

Adaptive Dispersal Strategies and the Dynamics of a Range Expansion

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ABSTRACT: In species undergoing range expansion, newly established populations are often more dispersive than older populations. Because dispersal phenotypes are complex and often costly, it is unclear how highly dispersive phenotypes are maintained in a species to enable their rapid expression during periods of range expansion. Here I test the idea that metapopulation dynamics of local extinction and recolonization maintain distinct dispersal strategies outside the context of range expansion. Western bluebirds display distinct dispersal phenotypes where aggressive males are more dispersive than non-aggressive males, resulting in highly aggressive populations at the edge of their expanding range. I experimentally created new habitat interior to the range edge to show that, as on the range front, it was colonized solely by aggressive males. Moreover, fitness consequences of aggression depended on population age: aggressive males had high fitness when colonizing new populations, while nonaggressive males performed best in an older population. These results suggest that distinct dispersal strategies were maintained before range expansion as an adaptation for the continual recolonization of new habitat. These results emphasize similarities between range expansion and metapopulation dynamics and suggest that preexisting adaptive dispersal strategies may explain rapid changes in dispersal phenotypes during range expansion.

Keywords: dispersal polymorphism, environmental heterogeneity, *Sialia*, kin cooperation, aggression.

Species that are expanding their range present a paradox because they commonly have both high dispersal ability and the ability to rapidly adapt to novel environmental conditions (Hill et al. 1999; Huey et al. 2000; Lee 2002; Holt 2003; Simmons and Thomas 2004; Badyaev 2005; Bearhop et al. 2005; Phillips et al. 2006). Yet theoretical models state that these two processes should oppose one another (Endler 1973; Slatkin 1985, 1987) because spatial

variation in selection pressures (e.g., in edge vs. interior populations) facilitates the evolution of local adaptation and population differentiation (Hoffman and Blows 1994; Holt and Keitt 2005), whereas high dispersal—and hence high migration between populations—prevents the evolution of local adaptation (Slatkin 1987; García-Ramos and Kirkpatrick 1997; Kirkpatrick and Barton 1997; Case and Taper 2000). These theoretical predictions are based on population genetic theory, which assumes that dispersal is random with respect to phenotypic variation and the fitness of an individual in its natal and recipient populations (Barton 2001; Armsworth and Roughgarden 2005a).

Yet these assumptions are unlikely to be met in most natural populations because dispersal behavior is often itself under strong selection and is commonly integrated with a suite of morphological, physiological, and behavioral traits (Roff and Fairbairn 2001). For example, many insect and plant species show distinct morphologies associated with dispersal (Sorensen 1978; Harrison 1980; Venable and Levin 1985; Zera and Denno 1997), and in many vertebrates the propensity to disperse is linked to variation in morphological and behavioral traits (Gaines and McClenaghham 1980; Dingemans et al. 2003; Garant et al. 2005; Phillips et al. 2006; Duckworth and Badyaev 2007; Skjelseth et al. 2007). Ultimately, such integration can lead to rapid population differentiation in the traits associated with dispersal and may explain patterns of rapid evolution observed during range expansion (Holt 2003; Garant et al. 2005; Duckworth and Badyaev 2007; Phillips et al. 2008).

Distinct dispersal strategies are favored in species that depend on patchy and ephemeral habitat (Harrison 1980; McPeck and Holt 1992; Roff 1994). Dispersal is generally thought to be costly because of the risks of leaving a familiar environment, the energetic expense of searching for new habitat, and the difficulty of settling in a new area where an individual must compete with prior residents for space and resources (Roff 1984; Alberts and Altmann 1995; Zera and Denno 1997). Such costs should favor a lower dispersal rate. However, when species depend on successional or ephemeral habitat, dispersal from the natal pop-

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ulation will eventually be necessary to escape a habitat patch that is destroyed or declining in quality (Levin et al. 1984; Crespi and Taylor 1990; Olivieri et al. 1995). When dispersal is unavoidable, traits that enable efficient dispersal or reduce the costs of dispersal should be favored (Roff 1986). However, these dispersal-related traits are often themselves costly to maintain (e.g., Roff 1984; Hughes et al. 2003). This produces a tension between the benefits of maintaining dispersal-related traits in the event of habitat destruction and the costs of bearing these traits once a new habitat patch is colonized (Roff 1986, 1994).

While these costs and benefits should maintain distinct dispersal phenotypes on a global scale, it is unclear how they are maintained within a population. One possibility is that the dynamics of local extinction and colonization leads to changing selection pressures within populations associated with changes in population density (Olivieri et al. 1990; Hanski 1999). In this case, the costs and benefits of both dispersal behavior and the suite of traits associated with dispersal will vary within populations according to the age of the population. This would produce temporal variation in selection within populations and spatial variation in selection among populations of differing ages and would provide a mechanism for the maintenance of variation in dispersal as well as in the traits correlated with dispersal.

Demonstrating that the fitness consequences of dispersal strategies vary both spatially and temporally is difficult because the colonization process is dynamic, and patterns of fitness variation can be interpreted only if colonization stage is known. This requires a system in which the process of colonization can be experimentally manipulated and dispersal phenotypes and their fitness consequences can be compared across populations of known age. Western bluebirds (*Sialia mexicana*) are undergoing a range expansion in the northwestern United States and are well suited to the investigation of temporal and spatial variation in fitness of dispersal strategies because the colonization of populations across the range expansion is well documented (Duckworth and Badyaev 2007) and because their settlement patterns are amenable to experimental manipulation by creating new habitat patches through the placement of nest boxes. Moreover, this species displays behavioral variation associated with dispersal: aggression is phenotypically and genetically integrated with a male's dispersal strategy such that highly aggressive males disperse more often and nonaggressive males are more likely to be philopatric (Duckworth and Badyaev 2007; R. A. Duckworth and L. E. B. Kruuk, unpublished data).

