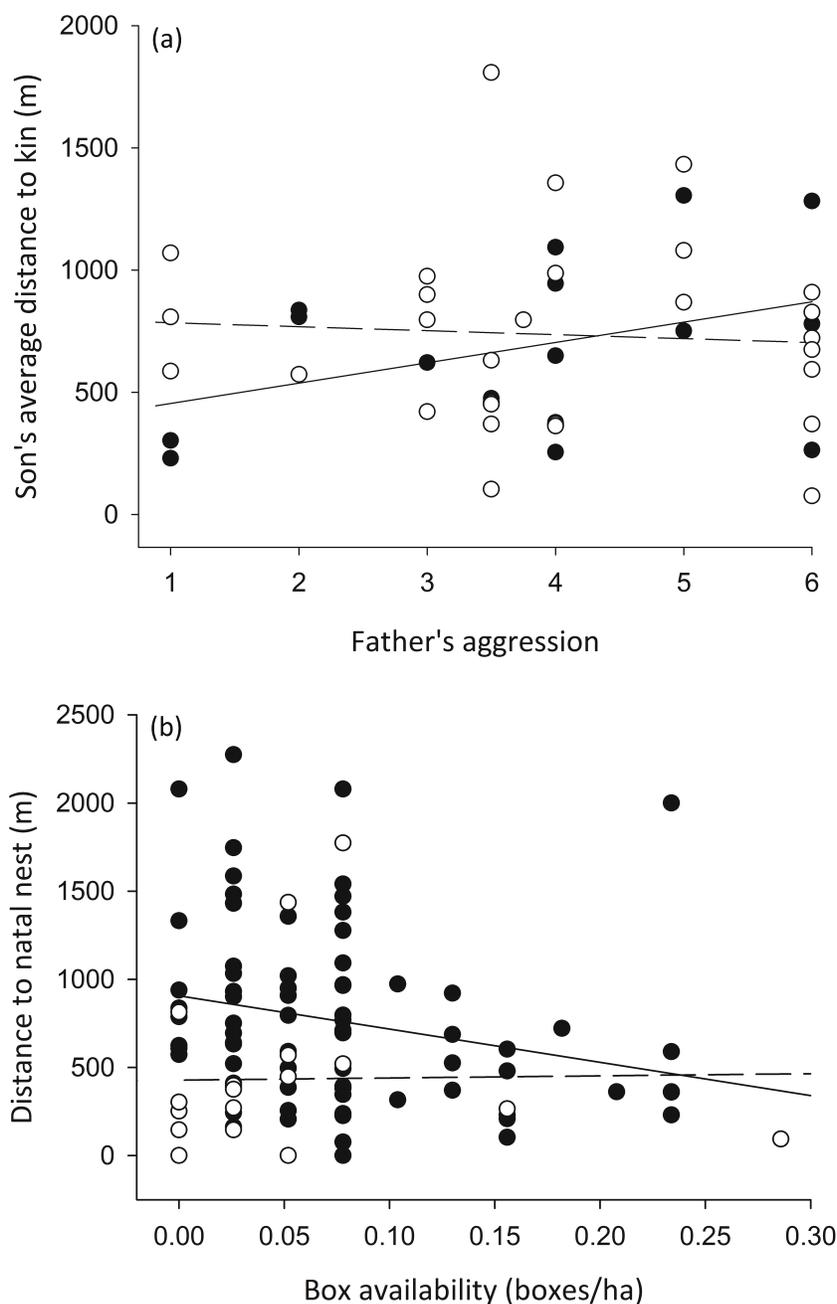


Figure 3 (a) Interaction between western bluebird fathers' and sons' aggression on sons' distance dispersed from kin. When sons are aggressive (open circles and dashed line, $N = 29$), there is no relationship between father's aggression and distance dispersed from kin. However, when sons are nonaggressive (closed circles and solid line, $N = 16$), they disperse less when fathers are also nonaggressive. The analysis was conducted as a mixed model, but the results presented are raw data with best-fit lines. (b) Negative relationship between resource availability and natal dispersal distance with kin present (closed circles and solid line, $N = 79$) and no relationship between resource availability and natal dispersal with kin absent (open circles and dashed line, $N = 18$). The analysis was conducted as a mixed model when males had kin present and a GLM when males had kin absent, but the results presented are raw data with best-fit lines.

