

Kin aggression and resource availability influence phenotype-dependent dispersal in a passerine bird

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Abstract Understanding the causes of dispersal is important as it strongly influences population dynamics and evolution. However, context dependency of dispersal decisions, such as effects of social interactions and resource availability, is rarely disentangled from intrinsic factors, such as animal personality. Western bluebirds provide a unique opportunity to investigate the relative importance of intrinsic versus extrinsic factors in dispersal decisions because they display distinct aggressive personality types, have high recruitment of sons to the natal population, and depend on nest cavities, a resource that is easy to quantify. Here, we measured territorial interactions among kin and non-kin, resource availability, and aggressive behavior over an 11-year period to determine how they influenced dispersal decisions of male offspring. We found that distance dispersed from kin was driven by a male's own aggression, the aggression of his nearest kin, and the resources available on the natal territory. Both aggressive males and males with aggressive kin dispersed longer distances, as did males who had fewer resources on their natal territories. Thus, dispersal in this species is influenced jointly by intrinsic and extrinsic factors. Because resource acquisition and personality type are interdependent in this species, changes in the social environment are likely to have important 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) because the decision to disperse depends not only on an individual's phenotype (Fraser et al. 2001; 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. 2001; Dingemanse et al. 2003; Cote and Clobert 2007; Duckworth and Badyaev 2007), 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

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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. 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 alone (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 promotes dispersal (Strickland 1991; Ekman et al. 2002; Pasinelli and Walters 2002) and cooperation with or tolerance of kin results 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).

In addition to the personality of interacting kin, resources in the natal population are known to have a strong influence on dispersal (Stacey and Ligon 1991; Brown and Brown 1993) either by directly affecting an individual's propensity to disperse or by influencing parental tolerance. For example, when resources are scarce, parents may be less tolerant of offspring remaining close to the natal territory and may actively displace them to avoid the negative fitness costs associated with competition between kin (Strickland 1991; Bach et al. 2006). Whereas when resources are abundant, relatives may be more willing to tolerate and may even actively promote offspring settlement nearby. Resource availability may also interact with kin personality type, such that individuals that have a less tolerant personality in general (e.g., because they are less social or more aggressive) may uniformly force offspring to disperse, whereas kin pre-disposed to be more tolerant may only become intolerant when resource competition is high. In general, 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 depends on the focal individual's personality alone (Clobert et al. 2009). In the former case, emigration rates from the population will be more closely tied to the overall mean expression of personality variation of a population, whereas in the latter situation, cohort effects will be most important for understanding emigration rates.

Aggression, in particular, has been linked to dispersal (Myers and Krebs 1971; Duckworth and Badyaev 2007; Duckworth and Kruuk 2009), yet it is unclear if this link is direct or indirect as aggression also mediates social interactions and enables individuals to defend and acquire resources (Ekman and Griesser 2002; Eikenaar et al. 2007). Nonaggressive individuals may be more tolerant of conspecifics compared to their more aggressive counterparts. This difference in tolerance can have important implications for dispersal behavior if aggressive individuals avoid interacting with or even actively drive kin away, whereas less aggressive individuals seek interactions with kin or at least tolerate their presence nearby. Alternatively, if tolerance of conspecifics depends solely on resource availability, then highly aggressive individuals that are better at procuring resources may be more tolerant of kin and allow them to settle closer, while nonaggressive individuals that are unable to procure excess resources may be less tolerant and drive kin away. Thus, there are multiple ways that the aggressive phenotypes of related individuals can interact to produce an association between aggression and dispersal.

Western bluebirds (*Sialia mexicana*) provide a unique opportunity to determine the relative importance of these factors 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 as aggressive males outcompete nonaggressive males for larger territories with more nest cavities (Duckworth 2006a, 2014). Aggressive behavior in this species shows consistent individual differences over time (Duckworth 2006a; Duckworth and Badyaev 2007) and across contexts (across breeding stages and toward con- and heterospecifics; Duckworth 2006b), and thus classifies as animal personality (Dall et al. 2004). Moreover, male offspring show highly variable dispersal behavior ranging from zero to more than 200 km with a high percentage (10–20 %) of fledged sons remaining in their natal population to breed (Duckworth 2008). Kin interactions are thought to play an important role in the dispersal decision, as family groups often overwinter together, participate in joint territorial defense and a small percentage of sons even delay breeding to help at their parents' nests (Dickinson and Akre 1998; Duckworth and Badyaev 2007). Finally, aggression is both phenotypically and genetically correlated with dispersal, such that aggressive males are more likely than nonaggressive males to disperse from their natal population (Duckworth and Badyaev 2007; Duckworth and Kruuk 2009).