The integration of dispersal and aggression has led to rapid changes in aggression across the range that correspond to western bluebird's history of colonization and the competitive displacement of their close congener, mountain bluebirds (*Sialia currucoides*; Duckworth and

Badyaev 2007). New populations at the edge of the range were colonized by highly aggressive males, and aggression rapidly decreased in these populations over time. These rapid shifts were concordant with current selection: more aggressive males invested less in offspring care, and this led to a substantial fitness cost of aggression (Duckworth 2006b); yet highly aggressive males have an advantage over less aggressive males in competition for territories (Duckworth 2006a; Duckworth and Badyaev 2007). While these observations make it clear that the association of dispersal and aggression has important consequences for the dynamics of the range expansion, two questions remain. What is the origin of the link between these behaviors, and what maintains variation in aggression within populations?

One possibility is that the integrated expression of dispersal and aggression evolved as an adaptation to the historical distribution of this species' main limiting resource, nest cavities. Before man-made nest boxes, forest fire was critical to the survival of secondary-cavity nesters such as western bluebirds because it opens up the forest and creates areas with a high density of dead trees with nest cavities (Zarnowitz and Manuwal 1985; Hutto 1995). Although such habitat patches can last for several decades, over time, habitat suitability decreases as new trees grow and dead snags that harbor natural nest cavities decay (Raphael et al. 1987).

Such a moderately stable yet patchy and ephemeral resource distribution may have favored the link between aggression and dispersal. Western bluebirds are facultative cooperative breeders, and family groups are known to cooperate in territory defense (Kraaijeveld and Dickinson 2001). Thus, philopatric males may benefit from being nonaggressive if interactions with kin are more important than competitive ability for territory acquisition in the natal population, whereas males colonizing new habitat patches, where there is no opportunity for kin interactions, may benefit by being more aggressive and hence better competitors. Under this hypothesis, aggressive males should colonize new habitat patches even in areas interior to the range front, and aggressive dispersers and nonaggressive philopatric males should perform best during different stages of colonization (fig. 1). Such dependence of fitness on the stage of colonization leads to spatial and temporal variation in selection pressures and provides a mechanism for the maintenance of variation in aggression and dispersal.

An alternative scenario is that the association between aggression and dispersal evolved only recently as a result of the unique ecological context of the range expansion. Western bluebird colonizing populations at the edge of the range face interspecific competition from mountain bluebirds, whereas mountain bluebirds have been excluded from many populations that are interior to the range edge

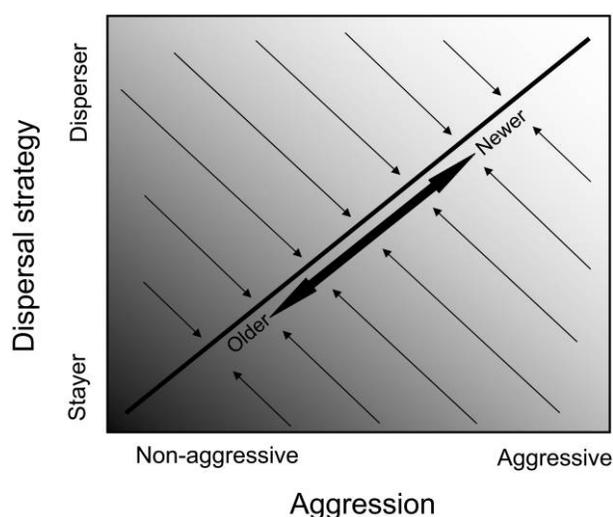


Figure 1: Conceptual illustration of the evolution of integrated expression of aggression and dispersal strategy. Direction of single-headed arrows indicates combinations along the solid line that are favored by selection. Nonaggressive philopatric males and aggressive dispersers are both expected to have high fitness; however, the fitness of each combination should vary in relation to patch age (indicated by shade gradient and double-headed arrow). Nonaggressive philopatric males are expected to excel in older habitat patches, whereas aggressive dispersers should perform best when colonizing new habitat patches (see text).

(Duckworth and Badyaev 2007). Heightened interspecific competition in edge populations may preclude settlement by less aggressive individuals. Under this scenario, the association of aggression and dispersal would be unique to the range front and not necessarily adaptive outside the context of the range expansion. Moreover, maintenance of variation in aggression may also be due to nonadaptive processes. For example, positive selection on either aggression of females or genetically correlated dispersal behavior (R. A. Duckworth and L. E. B. Kruuk, unpublished data) could counterbalance negative selection on aggression of males and maintain variation in this behavior.

To distinguish among these hypotheses, I combined observations of lifetime reproductive success in an established population with evidence from experimentally created new habitat patches that were paired with older habitat patches of known age. I predicted that, if the integrated expression of aggression and dispersal evolved in response to a patchy and ephemeral resource distribution, then even though the experimental habitat patches were not located at the edge of the range (fig. 2), males colonizing new patches should be similar in aggression to males colonizing new populations at the edge of the range. Moreover, I predicted that aggressive immigrants should perform best when colonizing new patches, whereas nonaggressive philopatric

individuals should perform best in the older, established population (fig. 1). However, if the link between dispersal and aggression is unique to the circumstances at the edge of the range (e.g., because of higher interspecific competition from mountain bluebirds), then males breeding in the newly created habitat patches should have lower aggression than males breeding at the range edge and should not differ in either aggression or fitness from males breeding in older populations with which they were paired. I also investigated the role of local density and kin interactions as factors contributing to spatial and temporal variation in selection pressures. Specifically, I measured territory spacing of males colonizing new versus old habitat patches and investigated whether nonaggressive males were more likely than aggressive males to settle adjacent to a relative.

Methods

Experimental Sites

This study was conducted in western Montana in an area that spans the easternmost edge of western bluebird's recent range expansion (fig. 2). Paired replicates of old and new habitat patches were created in two populations that are ~100 km apart, one near St. Regis (site 1 in fig. 2) and the second near Missoula (site 3 in fig. 2). The old habitat patches were colonized by western bluebirds more than 30 years ago at St. Regis and 13 years ago at Missoula. New habitat patches were created by placing nest boxes along fences in open rangeland that was previously uninhabited by bluebirds. The new and old habitat patches were separated by ~5 km at St. Regis and ~10 km at Missoula. Nest boxes were added to the new sites at a density similar to that of the old sites (mean \pm SE distance between adjacent boxes: St. Regis, 239.03 \pm 28.41 m at the old site, 273.71 \pm 28.40 m at the new site; Missoula, 122.58 \pm 8.73 m at the old site, 144.00 \pm 10.04 m at the new site; $P > .05$). Fourteen boxes were placed at the new site at St. Regis, and 20 were placed at Missoula. Measures of fitness and aggressive behavior were collected at St. Regis in 2004 only, whereas at Missoula, measurements used in the among-site comparisons were collected from 2005 to 2007. The St. Regis population was used for a concurrent experiment in 2004 in which half the territories at both old and new sites received a second box within 10 m; however, this treatment did not vary across sites (see Duckworth 2006a for details).