APPENDIX B: RESOURCES AND BEHAVIOR DRIVE POPULATION DYNAMICS IN A
BIRD

ABSTRACT

Dispersal and population dynamics are intimately tied, yet we often consider the mechanisms underlying each separately. However, intrinsic mechanisms such as aggression and social behavior can influence population dynamics through direct or indirect means. If aggression also influences dispersal propensity, the relationship between aggression and population dynamics may become more complex as dispersal controls the relative proportion of aggressive and nonaggressive phenotypes present in the population. Moreover, the importance of aggression may be mediated by the availability of resources. A system in which aggression influences dispersal propensity and populations cycle between different proportions of aggressive phenotypes is necessary to determine the underlying mechanisms. Here, we examine how aggression and resources influence recruitment and population density across a ten-year period in a passerine bird. We found that resource availability and the interaction of population aggression and recruitment strongly predict population density across years. Furthermore, nonaggressive males and males that bred for multiple seasons, once population saturation was reached, recruited more offspring into the population as breeders than aggressive males and males that bred for a single season. Nonaggressive males were more likely to breed for multiple seasons, which suggests aggression has a survival cost in this species. The results of this study show the importance of understanding the consequences of behavioral interactions between individuals and how these may scale up to influence overall population dynamics.

Keywords: population density, personality-dependent dispersal, recruitment, aggression, *Sialia mexicana*

INTRODUCTION

Individual behavior has important consequences for population dynamics and species interactions (Sih 1987; Sutherland 1996; Cote et al. 2010). However, scaling from individual mechanisms to population-level consequences is often difficult as it requires the collection of fine-scale detail over a long period of time, and as a result has been addressed in only a few systems (Korpimäki et al. 2002; Krebs 2011; Martínez-Padilla et al. 2014). Social interactions and aggression are intrinsic factors that have been shown to influence population dynamics (Watson et al. 1994; Mougeot et al. 2003). These also play a key role in dispersal behavior in many species (Rusu and Krackow 2005; Cote and Clobert 2007; Duckworth 2008; Raihani et al. 2008) and thus it is unclear whether their influence on population dynamics are direct or indirect.

Aggression may influence population dynamics directly or indirectly through a number of mechanisms. For instance, changes in individual aggression may directly influence population density through territorial behavior and changes in territory size (Moss et al. 1994; Adams 2001). More aggressive individuals often acquire larger territories (Moss et al. 1994; Duckworth 2006a), and so an increase in population level aggression should result in reduced population density. Moreover, aggression is also frequently linked to sociality, with more aggressive individuals often being less social and avoiding social groups (Ward et al. 2004; Pruitt et al. 2008; Clark and Fewell 2013). Thus, changes in aggression may indirectly influence population dynamics through an individual's tolerance of conspecifics, if this tolerance or lack thereof influences recruitment of offspring into the population (Mougeot et al. 2005). If more aggressive individuals are less tolerant of others, they may recruit less of their offspring into the population as adults and discourage the recruitment of other young of the year, which will influence population density. Both of these mechanisms have been shown to be working in concert in red

grouse (*Lagopus lagopus scoticus*), in which population cycles are driven by changes in the aggressive behavior of breeding adults that influence territorial spacing behavior and subsequent offspring recruitment (Matthiopoulos et al. 2002; Mougeot et al. 2003), in addition to other extrinsic mechanisms (Hudson 1986; Sievwright et al. 2005; New et al. 2009).