Although aggression and dispersal are clearly linked in this species (Duckworth 2006a, 2008; Duckworth and Badyaev 2007), it is not known whether kin interactions and access to resources may also influence dispersal and may at least partially underlie the association between aggression and dispersal. In this study, we combine a unique dataset in which aggression, dispersal, relatedness, and resource availability

have been measured over an 11-year period to investigate the relative importance of variation in aggression (of both male offspring and their kin), kin interactions, and resource acquisition on dispersal decisions. We focus on male dispersal as dispersal in western bluebirds is sex-biased, with females tending to disperse farther distances and rarely recruiting into their natal population (Duckworth 2008).

First, we compare males that have kin present during their first year of breeding to those with kin absent to determine whether the presence of kin influences dispersal. We next use data from aggressive interactions at territory boundaries over 6 years to determine whether kin breeding close together are more tolerant of one another than non-kin. Finally, we compare how the availability of resources and the aggression of males and their kin (parents and brothers) influence the dispersal decision. We predicted that if access to resources is the most important factor influencing male dispersal, then offspring should disperse farther when cavity resources are scarce near the natal territory. This may lead to a negative relationship with kin aggression as prior work has shown that more aggressive individuals acquire larger territories with more nest cavities (Duckworth 2006a). This hypothesis assumes that the aggression of kin does not influence offspring dispersal directly, but only through resource acquisition. Alternatively, if aggression is linked to tolerance, we expected a positive relationship between a male's dispersal and his kin's aggression because less aggressive kin would be more likely to tolerate relatives nearby and more aggressive kin more likely to compete with relatives and drive them away. However, if only the male's own aggressive phenotype is related to dispersal, then we predicted that dispersal should not be correlated with the aggressive phenotype of their relatives or resources and instead, aggressive males should disperse farther than nonaggressive males regardless of variation in these other factors. These hypotheses are not mutually exclusive, and all three factors could simultaneously influence offspring dispersal or interact with one another to produce more complex dispersal dynamics. For example, the aggression of kin may only be important when resources are scarce which would lead to an interaction between kin aggression and resource availability if aggressive kin tolerate offspring to stay close only when resources are abundant, but nonaggressive kin are uniformly tolerant of offspring. Therefore, we test all first-order interactions to investigate the possibility that these more complex dynamics are also important.

Methods

Study system and general methods

Data were collected over 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 seminatural as many are placed on dead snags with natural nest cavities, and thus the distribution is also highly variable, which provides the opportunity for males to acquire multiple nest boxes on their territory. 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 US Fish and Wildlife Service (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 for individual recognition.

Measurement of dispersal 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 the effect of prior residency. There were a total of 99 sons recruited to the population between 2002 and 2012, and of these, 17 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 nonsocial kin that may arise due to extra-pair paternity (ca. 15 % of offspring and 30 % of nests; Duckworth 2006b; Duckworth and Kruuk 2009) or siblings that result from the prior breeding attempts of parents. This assumption is supported by a cross-fostering experiment that showed that the behavior of fathers toward their own and extra-pair offspring does not differ (C. Gurguis and RAD, unpublished data).

Natal dispersal distance was measured as the distance from natal nest to first breeding nest. We also measured the distance from a focal individual's breeding nest to his nearest kin under the assumption that in a social species such as western bluebirds, dispersal distance from the natal social environment is as important biologically as dispersal distance from an individual's natal nest site and may more accurately reflect the influence of social interactions on dispersal. For males with kin absent from the site, it was only possible to measure dispersal distance from the natal nest site, and hence it is only possible to compare males with kin present to those with kin absent using this measure. Because our primary focus is on the influence of interactions between kin on dispersal, all other analyses use the distance to nearest kin as the measure of dispersal. If a male was affiliated with multiple nest boxes

during the breeding season (breeding or defending), the box in which he first initiated a nesting attempt was assigned as his breeding location for dispersal measures. Any movement between boxes during a breeding season was typically between boxes a short distance apart and generally adjacent, so choosing the first box did not substantially change dispersal distance measures (distance to natal nest would change from mean \pm SD=709 \pm 521 to 744 \pm 529 m if using the second nest).