I also compared aggression of birds at the experimental sites to aggression of birds in the six populations that span the area of western bluebirds' range expansion in Montana (fig. 2) and are of known age (Duckworth and Badyaev

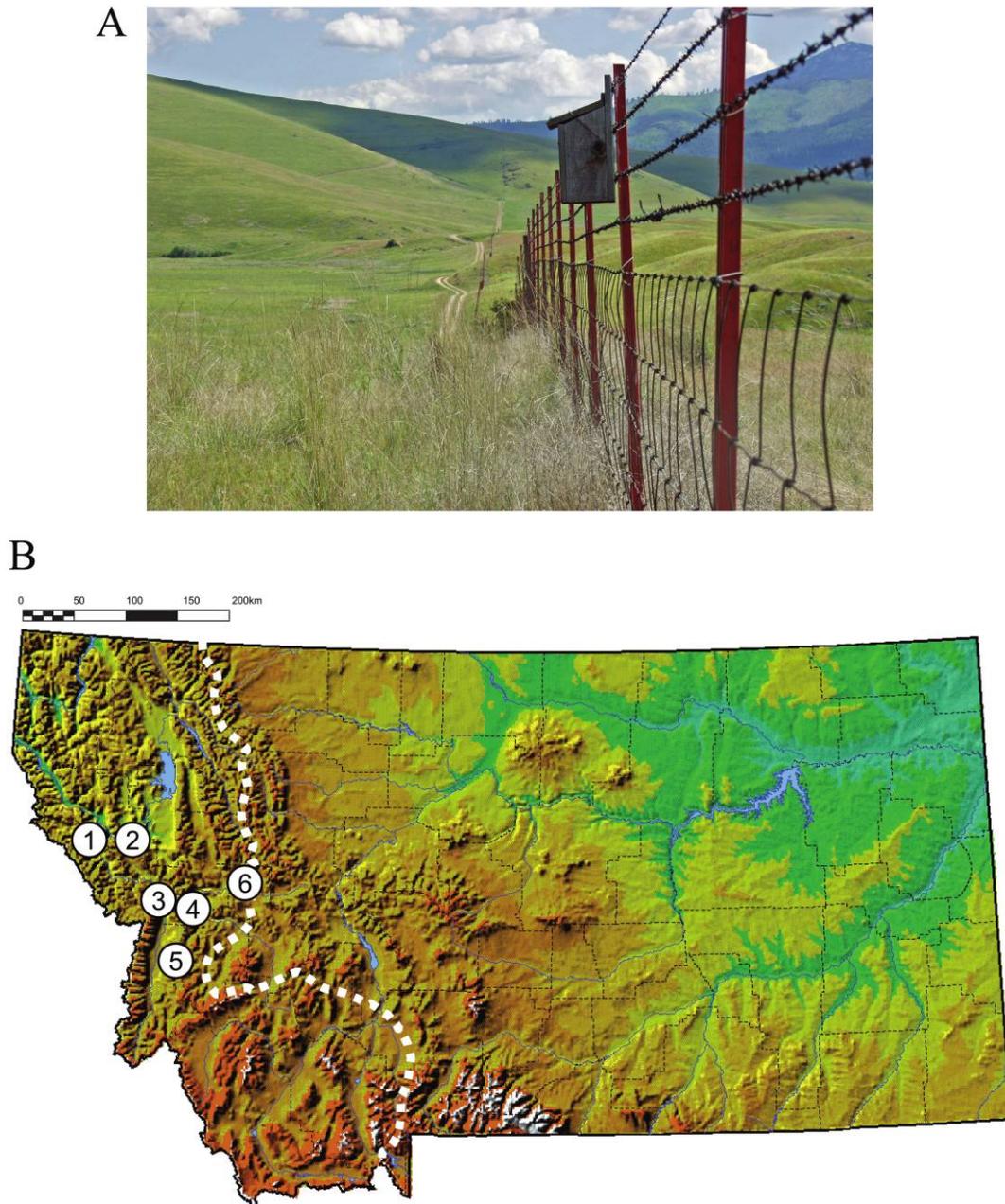


Figure 2: A, Example of open ranchland in Montana where the placement of nest boxes makes these areas suitable for western bluebirds to breed and thereby enables the experimental creation of new habitat patches. B, Location of study populations in western Montana. Numbers refer to the order of colonization of populations and population age rank. White dashed line indicates the current approximate edge of the range expansion. St. Regis and Missoula populations are indicated by numbers 1 and 3, respectively. Map courtesy of Montana Natural Resource Information System.

2007). The current analysis expands on previous population-level comparisons by including new data from the most recently colonized populations and also by investigating patterns of female aggression.

Measurement of Aggression

Aggression of bluebirds was measured by simulating a territorial intrusion of a common interspecific competitor,

the tree swallow (*Tachycineta bicolor*). Tree swallows were used because previous work showed that a male's aggressive response to tree swallows reliably indicated his aggressiveness toward conspecific males (Duckworth 2006b) and because using conspecific males can lead to infanticide and/or divorce, which is never observed after presenting a heterospecific competitor (R. A. Duckworth, personal observation). To simulate territorial intrusions, birds were presented with a live tree swallow in a wire cage placed on the nest box. I recorded the number of times an individual attacked, flew by, or hovered near the model during a 2-min trial. These behaviors were summarized into an aggression score that varied from 1 to 6, with 1 indicating the least aggressive response and 6 indicating the most aggressive response. Aggression is highly repeatable and consistent within individuals (Duckworth 2006b), and for individuals measured multiple times, I used the average of repeated measures for statistical analyses.