However, if aggression is also influencing an individual's propensity to disperse, the relationship between aggression and population dynamics may become more complex. Dispersal will control the relative proportions of aggressive and nonaggressive phenotypes in the population and as a result will influence the overall population dynamics through the mechanisms described above. If nonaggressive individuals remain philopatric in previously established populations, while aggressive individuals disperse and colonize new areas, populations will experience these mechanisms differentially across stages. In a newly colonized population, aggressive individuals will be prevalent, so direct mechanisms influencing population density through territory size may prevail. However, in older populations with more nonaggressive individuals, indirect mechanisms influencing tolerance of conspecifics will be more important and population density will be influenced as a result.

A system in which aggression influences dispersal propensity in a predictable direction and populations cycle between higher proportions of aggressive and nonaggressive individuals is needed to effectively address these mechanisms. Western bluebirds (*Sialia mexicana*) provide a unique opportunity to investigate the influence of aggression on population dynamics.

Aggression is both phenotypically and genetically correlated with dispersal in this species, such that aggressive individuals tend to disperse farther than nonaggressive individuals (Duckworth and Badyaev 2007; Duckworth and Kruuk 2009). Additionally, aggression is stable across an individual's life and does not change substantially with age or environmental context

(Duckworth 2006b; Duckworth and Sockman 2012). Western bluebirds depend on tree cavities created during forest fires to breed. Their sister species, mountain bluebirds, are often the first colonizers of new habitat following fire (Hutto 1995), whereas western bluebirds generally arrive later (Saab et al. 2004; Kotliar et al. 2007) and then rapidly replace the less aggressive mountain bluebirds (Duckworth and Badyaev 2007). Aggressive males tend to leave their natal population and disperse to new areas to breed, while nonaggressive males tend to remain in their natal population, which are generally older and denser (Duckworth and Badyaev 2007; Duckworth 2008).

Aggression, resource availability, and kin interactions have been shown to influence the spacing behavior of first-year males (Aguillon and Duckworth submitted), and these are likely to also be influencing recruitment into the population and population density across years. Nonaggressive sons often gain a territory by budding off their parent's territory (Duckworth 2008) and both father and son must be nonaggressive for sons to remain close, suggesting that aggressive males actively repel their sons (Aguillon and Duckworth submitted). If these patterns manifest at the population level, we predict that aggressive males will recruit fewer offspring into the population than nonaggressive males. Additionally, for males that return to their natal population to breed, resource availability around a male's natal nest influences his dispersal distance (Aguillon and Duckworth submitted). Further, aggressive males are able to acquire territories with more cavity resources than nonaggressive males (Duckworth 2006a). Thus, resource availability may also influence whether males decide to remain in their natal population or to disperse to habitat outside their natal area. If so, we expect resource availability at the population level to strongly influence population density across years.

MATERIALS AND METHODS

Study system and general methods

Data were collected for 10 breeding seasons (2003 – 2012) from a nest box population of western bluebirds in western Montana, USA (see Duckworth 2006a for a detailed description of the study site). This time period includes a period of rapid population growth from 2003 – 2005 when density was increasing from year to year and a period of population saturation from 2006 – 2012 when density peaked and subsequently fluctuated from year to year. Nest boxes were visited at least twice weekly during the breeding season (April – August) each year to monitor nest progress, to determine the affiliation of breeding pairs with specific boxes, and to band offspring and adults. Breeding adults and male offspring were banded with a unique color combination of plastic bands plus a USFWS metal band, while female offspring were banded with a USFWS metal band and a year color as they are unlikely to return to their natal population to breed (Guinan et al. 2000).

Aggression for all breeding adults was measured by simulating a territorial intrusion by a live tree swallow (*Tachycineta bicolor*), a heterospecific nest competitor (Robertson et al. 1992; Meek and Robertson 1994), during the incubation stage. See Duckworth (2006b) for a detailed description of aggression trials. Briefly, a tree swallow in a wire cage was placed on top of a bluebird pair's nest box for 2-min trials. The number of times an individual bluebird attacked, flew by, or hovered near the cage was counted and a score of 1 – 6 was assigned, with 1 indicating a nonaggressive response and 6 indicating the most aggressive response. We assessed aggression toward this heterospecific competitor because this measure is positively correlated with conspecific aggression and measuring aggression towards a conspecific can result in

infanticide (RAD personal observation). Aggression trials are repeatable across stages, across contexts, and over a bird's life (Duckworth 2006a, 2008; Duckworth and Kruuk 2009).

