Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird

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Behaviors can facilitate colonization of a novel environment, but the mechanisms underlying this process are poorly understood. On one hand, behavioral flexibility allows for an immediate response of colonizers to novel environments, which is critical to population establishment and persistence. On the other hand, integrated sets of behaviors that display limited flexibility can enhance invasion success by coupling behaviors with dispersal strategies that are especially important during natural range expansions. Direct observations of colonization events are required to determine the mechanisms underlying changes in behavior associated with colonization, but such observations are rare. Here, we studied changes in aggression on a large temporal and spatial scale across populations of two sister taxa of bluebirds (*Sialia*) to show that coupling of aggression and dispersal strongly facilitated the range expansion of western bluebirds across the northwestern United States over the last 30 years. We show that biased dispersal of highly aggressive males to the invasion front allowed western bluebirds to displace less aggressive mountain bluebirds. However, once mountain bluebirds were excluded, aggression of western bluebirds decreased rapidly across consecutive generations in concordance with local selection on highly heritable aggressive behavior. Further, the observed adaptive microevolution of aggression was accelerated by the link between dispersal propensity and aggression. Importantly, our results show that behavioral changes among populations were not caused by behavioral flexibility and instead strongly implicate adaptive integration of dispersal and aggression in facilitating the ongoing and rapid reciprocal range change of these species in North America.

genetics of behavior | geographical range | competition | colonization | behavioral integration

The successful colonization of a novel environment is a crucial first step in many models of speciation, is central to source-sink population dynamics, and is a key component of natural and human-induced changes in species distributions. Yet, the mechanisms underlying the colonization of new environments, from the initial arrival of new individuals to population establishment, remain poorly understood (1–3). Because the success of colonizers depends on their ability to survive and reproduce in novel ecological conditions, they must either be preadapted to the new environment or be flexible enough to respond rapidly and adaptively to novel conditions (4).

Behavioral flexibility is thought to aid colonization success by facilitating a rapid response to new conditions (5), thus enabling initial population persistence before adaptive evolution can occur (4, 6–8). In support of this idea, behavioral flexibility has been linked to the success of human-introduced invasive species (9, 10), yet its role in a natural range expansion has never been documented directly. Natural range expansion differs from colonization by invasive species, because, unlike invasive species that are often introduced to a novel environment by humans, a natural range expansion depends on both an organisms' ability to adapt quickly to novel conditions and on dispersal processes (2, 11–13) that may be unrelated to behavioral flexibility (14). In fact, limited behavioral flexibility may be advantageous when it enables the coupling of behaviors that are favored in a novel environment with the propensity to disperse to that environment (15, 16); yet, this idea has never been tested directly.

A major obstacle to testing this idea is the difficulty of identifying the mechanisms underlying behavioral changes during a range expansion. Although adaptive behavioral differences are often observed during species range changes (7, 17, 18), it is unclear whether these changes reflect flexibility of behavior, differential selection across populations, or a founder's effect. This is because direct observations of a colonization event are rare, and differentiating among these mechanisms necessitates making multiple measurements of behavior in the same individuals over time as well as tracking behavioral changes in new and established populations across generations.

The ongoing range expansion of western bluebirds (*Sialia mexicana*) across the northwestern United States provides a unique natural experiment to test the mechanisms underlying behavioral change during a range expansion. Western bluebirds, an obligatory secondary cavity nester, were common in western Montana (the site of this study) before the early 20th century; however, in the late 1930s, changes in logging and agricultural practices that severely limited the availability of mature trees with nest cavities in the mountain valleys across the Northwest coincided with their extirpation from the state (19, 20). However, in the last 35–40 years, the widespread implementation of nest box programs throughout the northwestern United States led to the rapid recolonization of western bluebirds' historical range (20–22). As western bluebirds recolonize their historical range, they are frequently coming into contact with populations of a close congener, mountain bluebirds (*Sialia currucoides*) (23). Although mountain bluebird populations were also affected by natural nest cavity limitation, their broader elevational range enabled them to persist in less affected higher elevation areas. When nest boxes were placed throughout the valleys of Montana, mountain bluebirds reached these areas first so that when western bluebirds' returned to these areas, mountain bluebirds were already present in high densities (24–26).