Comparisons of Reproductive Success

At all sites, nest boxes were checked at least once weekly during the breeding season, and the number of offspring that fledged was recorded. The old site at Missoula differs from all other sites in that it has been monitored closely since 2001 and all nestlings and adults have been banded each year. Moreover, it is surrounded by habitat that is unsuitable for bluebird breeding; the closest suitable habitat is >5 km away. Therefore, I categorized adult breeders that were banded as nestlings at the study site as philopatric and unbanded adults that settled in the population as immigrants. Pair affiliations of breeding adults were determined through extensive behavioral observations. I constructed a detailed, molecularly verified pedigree (see below), and, for a subset of individuals, collected data on lifetime reproductive success ($n = 156$; 77 males and 79 females; Duckworth and Badyaev 2007). Thus, at this site, I am able to compare lifetime fitness consequences of dispersal and aggression in both sexes and examine the effects of relatedness among individuals on settlement patterns.

Lifetime reproductive success was calculated as the number of genetic offspring that fledged across an individual's life. Adult western bluebirds have high site fidelity (Guinan et al. 2000), and adults that failed to return to the study site were assumed to have not survived the winter. Individuals that were still alive at the end of the 2007 breeding season were excluded from analyses. Juvenile western bluebirds undergo only a partial prebasic molt, which makes it possible to age individuals that were not banded as nestlings as "second year" (i.e., in their first year of breeding) or "after second year," depending on whether they had molted all of their greater secondary wing coverts (Shizuka and Dickinson 2005). Most indi-

viduals that bred at the site for the first time were aged as second year; however, 8.5% were either after second year or could not be aged because they were caught too late in the season and had already started to molt their wing coverts. Because the prior breeding history of these individuals was not known, I conducted analyses of fitness with and without these individuals and found that their inclusion/exclusion did not change the results. I report here the results of analyses in which these individuals were included. Individuals were assigned to cohorts based on their birth year. Individuals born before 2001 were grouped as cohort 1, and all other cohorts corresponded sequentially to an individual's birth year (cohort 2 hatched in 2001, cohort 3 hatched in 2002, etc.).

To verify measures of fitness, nestlings and adults were genotyped at four polymorphic microsatellite loci: *Cu μ 02*, *Cu μ 04*, *Ssi 8-19*, and *Ssi 9-32* (Duckworth 2006b). Parentage was assessed for each nest by comparing genotypes of offspring and the attending adults. All females matched their offspring's genotype, and the attending male was excluded as the father if one or more loci did not match. Extrapair offspring were assigned to a sire if their genotypes matched completely and there was no other male in the population with a matching genotype. Thirteen percent of all nestlings were extrapair, and more than 98% of these extrapair offspring were assigned to a sire.

For fitness comparisons among sites, I calculated reproductive success as the number of offspring fledged from a focal male's nest during the breeding season of 2004 at St. Regis and as the mean number of offspring that fledged per year during 2005–2007 in Missoula. For between-site comparisons, reproductive success for each male was not corrected for gains and losses of extrapair paternity because many attendant males in St. Regis and the experimental site at Missoula could not be captured for DNA sampling. However, this should not bias analyses because extrapair paternity is not related to male aggression, and correcting for extrapair paternity did not alter patterns of selection on aggression (Duckworth 2006b, 2006c). In the old patches, philopatric males were identified through banding data and were excluded from analyses of reproductive success of aggressive dispersers. At St. Regis, although some adults and nestlings were banded in 2002 and 2003, the banding at this site was not as complete as at the old site at Missoula; therefore, some philopatric males might have been categorized as immigrants. However, this should provide a conservative test of the prediction that fitness of aggressive dispersers is higher in new sites than in old sites because there is a general cost of dispersing (see "Results"), and including philopatric males should, if anything, decrease fitness differences among the sites at St. Regis. All males in the experimental sites were necessarily immigrants because there were no bluebirds

breeding in these areas before the addition of nest boxes. I compared the mean aggression scores of all males across sites and then, to test the predictions that aggressive males perform best when colonizing new patches, I compared measures of fitness of aggressive immigrants only. For this analysis, I categorized males as aggressive if their aggression score was >3 .

Mechanisms Underlying Fitness Consequences

To investigate the potential for kin cooperation in territory defense to occur in older populations, I used pedigree information from the old site at Missoula to compare aggressive behavior of philopatric males with territories adjoining their relatives to that of philopatric males that did not settle next to relatives. Territories were considered adjacent to a relative if the focal male's nest box was <300 m from either an attending parent's or nestmate's nest box and there were no other bluebird territories between them. Only first-order relatives that the focal individual had had contact with from hatch were considered. I chose 300 m as the limit because previous work has shown that bluebirds with nest boxes <300 m apart typically share territorial boundaries (Duckworth 2006a).

To investigate the importance of patch age on the spacing and settlement patterns of aggressive immigrants, I measured the spacing among adjacent territories by calculating the distance from a focal male's nest box to his nearest neighbor's nest box (Duckworth 2006a). For males with multiple observations across years, only their first year of breeding was used.

Statistical Analysis

To determine whether dispersal changed across consecutive cohorts, I used the ordered-heterogeneity test (Rice and Gaines 1994). For each sex, the complement of the probability (P_c) was calculated from an ANOVA that included cohort as the independent variable. Spearman's rank correlation coefficient (r_s) was calculated from the relationship between cohort and percent of individuals classified as immigrants.

The lifetime fitness consequences of aggression and dispersal in the Missoula population were first analyzed using a general linear model (GLM) with aggression, dispersal, sex, and their interactions as independent variables and the number of genetic offspring fledged as the dependent variable. There were no significant interactions (see "Results"), and selection gradients (β) were very similar for both sexes (table 1), so for subsequent analyses the sexes were pooled. I first estimated standardized selection gradients for each trait separately from a regression of relative fitness on the standardized trait values. To evaluate the

Table 1: Comparison of standardized selection gradients (β) and standard error (SE) from univariate and multivariate regression models for dispersal and aggression using lifetime reproductive success in male and female western bluebirds at the old site in Missoula

Trait	N	Univariate		Multivariate	
		β	SE	β	SE
Females:					
Aggression	79	-.20	.11	-.18	.11
Dispersal	79	-.14	.24	-.11	.24
Males:					
Aggression	77	-.26	.12	-.22	.13
Dispersal	77	-.21	.10	-.16	.10

Note: Values in bold indicate significance at $P \leq .05$.

strength and direction of natural selection after accounting for correlations among traits, I estimated selection gradients from a multiple-regression model with both aggression and dispersal included. To compare aggression, territory size, and reproductive success among sites, I limited analysis to males only because the restricted data set for this experiment meant that there was little opportunity for reproductive success of pair mates to differ.