Individual recruitment measures

We focused on males breeding on the site that successfully fledged offspring ($N = 130$). As western bluebirds display sex-biased dispersal and females were unlikely to return to their natal site to breed (Guinan et al. 2000), we were most interested in the recruitment of male fledged offspring into the population. We counted a son as recruiting into the population if he returned to breed on the site in the year after hatching. If a son did not return to his natal site to breed, we assumed he either dispersed or did not survive the winter (Guinan et al. 2000). To ensure that variation between males in the number of sons fledged did not influence our results, we first performed all analyses with recruitment measured as the proportion of sons that returned to breed out of the total number of sons survived to fledging. We verified that this did not differ statistically from the results using counts of offspring recruited, and so report these numbers here. Males that were present during the 2013 breeding season have been excluded from these analyses.

Annual measures of recruitment, density, and resource availability

To measure recruitment for each year of our study, we calculated the proportion of sons recruited to breed in the population out of all sons fledged out of all nests during each year. If the number of sons fledged was uncertain (e.g. because we were unable to sex all offspring before fledging), the highest possible value was used to calculate the proportion of sons recruited as this would result in the most conservative estimate of recruitment. For males that bred during multiple

seasons, we included them in each year they bred, but values differed based on the individual success of each brood. Because our recruitment measure is calculated as a proportion of all sons fledged during a single breeding season, we have accounted for any differences in production of offspring and offspring survival to the fledging stage across years.

We measured density and resource availability over the entire site for each year of our study. Density was calculated as the number of breeding adults within the total area of the site, while resource availability was calculated as the number of empty nest boxes within the total area of the site. If a breeding pair was noted as defending or nesting in multiple boxes over the course of the breeding season, only one box was counted as occupied for the resource availability measurement.

Statistical analyses

All statistical analyses were performed using SAS version 9.2 (SAS Institute 2008). We first assessed if recruitment of sons or aggression differed based on if a male was born on the site or on the number of seasons he bred and if recruitment of sons differed based on the father's aggressive phenotype. We classified each male as a resident if he was born on the site or as an immigrant if he was not born on the site. We then classified each male as breeding during a single year or breeding during multiple years. To perform these comparisons we used Wilcoxon rank sum tests and Spearman's rank correlation because the data for recruitment and aggression were skewed and unable to be compared using a standard parametric test. Because different dynamics are likely to occur during colonization of a site, we first performed these analyses over all years and then performed them separately during the years of rapid population growth (2003 – 2005) and the years once population reached saturation (2006 – 2012).

General linear models (GLMs) were used when analyzing the importance of resource availability, recruitment, and population aggression on variation in annual density. Population aggression was calculated by taking the average of aggression scores for all breeding males in a given year. For males that had been trialed for aggression multiple times across years, we included individual trials in each of the years that they were performed. The influence of resource availability, recruitment, and population aggression in year $t - 1$ on the subsequent population density in year t were determined.

RESULTS

The influence of site residency and aggression on individual recruitment of offspring Aggression was significantly higher in males that bred for a single season compared to those that bred for multiple seasons ($N = 130$, $Z = -2.672$, $P = 0.0075$; Figure 1). Resident and immigrant males did not differ in the number of seasons they breed ($N = 130$, $\chi^2 = 0.582$, $P = 0.399$) or the number of sons they recruited into the population ($N = 114$, $Z = 0.238$, $P = 0.812$). However, recruitment was significantly higher in males that bred in multiple seasons once the population became saturated ($N = 82$, $Z = 3.994$, $P < 0.0001$; Figure 2B), but did not differ between males that bred for a single season and those that bred in multiple seasons during the rapid population growth ($N = 32$, $Z = 0.250$, $P = 0.803$; Figure 2A). Moreover, overall levels of recruitment did not differ between the period of rapid growth and population saturation ($N = 114$, $Z = -0.124$, $P = 0.901$). The overall number of male offspring fledged was significantly negatively correlated with father aggression ($N = 117$, $\rho = -0.331$, $P = 0.0003$), as was the total number of offspring fledged ($N = 130$, $\rho = -0.199$, $P = 0.023$). Moreover, the number of male offspring recruited into the population was significantly negatively correlated with father aggression once the population

became saturated ($N = 82$, $\rho = -0.285$, $P = 0.0094$; Figure 3A), but not during the period of rapid growth ($N = 32$, $\rho = 0.032$, $P = 0.863$; Figure 3B).