We measured local resource availability by creating a 350-m radius buffer around each focal male's natal nest box, which measures the availability of resources on the parents' and neighboring territories. At this site, the distance between nearest nest boxes ranges from 38 to 276 m with a mean \pm SD of 157 \pm 62 m. Thus, using a 350-m buffer takes into account the area in which individuals on adjacent 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 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. This measure is taken during the natal year because this is when fledglings are assessing the neighborhood around their natal box and forming 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. In some cases, the same swallow was used for multiple trials that occurred on the same day; however, using a subset of males over a 7-year period where swallow identity was recorded, we verified that bluebird response was not influenced by swallow identity (ANOVA with swallow identity as a fixed factor: $N=111$, $F_{41,69}=0.92$, $P=0.61$). We assessed aggression toward this heterospecific competitor because it is highly correlated with the response to conspecifics ($r=0.63$ from Duckworth 2006b), and measuring aggression toward a conspecific can result in infanticide. Moreover, using a heterospecific nest competitor 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 related to resource acquisition (more aggressive males attain territories with more nest cavities; Duckworth 2006b) and is also repeatable across nest stages, contexts, and years (repeatability ranges from 0.80 to 0.96; Duckworth 2006b; Duckworth and Sockman 2012).

Important behavioral 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. For the focal male and his brothers, we use aggression measured during the first year of breeding, as this is the first possible measurement (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 focal males and their brothers), we used the measurement from the next available year. This is justified given the high repeatability of aggressive behavior across years in this species (Duckworth and Sockman 2012).

To determine whether kin with adjacent territories had fewer territorial disputes compared to unrelated individuals sharing territorial boundaries, we recorded aggressive interactions between conspecifics during the 2004–2009 breeding seasons. Weather permitting, during the pre-breeding period from mid-March through April, we randomly selected a region of the study site consisting of six to eight bluebird territories for intensive observation between 6:00 and 10:00 am. Aggressive interactions (such as chases and fights), the individuals or pairs that were involved, and the locations in which interactions occurred were noted. We spent at least 30 min 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 regular nest checks. These additional observations were conducted equally across all nests, as the protocol for nest checks and trapping/banding is the same for all nests. 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 Inc., Cary, NC). 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 was used. In these males, the influence of the natal site is not confounded with the influence of kin, so it provides a baseline measure of dispersal

in the absence of kin influence. 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 number of territory boundaries on the site that were between related or unrelated individuals, respectively.

Throughout the subsequent analyses, we used a mixed model analysis with birth nest as a random factor to account for the dependency of observations when brothers from the same clutch both returned to breed ($N=31$). We included year as a covariate in all initial analyses but determined it was nonsignificant ($N=66$, $F_{10,49}=0.54$, $P=0.85$) and have not included it in the final analyses presented here. We created a model including resource availability, male's aggression, the aggression of his nearest kin, and their interactions to determine their relative importance on a male's dispersal distance.

As males are most likely to engage in competitive or cooperative interactions with kin in closest proximity to them, we use the aggression of this individual (mother, father, or brother) in the analysis. If both parents remain together during their son's first breeding year and are the nearest kin, we use the average of their aggression scores (i.e., a mid-parent score) in the analysis. 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 on dispersal in these males. All data were standardized to a mean of 0 and a standard deviation of 1 before analyses. Distance measurements were normalized with a square-root transformation to allow zero distance measurements to remain in the analysis. Aggression scores were not available for all males and their nearest kin; thus, sample sizes vary accordingly.

Results

How does kin presence influence dispersal?

First-time breeding males with kin absent from the study site remained closer to the natal nest site than expected under a random dispersal strategy (Wilcoxon signed-rank test: $N=17$,

$W=11$, $P<0.001$). Males that had kin present dispersed farther from the natal nest site (mean \pm SE=768.4 \pm 54.9 m) compared to males that did not have kin present (mean \pm SE=410.9 \pm 117.8 m; $N=99$, $F_{1,97}=14.05$, $P=0.0003$, Cohen's $D=0.759$; Fig. 1). To ensure that this result was not a consequence of males breeding at their natal nest site when kin were absent, we repeated the analysis removing the individuals that returned to breed at their natal nest site ($N=3$) and obtained the same result (mean \pm SE=499.0 \pm 131.7 m, $N=96$, $F_{1,94}=5.03$, $P=0.027$, Cohen's $D=0.460$). Finally, neither the presence of fathers ($N=56$, $F_{1,54}=0.76$, $P=0.388$) nor the presence of mothers ($N=44$, $F_{1,42}=1.67$, $P=0.204$) at the natal nest influenced the distance sons dispersed.