Results

Aggression and Population Age

For both males and females, mean aggression scores were significantly related to population age, with newly colonized populations being more aggressive than older populations (males: $r = -0.93$, $P < .01$; females: $r = -0.79$, $P = .02$; $n = 6$ populations). Males were more aggressive than females (mean \pm SE aggression of males = 3.90 ± 0.12 , females = 3.39 ± 0.13 ; $F = 10.71$, $df = 1, 290$, $P = .001$), but patterns of population variation were similar between the sexes (interaction between sex and population: $F = 0.31$, $df = 1, 290$, $P = .91$; fig. 3). Males colonizing the two newly created habitat patches did not differ in aggression from males colonizing the two most recently established populations at the edge of the range ($F = 0.09$, $df = 3, 27$, $P = .96$; fig. 3).

Within-Population Analysis of Selection on Aggression and Dispersal

Data on lifetime reproductive success corrected for both within and extrapair paternity from the old site at Missoula showed a significant fitness cost of aggression ($F = 7.25$, $df = 1, 155$, $\beta = -0.21$, $P < .01$; fig. 4A), and the pattern of selection did not differ among the sexes (interaction between sex and aggression: $F = 0.36$, $df = 1, 155$, $P = .55$; table 1). Moreover, immigrants had lower reproduc-

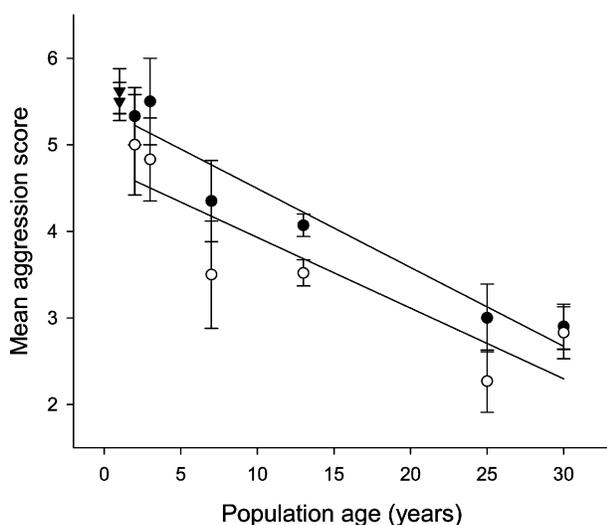


Figure 3: Relationship between mean aggression score and population age. Open circles indicate females, and filled circles indicate males. Filled triangles indicate mean aggression of males in “new” experimental patches. Bars indicate standard error. Data from experimental patches were not used in calculation of regression line. From right to left, populations correspond to numbers 1–6 in figure 2.

tive success than philopatric individuals ($F = 4.87$, $df = 1, 155$, $\beta = -0.18$, $P = .02$; fig. 4A), which also did not differ between the sexes (interaction between sex and dispersal: $F = 0.19$, $df = 1, 155$, $P = .66$; table 1). Fitting a model with both traits did not substantially alter selection gradients for either aggression or dispersal (aggression: $t = -2.59$, $\beta = -0.20$, $P = .01$; dispersal: $t = -2.09$, $\beta = -0.16$, $P = .04$).

At the old site at Missoula, among philopatric males, nonaggressive males were more likely than aggressive males to share a territorial boundary with a relative ($t = 2.26$, $P = .03$, $n = 44$; fig. 4B). Dispersal status was influenced by sex (8.3% of breeding females were philopatric vs. 43.1% of breeding males; $\chi^2 = 47.26$, $P < .0001$, $n = 237$; fig. 5) and cohort ($\chi^2 = 21.04$, $P < .01$). In both sexes, the proportion of adult breeders consisting of immigrants significantly decreased across consecutive cohorts (ordered-heterogeneity test, $n = 7$ cohorts; males: $r_s = -0.81$, $P_C = 0.92$, $P < .01$; females: $r_s = -0.78$, $P_C = 0.92$, $P < .01$; fig. 5).

Among-Patch Comparisons

Males breeding in new habitat patches were more aggressive than males breeding in older patches (Fisher’s test for combined probability: $\chi^2 = 28.64$, $P < .001$, $n = 96$; fig. 6A, 6B). In both St. Regis and Missoula, 100% of the males colonizing new habitat patches were categorized as ag-

gressive (i.e., aggression score > 3), whereas 38% of males breeding in older patches were nonaggressive. Among aggressive immigrants (score > 3), males settling in older patches had lower reproductive success than males settling in new patches (Fisher’s test for combined probability: $\chi^2 = 9.42$, $P = .05$; fig. 6C, 6D) and obtained smaller territories than males colonizing new habitat patches (Fisher’s test for combined probability: $\chi^2 = 14.10$, $P < .01$; fig. 6E, 6F). There was no significant difference between Missoula and St. Regis in either territory size or mean aggression score (all $P > .45$); however, individuals breeding at St. Regis had higher reproductive success than individuals breeding at Missoula ($F = 15.70$, $df = 1, 46$, $P < .01$; fig. 6C, 6D). Within each of these populations, no offspring or adults dispersed between the old and new sites.

Discussion

When habitat is ephemeral and patchy, species persistence depends on the recolonization of new habitats (Levin and Paine 1974; Sousa 1984; Roff 1994), creating temporal and spatial variability in population densities and leading to distinct selection pressures on dispersal in new and old areas (Olivieri et al. 1995). Specifically, highly dispersive individuals are favored when older patches are either destroyed or become oversaturated, yet once a new population is colonized, intrinsic costs of dispersal favor philopatric individuals (Olivieri et al. 1995; Hanski 1999). Dispersal is thought to be costly because dispersing from a familiar area can be risky and can involve a substantial energy investment and because immigrants may be at a disadvantage when settling in a new area (Alberts and Altmann 1995; Gandon and Michalakis 1999; Clobert et al. 2001; Hughes et al. 2003). The integration of dispersal with traits that enhance an individual’s chances of successfully dispersing and settling in a new area can reduce the costs of dispersal and lead to the maintenance of distinct dispersal strategies within a species (Olivieri et al. 1990, 1995; Roff 1994; Ravigné et al. 2004). In turn, such phenotype-associated dispersal affects the ecological and evolutionary dynamics of populations (Armsworth and Roughgarden 2005b; Garant et al. 2005) and may explain rapid divergence in traits among populations as species undergo range expansion.