Influence of aggression, resources, and recruitment on density across years

Density in year t was significantly positively correlated with resource availability in year $t - 1$ ($N = 11$, $t = 3.60$, $b_{st} = 0.769$, $P = 0.006$; Figure 4). Moreover, density in year t was also influenced by population aggression, population recruitment, and their interaction in year $t - 1$ (Table 1; overall model: $N = 10$, $F = 18.89$, $P = 0.0018$).

DISCUSSION

Individual behavior can have important consequences for population dynamics and species interactions (Sih 1987; Sutherland 1996; Cote et al. 2010), yet identifying mechanisms at the individual level that influence population dynamics is often difficult to accomplish. Aggressive behavior, in particular, has been shown to influence population dynamics directly through changes in territory size (Moss et al. 1994; Adams 2001) and indirectly through offspring recruitment (Mougeot et al. 2005). However, aggression's influence on population dynamics has yet to be studied in a system in which aggression has the added function of influencing dispersal propensity. Dispersal can change the relative proportions of aggressive and nonaggressive phenotypes in a population. The mixture of behavioral types in a population has been implicated as a mediator of direct and indirect species interactions (Pruitt et al. 2012), so it likely also mediates intraspecific interactions and population dynamics as a result. Here, we use a long-term dataset to explore how aggression influences population dynamics in a species with phenotype-dependent dispersal.

We found that western bluebird population density across years was strongly influenced by average population aggression, population recruitment, and their interaction during the previous year (Table 1). This seems to directly follow from aggression's known influence on dispersal into and out of populations (Duckworth and Badyaev 2007), as well as the kin interactions that influence within-site spacing behavior (Aguillon and Duckworth submitted). Furthermore, density was also explained by the nest box resources available in the previous year, with higher densities when more resources were available in the previous year (Figure 4). These results are consistent with what is known about this species and how decisions are being made at the individual level within years. At the local scale, resource availability around the natal nest influences the dispersal of males that return to breed on the site, with males dispersing less when more resources are available and dispersing farther when fewer resources are available (Aguillon and Duckworth submitted). The results from this study suggest that if too few resources are present on the site as a whole, most sons disperse out of the population rather than staying to compete for limited resources (consistent with the idea that less resources mean farther dispersal).

We also found that recruitment was negatively correlated with a male's aggressive phenotype once the population reached saturation, but not during the period of rapid population growth (Figure 3). This could simply be a result of aggressive males fledging less offspring, as has been found in a previous study (Duckworth 2006b) and was found over a longer period in this study (Results). However, when recruitment was measured as the proportion of male offspring that returned to breed out of all male offspring fledged, we get the same statistically significant result. This suggests that the differences between offspring recruitment of aggressive and nonaggressive males is not simply a reflection of reproductive success, but is a result of

nonaggressive males benefitting most from recruitment once the population was saturated. Furthermore, we found that recruitment was higher in males that bred for multiple seasons during the saturated years, but not during the period of rapid growth (Figure 2). This suggests a role for the formation of family groups, which is supported by this species being a facultative cooperative breeder and sons often gaining territories by budding off their parent's territory (Dickinson and Akre 1998; Duckworth 2008). Moreover, nonaggressive males were more likely to breed for multiple seasons (Figure 1), which further supports this idea, as nonaggressive phenotypes are necessary for fathers and sons to remain close together (Aguillon and Duckworth submitted) and may be the foundation on which family groups can be built. Additionally, this suggests that there are survival differences between nonaggressive and aggressive individuals because western bluebirds have high breeding site fidelity and are unlikely to disperse to another breeding site after their first breeding season (Guinan et al. 2000). Similar survival differences have been observed in other species (Moss et al. 1994).