As western bluebirds expand their range eastward, they are rapidly displacing mountain bluebirds (Fig. 1 *Inset*) from lower elevation areas, with complete species replacement occurring in <10 years in several populations that have been closely monitored for >30 years (Fig. 1). Thus, this system provides a unique opportunity to test the role of behavior in range expansion because, not only is the exact time of establishment of each western bluebird population in the newly colonized range known (Figs. 1 and 2*B*), but the continued displacement of mountain bluebirds also results in

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Fig. 1. Changes in the breeding range of western bluebirds in Montana from 1975 to 2005. Data on aggressive behavior were collected from eight nest box populations near the towns of St. Regis (STR), Perma (PER), Moiese Valley (MV), Missoula (BMT and UMC), Hamilton (HMT), Ovando (OVD), and Stanford (STF). Pie charts indicate the relative proportion of western (white) and mountain (black) bluebirds breeding in each of the study populations during 2001–2005 (summed over 5 years). Before 1975, all mapped populations were comprised of 100% mountain bluebirds. (*Inset*) Rapid displacement of mountain bluebirds by western bluebirds in BMT (*Upper*) (western: $n = 224$; mountain: $n = 78$) and UMC (*Lower*) populations (western: $n = 38$; mountain: $n = 134$). Dashed lines represent mountain bluebirds, and solid lines represent western bluebirds. Gray lines indicate estimated trend.

distinct competitive environments between new and old populations; newly arriving western bluebirds colonizing new populations are competing mainly with heterospecifics for territories, whereas those settling in older populations are mainly competing with conspecifics.

Western bluebirds in Montana are short-distance migrants that spend most of the year (March through October) on the breeding grounds. Females typically disperse away from their natal population to breed; however, males vary widely in their dispersal behavior. Similar to nonmigratory populations (27), western bluebirds in Montana are facultative cooperative breeders and 7.3% of males help at their parents' nest and 59.3% of returning males either inherit or settle territories adjacent to a relative's territory. Thus, juvenile males are faced with the decision to either remain in their
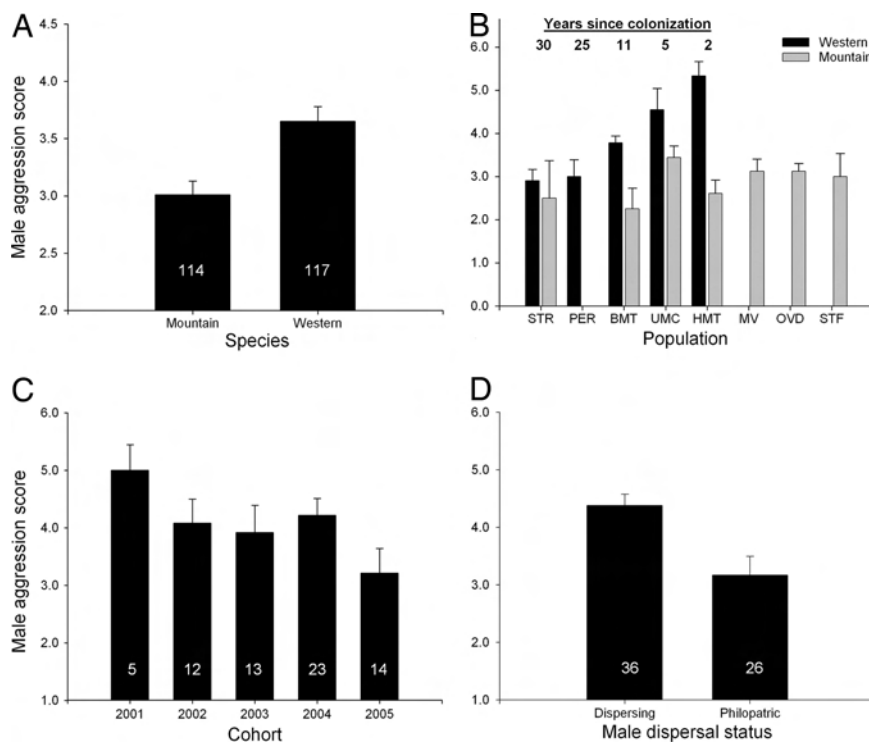
Fig. 2. Variation in aggression across species, populations, generations, and dispersal classes. (*A*) Western bluebirds were more aggressive than mountain bluebirds. (*B*) Aggression differed significantly among western bluebird populations and was related to the number of years since colonization of a population (numbers above bars) See Fig. 1 for location abbreviations and supporting information (SI) Table 1 for sample sizes. (*C*) Aggression significantly decreased across cohorts in the BMT population. (*D*) Males that dispersed away from their natal population to breed (*Left*) were more aggressive than males that remained in their natal population (*Right*). Shown are means ± SE. Numbers on bars indicate the number of males sampled.