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, resulting in a highly significant difference in frequency of territorial disputes between kin versus non-kin ($N=90$, $\chi^2=25.71$, $P<0.0001$). Even if, under the most conservative assumption, territorial interactions in which we could not identify both interacting individuals clearly (e.g., because it was not possible to read bands) are assumed to be an interaction between related individuals, territorial interactions still occurred significantly more often between nonrelatives than relatives ($\chi^2=4.85$, $P=0.028$).

How do aggression, resource availability, and their interactions influence dispersal?

Males remained closer to their natal territory when cavity resources were abundant near the natal territory, but only when kin were present ($N=82$, $\beta\pm$ SE=-0.244 \pm 0.101, $F_{1,80}=5.84$, $P=0.018$; Fig. 2); however, when kin were absent,

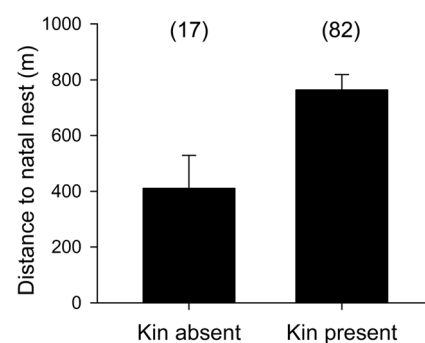


Fig. 1 Male western bluebirds with kin absent dispersed significantly shorter distances from the natal nest compared to males with kin present on the study site. Bars indicate mean \pm SE and the numbers above the bars indicate sample size

resource abundance near the natal territory did not influence natal dispersal (GLM: $N=17$, $\beta \pm SE=0.084 \pm 0.268$, $F_{1,16}=0.10$, $P=0.758$; Fig. 2). Furthermore, male's aggression, the aggression of his nearest kin, and the local availability of cavity resources were all found to be significantly related to a male's distance to his nearest kin (Table 1). Male's aggression (Fig. 3a) and the aggression of his kin (Fig. 3b) were positively related to the male's distance to his nearest kin, such that more aggressive males and males with more aggressive kin dispersed farther distances. Similar to the relationship with natal dispersal, males dispersed farther from kin when availability of cavity resources near the natal territory was low. The only significant interaction in our full model was between a male's own aggression and the aggression of his nearest kin (Table 1). There was no significant interaction between kin presence and resource availability ($F_{1,95}=1.96$, $P=0.165$).

Discussion

The influence of behavioral traits, such as aggression, boldness, and sociality, has added a new dimension to understanding the causes of dispersal. Thus far, the focus has been placed primarily on the influence of personality variation of the dispersing individual alone (Fraser et al. 2001; Dingemanse et al. 2003; Cote and Clobert 2007; Duckworth and Badyaev 2007; Cote et al. 2010b). Yet, it has long been known that kin interactions can influence dispersal (Eikenaar et al. 2007; Davis 2011) making the personality and resource holding potential of kin a potentially powerful influence on natal dispersal.

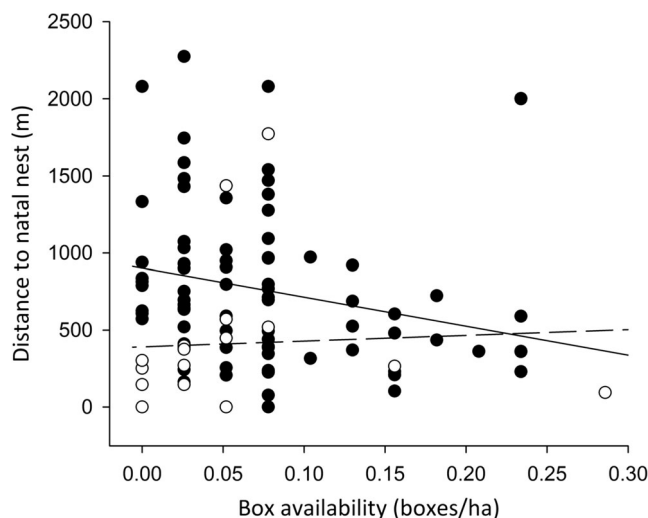


Fig. 2 The relationship between resource availability and natal dispersal distance of male western bluebirds with kin present (closed circles and solid line, $N=82$) and no relationship between resource availability and natal dispersal distance with kin absent (open circles and dashed line, $N=17$)