It is important, yet difficult, to identify how mechanisms that function at the individual level may influence dynamics at the population scale. Social interactions and aggression have been shown to influence both dispersal and population dynamics (Watson et al. 1994; Mougeot et al. 2003; Cote and Clobert 2007; Duckworth and Badyaev 2007). Here we show that aggressive behavior, resources, and recruitment in western bluebirds influence population density across years. Furthermore, we show that kin interactions and aggressive phenotypes, which were shown to be important for dispersal in previous studies (Aguillon and Duckworth submitted), influence recruitment into the population as breeders. These findings show the importance that mechanisms working at the level of the individual may have on overall population dynamics and indicate that this should be an area of future research.

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Table 1 Influence of average population aggression in year $t - 1$ and percent recruitment in year $t - 1$ on western bluebird population density in year t .

Effect	Estimate	SE	<i>t</i>	<i>P</i>-value
Population aggression	-0.104	0.020	-5.10	0.0022
Recruitment	-3.050	0.490	-6.22	0.0008
Aggression \times Recruitment	0.715	0.125	5.71	0.0013

FIGURE LEGENDS

Figure 1 Median aggression is significantly higher in western bluebird males that bred during a single season ($N = 76$, median = 4.875) compared to males that bred during multiple seasons ($N = 54$, median = 4). The shaded boxes represent the 25th to 75th percentile with the 50th percentile (median) represented as a line within.

Figure 2 A) Median recruitment of western bluebird sons did not differ between males that bred during a single season ($N = 17$; median = 0) compared to those that bred during multiple seasons ($N = 15$; median = 0) during the rapid population growth phase. B) Median recruitment was significantly higher in males that bred during multiple seasons ($N = 38$; median = 1) compared to those that bred during a single season ($N = 44$; median = 0) once the population became saturated. The shaded boxes represent the 25th to 75th percentile with the 50th percentile (median) represented as a line within, unless it did not differ from the 25th percentile.

Figure 3 A) The number of male western bluebird offspring recruited into the population as breeders was not correlated ($N = 32$) with father aggression during the rapid population growth phase. B) The number of male offspring recruited into the population as breeders was significantly negatively correlated ($N = 82$) with father aggression once the population reached saturation, such that more aggressive fathers recruited less offspring.

Figure 4 The population density of western bluebirds in year t was significantly positively correlated with the availability of resources in year $t - 1$, such that population density was high in years after many resources were available.