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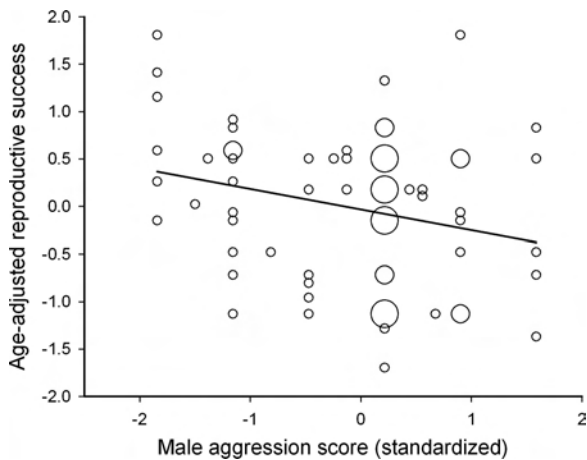
Fig. 3. Significant negative selection on aggression in the BMT population, where mountain bluebirds were excluded in 2001. Reproductive success is calculated as the residuals of a regression of a male's annual reproductive success and age. The sizes of the circles indicate the number of overlapping data points with the smallest size indicating a single point and the largest indicating three overlapping points.

natal population, cooperate with relatives and acquire a territory through nepotism, or disperse outside of their natal population and compete for a territory on their own. Previous experimental work has shown that more aggressive males have an advantage over nonaggressive males in competition for territories (28) but invest very little in parental care (29). Thus, we predicted that nonaggressive males would be more likely to remain in their natal populations, whereas aggressive males would be overrepresented at the edge of the expanding range because of their superiority at acquiring new territories. Here, we test these predictions by using a common nest site competitor of both bluebird species to experimentally assay aggression in multiple replicates of newly established and older populations across >75,000 km^2 on the eastern edge of the western bluebirds' current range. First, we show that aggression is changing rapidly across the range expansion. Second, we examine the relative contribution of behavioral flexibility, natural selection, and biased dispersal in producing rapid changes in aggression within and among the populations.

Results

Variation in Aggression Across the Range Expansion. Western bluebirds, the competitively superior species, were more aggressive than mountain bluebirds ($F = 24.50$, $P < 0.0001$; Fig. 2A). Aggression differed significantly among western bluebird populations (ANOVA: $F = 4.88$, $P < 0.01$, $n = 116$) such that males in newly colonized populations were more aggressive compared with males in older populations (ordered heterogeneity test, $r_s = -1$, $P_C = 0.99$, $P < 0.001$, $n = 5$ populations; Fig. 2B). Aggression did not differ among mountain bluebird populations ($F = 0.99$, $P = 0.44$, $n = 113$; Fig. 2B).