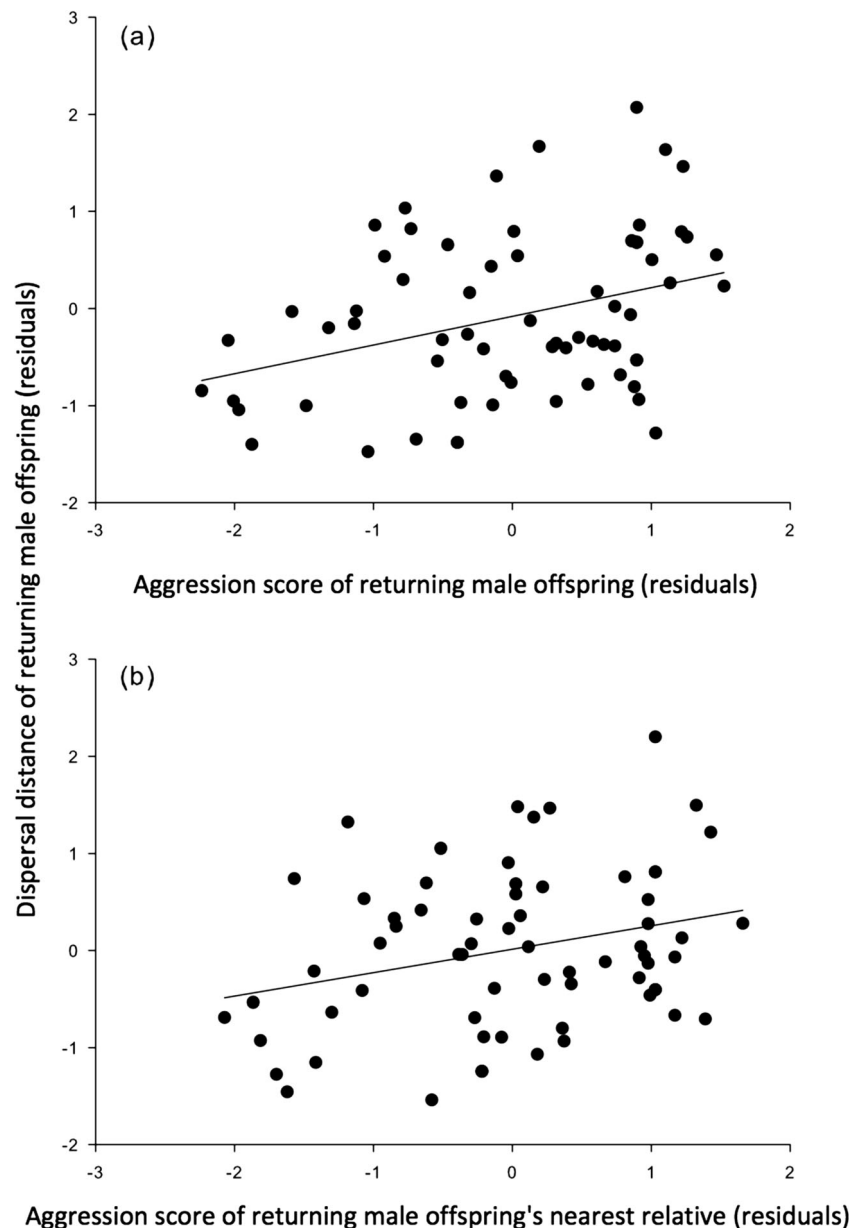
Table 1 Influence of aggression and resource availability on the distance to the nearest kin in western bluebirds ($N=66$)

Effect	$\beta \pm SE$	t	P value
Male's aggression	0.306±0.075	4.08	<0.001
Nearest kin's aggression	0.160±0.073	2.19	0.033
Local resource availability	-0.497±0.130	-3.82	<0.001
Male's aggression × nearest kin's aggression	0.179±0.088	2.04	0.045
Male's aggression × local resource availability	0.127±0.091	1.40	0.167
Nearest kin's aggression × local resource availability	-0.167±0.124	-1.35	0.182