The results of this study support the idea that the integrated expression of dispersal and aggression evolved in response to the historically patchy and ephemeral resource distribution of western bluebirds. I found that both new experimental patches and new populations on the range edge were colonized solely by aggressive males, demonstrating that the link between dispersal and aggression is not unique to the context of this species’ recent range ex-

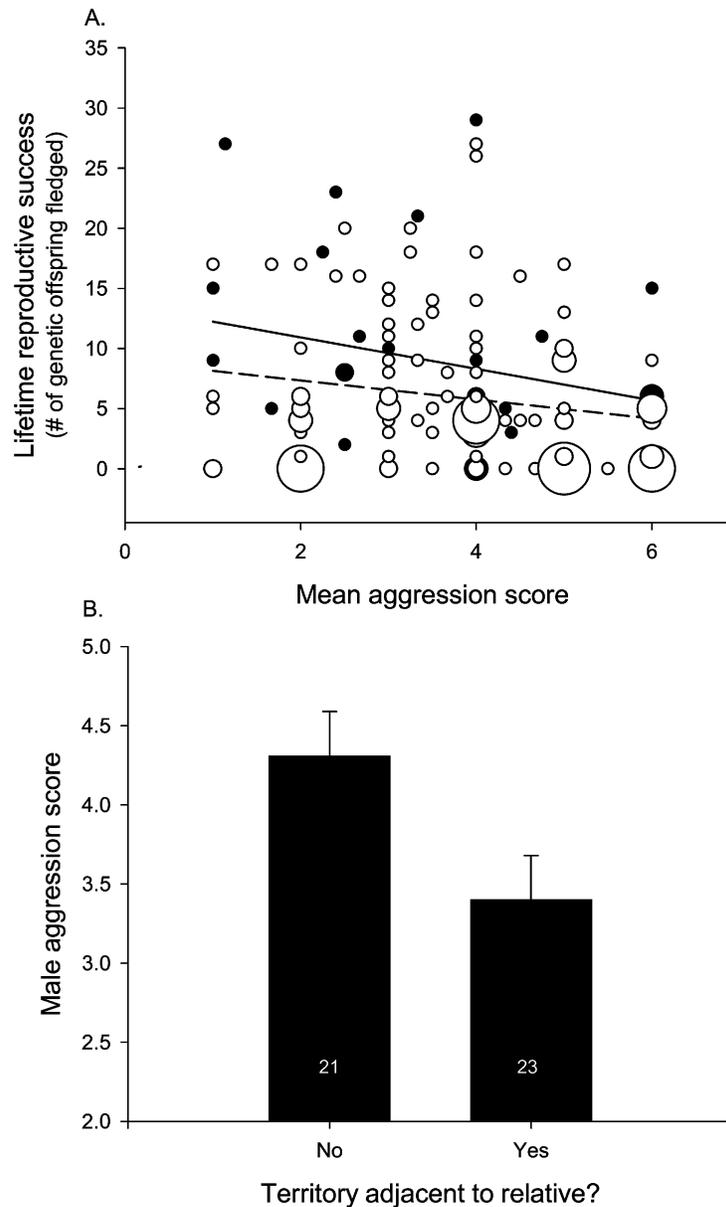


Figure 4: A, Relationship between lifetime reproductive success and mean aggression score for immigrant (*dashed line, open circles*) and philopatric (*solid line, filled circles*) western bluebirds. Size of circles indicates the number of overlapping data points, with the smallest size indicating a single point and the largest indicating six overlapping points. B, Among philopatric males, less aggressive males were more likely to settle adjacent to a relative than were highly aggressive males. Bars indicate mean + standard error. Data are from the old site at Missoula.

pansion. Moreover, as predicted, the fitness of aggressive immigrants depended on the age of the population they were colonizing. Aggressive immigrants had higher reproductive success when colonizing new versus old habitat patches (fig. 6C, 6D). In contrast, when all dispersal strategies in an older population were compared, nonaggressive philopatric males had the highest fitness. Comparison of fitness of nonaggressive males between new and old habitat

patches was not possible because not a single nonaggressive male settled in a new habitat patch. The absence of nonaggressive males from these areas may be because competitive sorting prevents them from colonizing new areas (see below).

Alternative hypotheses for the maintenance of variation in aggression were not supported. There was no evidence that positive selection on female aggression counterbal-

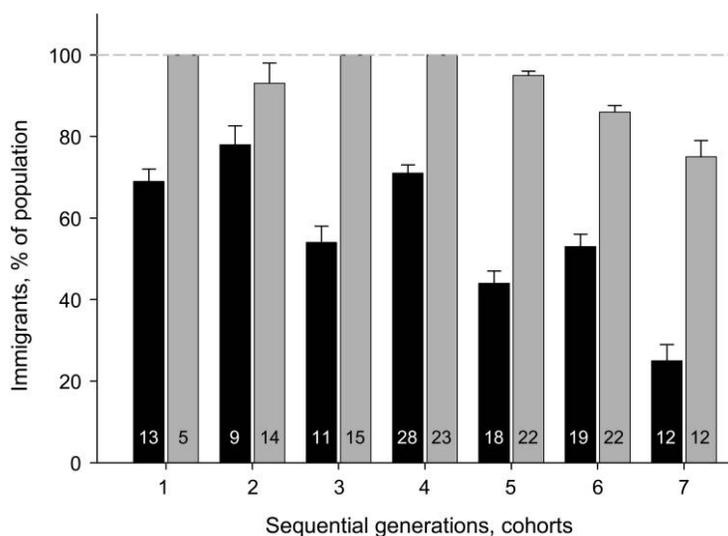


Figure 5: Percent of immigrant adult breeders has decreased across consecutive cohorts in the Missoula population. Gray bars indicate percent of females, and black bars indicate percent of males + binomial standard errors. Numbers on bars indicate sample size, and dashed line indicates 100%.

anced negative selection on male aggression; selection gradients were very similar among the sexes (table 1). Moreover, there was no evidence that positive selection on dispersal could impede the erosion of genetic variation in aggression through a correlated response. Selection on dispersal was also negative and was independent of negative selection on aggression (estimates did not differ between univariate and multivariate models). Taken together, the results strongly support the hypothesis that distinct dispersal strategies of western bluebirds are adaptive and are maintained by spatial and temporal variation in selection that is associated with the process of colonization.