Mechanisms Underlying Population Variation. We tested whether variation in aggression among populations was due to within-generation behavioral flexibility or across-generation changes. In the Blue Mountain (BMT) population (see *Methods*), we found that aggression was initially high but strongly decreased across years after the exclusion of mountain bluebirds in 2001 (ordered heterogeneity test, $P_{one-tailed} < 0.01$, $n = 5$ years; $r_s = -0.70$, $P_C = 0.99$). The decrease was not caused by age-related changes because aggression did not change with male age (paired t test, $t = 1.34$, $P = 0.20$, $n = 20$), and age was not a significant predictor of aggression in the mixed model ($F = 0.44$, $P = 0.51$). Further, results of the mixed model showed that individual differences among males

explained a significant amount of the variance in aggression ($z = 3.03$, $P = 0.001$, $n = 67$), corroborating findings that aggression is highly consistent within males in this species (28). Instead, we found that the change in aggression across years was caused by a strong decrease in aggression among consecutive cohorts of males (mixed model: $F = 6.80$, $P = 0.01$; Fig. 2C). We also found that males that dispersed were more aggressive than philopatric males ($t = -3.19$, $P = 0.003$, $n = 62$; Fig. 2D).

Heritability (h^2) of and Selection on Aggression. Maximum-likelihood analysis of the molecularly verified multigenerational pedigree (see *Methods*) revealed significant additive genetic variance for aggression ($V_A = 1.12 \pm 0.53$; $h^2 = 0.45 \pm 0.15$ SE, $P < 0.01$), no significant permanent environment effect ($V_{PE} = 0.00$), and residual variance of 1.39 ± 0.32 SE. We found significant negative fecundity selection on aggression in the BMT population even after correcting for extra-pair paternity ($F = 4.93$, $P = 0.028$, standardized regression coefficient = -0.27; Fig. 3). The predicted response to selection (see *Methods*), calculated with estimates of h^2 and selection was -0.12 SD per generation; however, the observed average change in aggression across cohorts of males was more than twice greater (more than -0.30 SD). The expected aggression score of emigrants (A_e), calculated with the observed change in aggression across generations (ΔA), h^2, the standardized selection differential (S), and the aggressive phenotype of immigrants (A_i) (see *Methods*), was 0.36 SD per generation and was not statistically different from the observed aggression score of immigrants (0.28 ± 0.13 SD per generation), indicating that both emigrants and immigrants of the BMT population are much more aggressive than philopatric males (observed aggression score = -0.52 ± 0.22 SD per generation).

Discussion

The striking differences in aggression among western bluebird populations correspond closely to this species' history of colonization of new environments (Fig. 2B), suggesting that behavioral changes play an important role in western bluebirds' ongoing range expansion. We found that aggression was highest among birds colonizing new populations, but once species replacement was complete, aggression decreased rapidly in only a few generations (Fig. 2 B and C), resulting in drastic population differences across western bluebirds' newly established range.

Our findings indicate that a combination of biased dispersal and strong natural selection on aggression are the primary causes of changes in aggression among western bluebird populations. The rapid across-generation decrease in aggression was concordant with patterns favored by current selection (Figs. 2C and 3; BMT population); however, the observed change in aggression among cohorts was more than twice that predicted by response to selection alone. We showed that the biased dispersal of aggressive and nonaggressive males (Fig. 2D), where aggressive males disperse and nonaggressive males remain in their natal population, greatly accelerated the observed divergence in aggression across populations. Evidence for a close integration of dispersal and aggressive behaviors in this species comes from the observed aggressive phenotypes of immigrants and philopatric males (Fig. 2D), the observed highly aggressive phenotype of initial colonizers of new populations (Fig. 2B), the predicted phenotype of emigrants from the BMT population, and recent evidence of a strong positive genetic correlation between these behaviors (R.A.D., unpublished work). Close association between dispersal strategies and aggressive behaviors provides an important mechanism for two key observations in this species: the colonization of new populations by aggressive males and the rapid decrease of aggression in older populations.