Here, we used a long-term dataset on western bluebirds, a species with phenotype-dependent dispersal, to show that personality of family group members and resource availability interact with an individual's own phenotype to influence the dispersal decision. Specifically, we found that a male's distance dispersed from his nearest kin was influenced not only by his own aggressive phenotype but also by the aggressive phenotype of his nearest kin in addition to resource availability (Table 1). The direction of the relationship between dispersal and kin personality (Fig. 3b) suggests that aggressive individuals are less tolerant of other individuals, such that males with aggressive kin are separated by farther distances from their relatives compared to males with nonaggressive kin. Previous work has shown that dispersal and aggression are genetically correlated in this species (Duckworth and Kruuk 2009), so an alternative explanation is that offspring from aggressive families disperse farther, not because of direct behavioral interactions, but because they have inherited a greater propensity to disperse from their fathers. However, the model we used corrected for variation in male aggression and still showed an effect of kin aggression, suggesting that such inheritance, while potentially important, cannot fully explain the patterns observed. It is also possible that variation in aggression may also be influenced by the dispersal decision itself as aggression of offspring is measured after dispersal. Whatever the specific mechanisms, it is clear from our results that aggression of kin and the focal individual's own aggression both have independent, but important, influences on dispersal.

These patterns could arise if 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 are facultative cooperators and also historically depended on successional, post-fire habitat. Aggressive males are most likely to colonize new areas that have a low density of conspecifics, and nonaggressive males are more likely to remain in their natal population (Duckworth 2008, 2012). Thus, a link between aggression and sociality also makes sense in this species, especially if more aggressive

Fig. 3 Partial regression plots ($N=66$) showing the relationship between the dispersal distance from nearest kin of male western bluebird offspring and **a** offspring aggression controlled for resource availability and kin aggression and **b** nearest kin aggression controlled for resource availability and offspring aggression



males are less tolerant of others breeding nearby and so disperse farther to avoid the high densities prevalent in older populations. Moreover, if nonaggressive individuals are more social, they may be more likely to cooperate with their kin, accounting for males returning to breed nearby when their kin are nonaggressive. Intense behavioral observations across years support this interpretation, as we observed no instances of aggression between related individuals sharing territory boundaries, despite frequent observations of aggression at territory boundaries between unrelated individuals. Sociality and aggression are linked in other systems, such as spiders (Pruitt et al. 2008), social insects (Clark and Fewell 2013), and fish (Ruzzante and Doyle 1991) suggesting a common tradeoff between these behaviors across a diverse group of taxa.

We found that individuals dispersed farther from the natal nest when local resource availability (encompassing resources on parents' own and neighboring territories) was scarce (Fig. 2), but only when males had kin present on the study site. Offspring without kin present almost uniformly dispersed very short distances suggesting that offspring that remain in their natal population prefer to stay as close to their natal territory as possible. If so, then this suggests that when resources are not readily available near the parental territory, parents may actively deter offspring settling nearby. Because parents often return to breed in the same or nearby nest box in subsequent years, their offspring are generally prevented from occupying the natal site. However, our results suggest that relatives prevent sons not only from occupying the natal nest cavity itself but also from settling too close to the natal site in

general. This makes sense as in the absence of abundant cavity resources nearby, offspring may compete with parents for access to their primary nest cavity which may in turn negatively impact parental fitness (Ronce et al. 1998; Cote and Clobert 2010). However, when resources are abundant, parents not only tolerate offspring remaining nearby but may also gain important fitness benefits if it leads to a neutral territorial border and reduces the cost of territory defense (Eikenaar et al. 2007; Davis 2011).

The preference of offspring to remain close to the natal territory, even in the absence of kin, may be due to the costs of dispersal (Clobert et al. 2001; Rousset and Gandon 2002; Bonte et al. 2012). Moreover, prior 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*) and great tits (*Parus major*), individuals with familiar neighbors had increased reproductive success compared to those with unfamiliar neighbors (Beletsky and Orians 1989; Grabowska-Zhang et al. 2011). Moreover, breeding near the natal nest is likely to ensure that a male breeds near his relatives, if they return, and may provide opportunities for joint territorial defense (Dickinson and Akre 1998) or neutral territorial boundaries (this study). Thus, the finding that presence of kin on the study site deters most offspring from breeding close to the natal site suggests that competition among kin is at least as, if not more, important than kin cooperation in this species.

Overall, dispersal of offspring that remain in their natal population appears to be driven by a balance between the propensity of aggressive males to disperse, the tolerance of kin, and the resource availability near the natal site. While resources and kin tolerance have been shown to influence dispersal in many other species, our study adds a new dimension to the study of dispersal dynamics by showing that kin tolerance might depend on their personality. Thus, the frequency of distinct personality types within a population as well as how these personalities are distributed across generations can have important 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 are 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. More generally, 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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Ethical standards This research was conducted under permits to RAD and complies with the current laws and ethical guidelines of the USA.

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