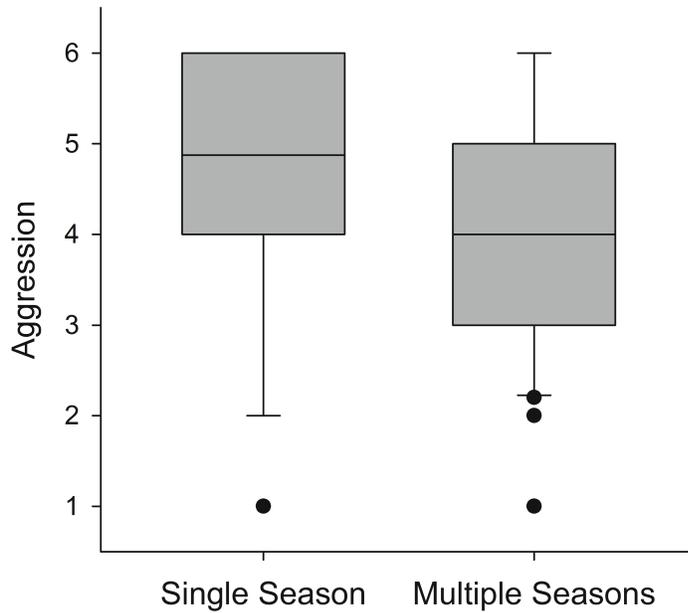


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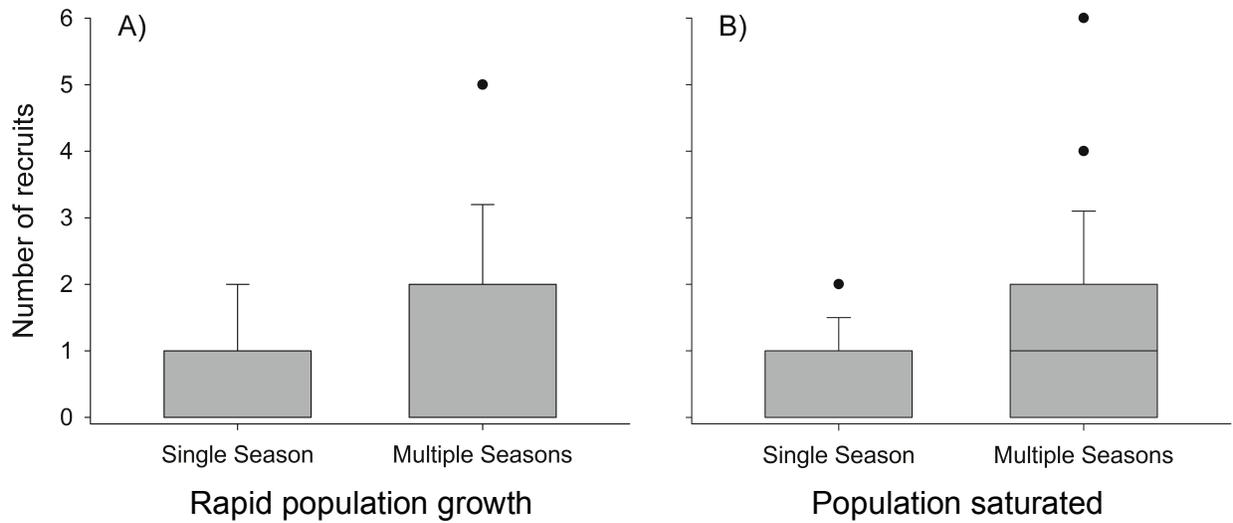