Alternatively, rapid behavioral changes within and across populations of this colonizing species can be caused by behavioral flexibility. However, several lines of evidence rule out this expla-

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nation. First, the decrease in aggression across years at BMT was caused by a progressive decrease in aggression among consecutive cohorts of males and not by age-related changes within individuals (mixed model analysis; Fig. 2*C*). Second, aggression was highly repeatable and consistent within individuals and was not affected by age or breeding stage and within-individual variation was significantly lower than among-individual variation. These findings corroborate earlier studies showing that males do not modify aggression across breeding stages and respond similarly to different nest site competitors (29). Third, previous studies found that males do not modify their aggressive response in relation to experimental manipulation of local competitor density and that the aggressive phenotype of males is formed before they settle territories (28). Finally, the finding of significant additive genetic variance for aggression indicates that a proportion of variance in aggression is stable not only within individuals but also across generations. This finding is further supported by the recent documentation of a strong positive genetic correlation between aggression and dispersal (R.A.D., unpublished work). Taken together, these results show that the observed patterns cannot be explained by behavioral flexibility, but instead, distinct dispersal strategies in combination with current natural selection on aggression strongly contribute to the observed across-generation and across-population changes.

An important question following from these results is whether these distinct dispersal strategies and the resulting shifts in aggression across populations are adaptive. Significant negative selection on aggression in the BMT population indicates that the rapid decrease in aggression of older populations is adaptive (Fig. 3); the negative selection is proximately caused by a link between aggression and paternal care; aggressive males provide almost no parental care, which leads to high offspring mortality (29). Thus, even though aggressive males perform better than nonaggressive males during competitive interactions, their lower reproductive investment leads to a substantial cost in fitness (28). This lack of parental investment by aggressive males may also explain why they disperse more often than nonaggressive males. Adult males of this species often nest near their parents or other close relatives and occasionally help provision their parents' offspring (20). Facultative cooperative behavior and nepotism may explain why nonaggressive males are able to obtain territories despite their poor performance during competitive interactions. Thus, the tradeoff between reproductive investment and competitive ability, in conjunction with facultative cooperative behavior, may be the ultimate reason that the integrated expression of aggression and dispersal has evolved in this species.

Further, the colonization of new populations by highly aggressive western bluebird males is likely to be adaptive. Highly aggressive males are able to exclude both less aggressive conspecifics and the less aggressive mountain bluebirds from breeding territories (28). In contrast, less aggressive western bluebird males, which show a level of aggression similar to mountain bluebirds (Fig. 2 *A* and *B*), are poorly suited for colonizing new areas. Thus, competitive sorting, a form of selection on aggression caused by the differential abilities of aggressive and nonaggressive males to acquire territories (31), could be an important mechanism that not only enables the displacement of mountain bluebirds in areas of recent overlap, but also accounts for the colonization of new populations by a subset of highly aggressive western bluebird males. Taken together, negative selection on aggression in older populations and the known link between aggression and competitive ability (28) suggest that the distinct dispersal strategies of aggressive and nonaggressive males are adaptive. By ensuring that highly aggressive males colonize new areas and by accelerating adaptive evolution of aggression in older populations, the link between dispersal and aggression plays a key role in the western bluebird's successful range expansion.