Mechanisms Underlying Patterns of Selection

The historical distribution of nest cavities undoubtedly played a key role in the evolution of a link between dispersal and aggression in this species. Historically, this resource not only was limited in the environment but also was patchily distributed and ephemeral. Many studies have demonstrated fierce competition both within and among secondary-cavity-nesting species for nest cavities (Gustafsson 1986; Brawn and Balda 1988; Newton 1994; Merilä and Wiggins 1995). Under such intense competition for nest sites, a successful colonizer of a new habitat patch would need to be highly aggressive to acquire a nest cavity. This benefit of aggression is balanced by a significant fecundity cost of aggression (Duckworth 2006*b*; fig. 4*A*), and once new areas are colonized, over time, the number

of aggressive males rapidly decreases in concordance with negative selection (Duckworth and Badyaev 2007).

If aggression is important in territory acquisition, how, then, do nonaggressive males acquire territories? Habitat patches that are newly created by forest fire can last for several decades (Russell et al. 2006), on the order of 10–15 bluebird generations. As the habitat patch ages, population density increases, and while this should increase the strength of intraspecific competition for nest sites, it also increases the opportunity for kin to interact. Thus, in established populations, the social structure of a population may be as important as an individual's competitive ability in determining the outcome of territorial interactions, and kin facilitation of territory acquisition may play an important role in enabling nonaggressive males to acquire territories (Waldman 1988; Matthiopoulos et al. 2000). In support of this, among philopatric males, nonaggressive males were more likely than aggressive males to acquire a territory next to a relative (fig. 4*B*). Kin facilitation of territory acquisition seems likely in this species because western bluebirds display many forms of cooperative behavior, including helping at the nest and defense of winter territories by sons (Kraaijeveld and Dickinson 2001). The results of this study indicate that there is also potential for kin to cooperate during breeding territoriality; if this is the case, reduced aggressive interactions among family members may enable nonaggressive males to acquire territories in their natal populations.

A secondary consequence of changes in breeding density with population age is that, compared to those in older

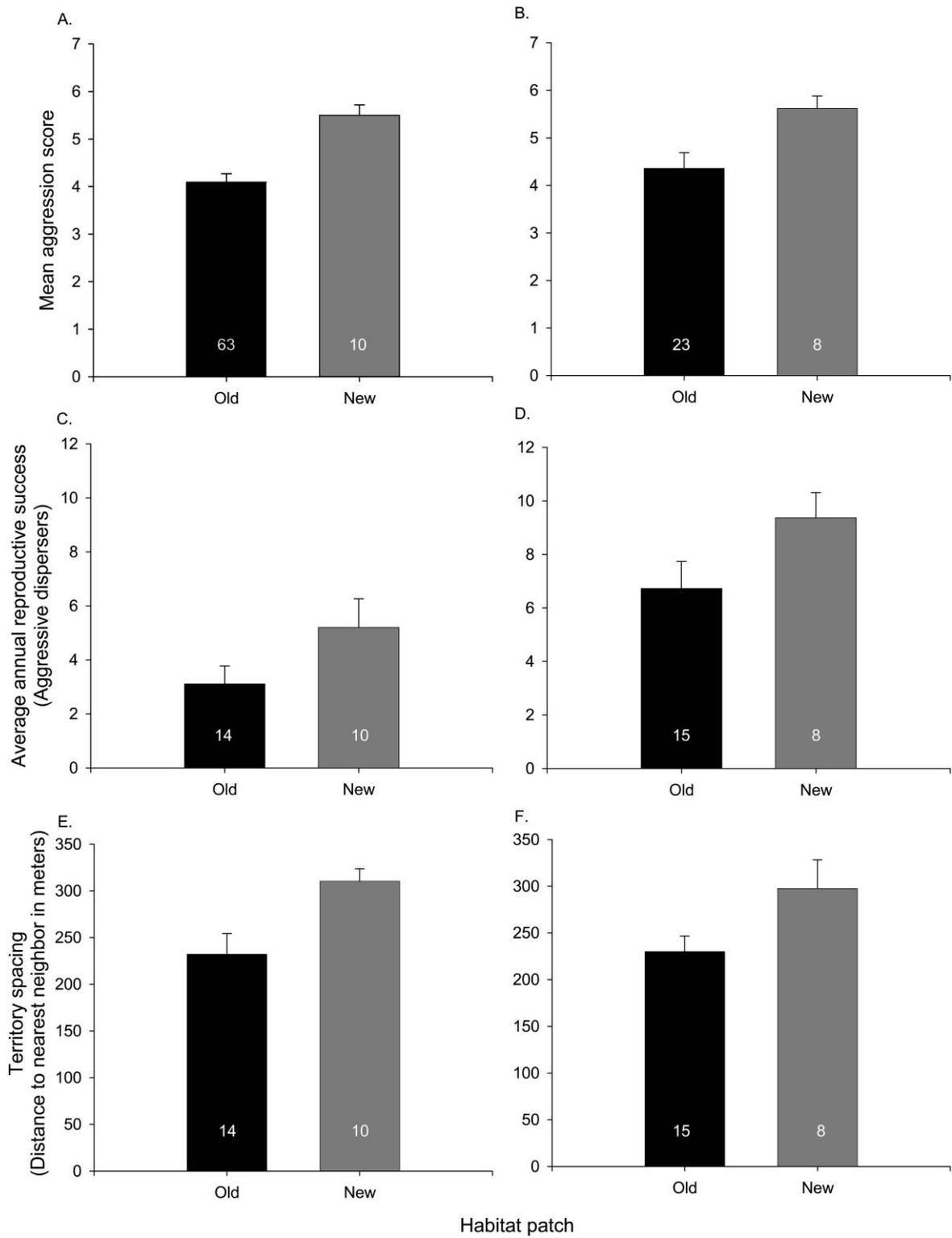


Figure 6: Differences in aggression, reproductive success, and territory size between males breeding in old (black bars) and those breeding in experimentally created new (gray bars) habitat patches in Missoula (A, C, E) and St. Regis (B, D, F) populations. In C–F, data include aggressive immigrants only (aggression score > 3).