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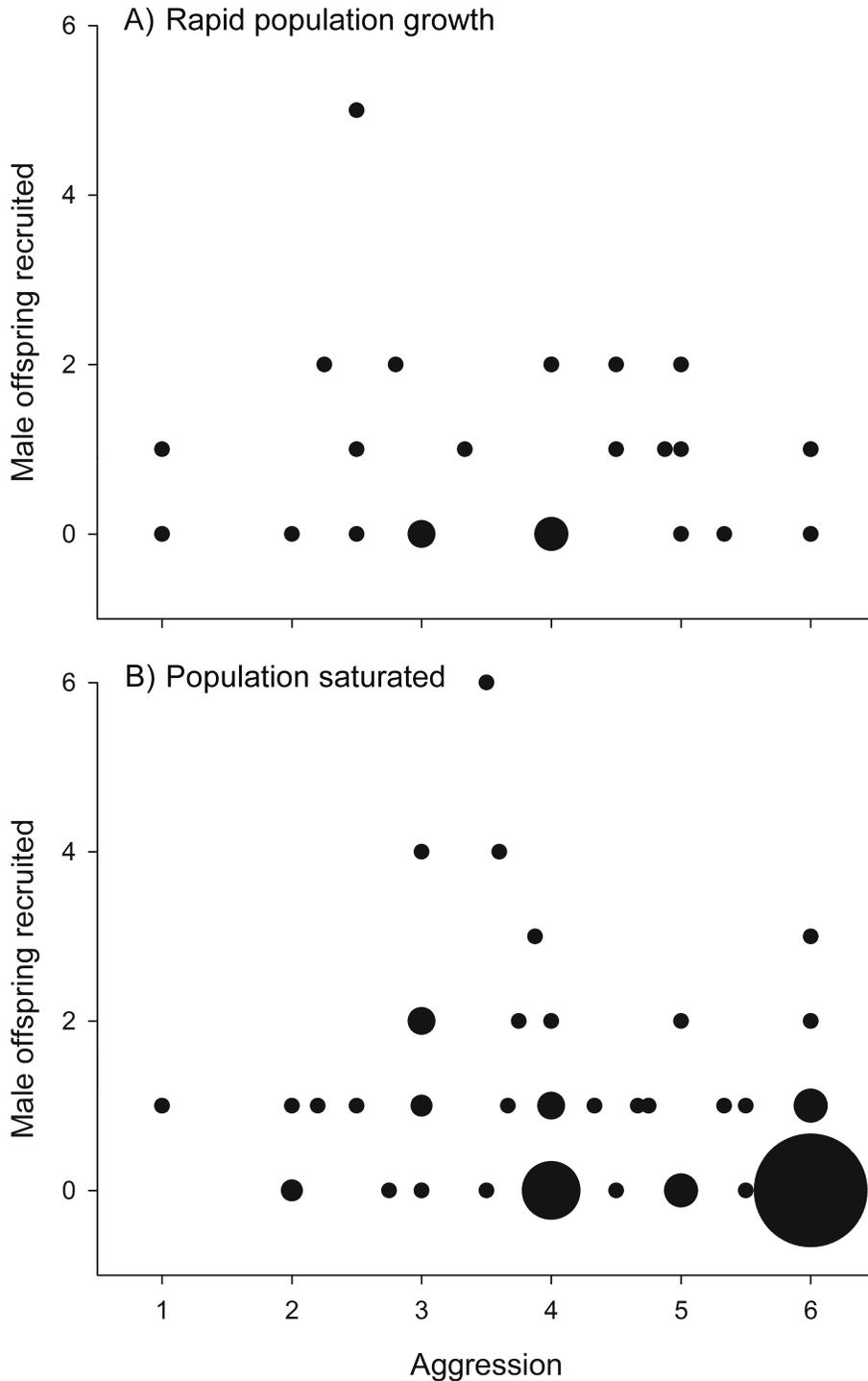


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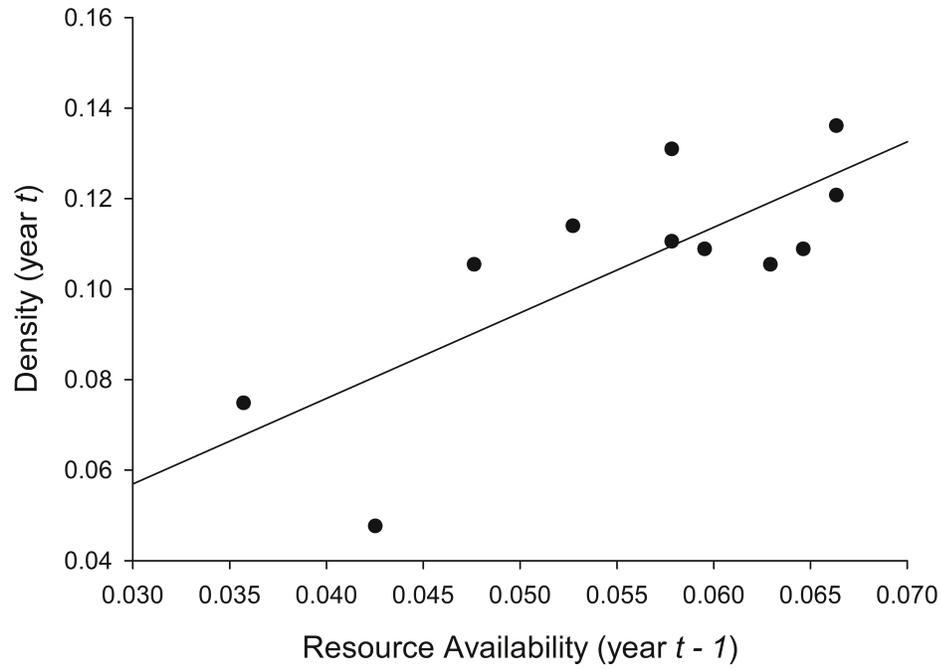


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