Western bluebirds current range expansion is likely too recent to have caused the evolution of distinct dispersal strategies. Instead, the existence of a link between dispersal and aggression likely predates the range expansion and has made western bluebirds preadapted to take advantage of the recent influx of nest boxes in the western United States. Natural nest cavities are a patchy and often ephemeral resource, and this particular resource distribution may have selected for functional integration of dispersal and aggression in this species. For example, forest fires often produce areas of high densities of natural nest cavities that can persist for several decades until succession makes these areas unsuitable for bluebirds (32). Thus, historically, the evolution of distinct dispersal strategies in this species may have been favored by alternations of a patchy and ephemeral resource with its relative intersuccessional stability. Regardless of the origins, our findings provide strong support for the idea that the integrated expression of ecologically important behaviors and dispersal can have large-scale ecological consequences by ensuring that the trait necessary for success in a new environment is reliably coupled with the propensity to move to that environment. More generally, these findings show that individual variation in behavior plays a central role in regulating population level processes, including those ultimately determining the distribution of species.

Methods

Study Populations. Data on abundance and historical and present-day breeding ranges of western and mountain bluebirds were obtained from personal observations (A.V.B.: 1995–1997; R.A.D.: 2001–2005), Bent (33), Aylesworth (34), U.S. Geological Survey Bird Banding reports (1961–2005), Mountain Bluebird Trails fledging reports (1987–2005), Skaar (26), Bergeron *et al.* (25), Lenard *et al.* (24), and Sauer *et al.* (23). Nestlings and breeding adults were banded each year in all populations, allowing us to account for multiple measurements of individuals in analyses of population and species differences in behavior. An experiment on the effects of nest box density on bluebird aggressiveness (28) was conducted in St. Regis in 2004–2005, and these years were omitted from analyses.

Measurement of Aggression. Aggressive behavior of 231 mountain and western bluebirds was measured in the eight study populations in May and June, 2001–2005 by simulating a territorial intrusion of a tree swallow (*Tachycinetas bicolor*), a common interspecific competitor of bluebirds, and recording males' aggressive responses (see SI Table 1 for sample sizes). Different models were used each time the same male was measured to avoid pseudoreplication. We focused on males in this study because previous work showed that female aggression was unrelated to territory acquisition (28). Assays used to measure aggression have been described in detail (29). Briefly, each male was assigned an aggressiveness score of 1–6 based on the number of times he attacked, flew by, or hovered at the tree swallow model with 1 indicating a low response and a 6 indicating a highly aggressive response. The behavioral trials are an objective measure of aggression as the number of attacks, flybys, and hovers is concrete and easy to score (35, 36). Moreover, the scorer rarely had knowledge of an individual's age, dispersal status, previous aggression score, and relatedness to other individuals in the population during the trials and therefore, the trials were blind with respect to these factors. This measure of aggression is not confounded by differences among populations in duration of co-existence of the two bluebird species and is highly repeatable across breeding stages and highly concordant with a male's aggressive response to a bluebird (29).

Data Collection in the BMT Population and Construction of Pedigree. Pairing and nesting affiliations of breeding adults were determined through extensive behavioral observations. Nests boxes were checked at least twice weekly throughout the breeding season to monitor adult breeding status and nestling survival. Blood samples were collected from all nestlings and adults. DNA collection and microsatellite genotyping methods have been described (29). Briefly, individuals were genotyped at four polymorphic microsat-

ellite loci: Cuμ 02, Cuμ 04 (34), Ssi 8–19, and Ssi 9–32 (28), all females matched their son's genotype, and links between fathers and sons were included in the pedigree only if there was a complete match of genotypes. One male offspring matched three potential fathers, and, therefore, his paternal link was omitted from the pedigree. The pedigree has 810 individuals with 83 paternal links, 95 maternal links, and a maximum depth of five generations.

The BMT population is isolated because it is surrounded by habitat unsuitable for bluebird breeding, by dense forest to the west and south and by housing subdivisions to the east and north (28). The closest suitable habitat is >5 km away. Therefore, we were able to categorize adult breeders as either locally born (when they were banded as nestlings at the study site) or dispersers (unbanded adult males breeding at the site for the first time) and compared their aggressive behavior (28). Unbanded adults were aged as either HY (hatch-year males in their first year of breeding) or AHY (after hatch-year males) based on whether they had molted all of their greater secondary wing coverts (37).