populations, individuals settling in new populations can gain larger territories and potentially more resources. The lower density of males breeding in new patches meant that their territories were spaced farther apart than males breeding in older patches despite a similar distribution of nest boxes between new and old patches (fig. 6E, 6F). In the absence of neighbors, bluebirds use a wide area around their nest site to forage (Power 1966; Pinkowski 1979). Thus, males settling in new patches should have larger foraging areas than the colonizers of older patches, and this may at least partially compensate for the trade-off between parental investment and competitive ability (Arcese and Smith 1988; Phillips et al. 2008).

While aggressive immigrants sometimes settle in older populations, no nonaggressive male colonized new populations or habitat patches. Nonaggressive males may be unable to colonize new patches because, despite the lower density of conspecifics in these patches, the high frequency of aggressive males, in combination with interspecific competition, may preclude their settlement through competitive sorting (Pearson and Rohwer 2000; Ravné et al. 2004). Alternatively, the link between aggression and dispersal may mean that nonaggressive males never attempt to settle in new habitat patches. However, if this were the case, then we would expect that nonaggressive males would never be immigrants. Yet, at the old site at Missoula, there are some nonaggressive immigrants, suggesting that nonaggressive males may be able to successfully acquire territories in older populations where aggression is lower. In sum, kin interactions may enable nonaggressive philopatric males to acquire territories in their natal population, whereas males colonizing new habitat patches, where there is no opportunity for kin interactions, may benefit by being more aggressive and hence better competitors. These results suggest that increasing density within newly colonized populations might have opposite fitness consequences on aggressive and nonaggressive males by simultaneously decreasing territory size and increasing the potential for kin interactions. Such opposing effects of density on fitness provide a mechanism acting within populations for the maintenance of variation in dispersal strategies.

Given that a patchy and ephemeral resource distribution was likely key to the evolution of dispersal strategies in this species, the current human-induced changes in the distribution of nest cavities may have profound effects on this species' evolution. In many parts of the western United States, there are now hundreds of miles of evenly spaced nest boxes that can provide an exceptionally stable resource base. The results of this study show that in established, stable populations, both dispersal and aggression are costly (fig. 4A). Thus, a prediction from this study is that, over time, western bluebirds, as a species, should

become less aggressive and more sedentary because, through human intervention, the stability of the resource distribution has been fundamentally altered.

Implications for Species Range Expansion

Because highly dispersive individuals are more likely to colonize new areas, models predict rapid changes in dispersal propensity with respect to population age (Olivieri et al. 1995; Hanski et al. 2004; Phillips et al. 2008). Within the Missoula population, I found an overall decrease in the proportion of adult breeders that were dispersers across consecutive cohorts (fig. 5), and this has been coupled with a rapid decrease in aggression across cohorts in this population (Duckworth and Badyaev 2007), resulting in older populations that are increasingly nonaggressive and less dispersive (Duckworth and Badyaev 2007; figs. 3, 5). Recent studies show analogous patterns of change in dispersal and dispersal-related traits during the course of a range expansion. In cane toads (*Bufo marinus*), individuals with longer legs dispersed faster and colonized new populations at the range front, whereas individuals in interior populations dispersed much shorter distances (Phillips et al. 2006). In two species of butterflies (*Hesperia comma* and *Aricia agestis*) and two species of bush crickets (*Conocephalus discolor* and *Metrioptera roeselii*), individuals from newly colonized populations at the edge of the range had adaptations for greater flight ability (e.g., larger thoraxes, longer wings) compared to individuals from older populations (Hill et al. 1999; Thomas et al. 2001; Simmons and Thomas 2004). All of these examples are consistent with a scenario of nonrandom colonization of new populations by highly dispersive individuals and subsequent evolution of decreased dispersal in older populations.

The dynamics of dispersal evolution during these range expansions shows patterns strikingly similar to the dynamics of patch colonization in metapopulation studies. A wide range of species, from ciliated protists (*Tetrahymena thermophila*; Fjerdingstad et al. 2007) to numerous plant (e.g., Peroni 1994; Piquot et al. 1998) and insect (e.g., MacKay and Lamb 1979; Taylor and Merriam 1995; Hanski et al. 2004) species, show a close association between patch age and dispersal-related traits. In these species, new patches are colonized by highly dispersive individuals, while individuals in older patches are much more philopatric. The main difference between these studies and studies of range expansion is that the observed colonization dynamics occur throughout the species' range and are not limited to the range edge. Such analogous variation in dispersal dynamics among populations of species that depend on the colonization of new habitat patches for survival and species that are undergoing range expansion suggests that the same processes underlie the dynam-

ics of both. These parallels also suggest that, because species that depend on patchy and ephemeral habitat are preadapted to continually colonizing new areas, they may be the first species to expand their range in response to climate change and other global processes that open up new habitat at range borders.

Nonrandom dispersal with respect to phenotypic variation is frequently overlooked as an explanation for population-level changes in traits, yet the results of this and other recent studies indicate that it may be a common occurrence, particularly because distinct dispersal strategies occur in a wide variety of taxa (Sorensen 1978; Olivieri et al. 1983; Zera and Denno 1997; Toonen and Pawlik 2001; Cote and Clobert 2007; Duckworth and Badyaev 2007). Biased dispersal may be an important mechanism for the often-observed rapid adaptation to novel environmental conditions documented during range expansions (Hill et al. 1999; Huey et al. 2000; Duckworth and Badyaev 2007). More generally, these results suggest that key assumptions of population and quantitative genetic models of trait evolution—that dispersal is random with respect to phenotypic variation and fitness across populations—may often be incorrect. Thus, to understand the adaptive evolution of complex phenotypes in natural environments, an evolutionary framework is needed that not only incorporates spatial ecology but also acknowledges that organismal movement is not a random process but itself is the target of adaptive evolutionary processes.

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