Estimation of Genetic Parameters. h^2 of aggression was estimated by using a restricted maximum-likelihood mixed model ("animal model"), which allowed us to accommodate an unbalanced data set, incorporate information from a complex pedigree, and include fixed effects that are known to influence trait means (38). In a concurrent study, we found a significant effect of an individual's size rank as a nestling on the expression of aggression in adulthood. Therefore, we included nestling size rank, sex, and the interaction between them as fixed effects in the model. We used wing length at 10 days of age to determine size ranks of nestlings. Random effects were included in the model as an additive genetic effect and permanent environment effect on aggression. Components of variance were estimated by using ASReml (VSN International, Hempstead, U.K.; www.vsn-intl.com), and the total phenotypic variance was split into three components: additive genetic variance, permanent environment variance, and residual variance. The total phenotypic variance was the sum of all variance components. Estimates of h^2 were calculated as the ratio of additive genetic variance to the total phenotypic variance. We assessed the significance of the additive genetic component by using a likelihood ratio test (39).

Statistical Analyses. Reproductive success was calculated for each male as their total number of within and extra-pair offspring that they successfully fledged during one breeding season. Reproductive success of males strongly depends on age ($F = 18.41$, standardized regression coefficient $= 0.47$, $P < 0.001$, $n = 48$), and because several males were present in the population in multiple years, we first used a mixed model to control for both age-dependent variation and multiple measurements of the same individuals. Because including individual identity in the mixed model did not affect the relationship between male aggression and fitness and did not improve the model (value of Akaike's information criterion increased with inclusion of individual identity), we used a least-squares regression to estimate selection. Specifically, we determined the strength of selection on aggression as the standardized regression coefficient of a model with age-adjusted reproductive success (the residuals of the regression of reproductive success on

male age) as the dependent variable and standardized male aggression score as the independent variable. The predicted response to selection was determined as the product of h^2 and S, the standardized selection differential, which was compared with the mean change in aggression across cohorts, measured in SD. To estimate the level of emigration needed to produce the observed changes, we used a modified version of the breeder's equation:

$$\Delta A = h^2 S + (A_i - A_e),$$

where ΔA is the change in aggression of the population across generations, A_i is the aggressive phenotype of immigrants, and A_e is the aggressive phenotype of emigrants.

To determine whether aggression differed among species or populations, we used a mixed model (Proc Mixed in SAS 9.13) with aggression score as the independent variable, species, population, and breeding stage as fixed factors with year and individual identity as random factors. Only significant terms were retained, and, therefore, in the final model we omitted breeding stage as it was unrelated to variation in aggression ($F = 0.17$, $P = 0.84$). For post hoc analysis of differences in aggression among populations, each species was analyzed separately by ANOVA, and only populations with multiple observations of each species were included. In these analyses, only the first measurement of aggression was included for males measured in >1 year. To determine whether aggression of western bluebirds decreased across years in BMT and whether mean aggression of western bluebirds varied with population age, we used the ordered heterogeneity test (30). For changes in aggression across years, P_C is calculated from a mixed model including year and male age as a fixed effects and individual identity as a random factor. For changes in aggression in relation to population age P_C was calculated from an ANOVA. To determine whether aggression decreased in males during their life, we used a paired t test in which we compared the aggression score of a male in his first year of breeding with his score in his second year of breeding. To determine whether changes in aggression across years were caused by differences in aggression among cohorts, we used a mixed model with aggression score as the independent variable, cohort and age as fixed factors, and individual identity as a random factor. An individual's cohort was assigned based on when it was born. Individuals born before 2001 were grouped as cohort 1, and all other cohorts corresponded sequentially to an individual's birth year (e.g., cohort 2 was born in 2001, cohort 3 was born in 2002, etc.). For analyses using regression, general linear models, or mixed models, residual plots were checked and Levene's test was used to verify that the assumptions of heterogeneity of variance and linearity were not violated.

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