

# Evolution of genetically integrated dispersal strategies

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## 7.1 Spatio-temporally varying environments and the evolution of dispersal

Dispersal is costly, so all else being equal, it is beneficial for an individual to remain in its natal population. Yet if habitat quality varies over time and space—as is often the case for species that depend on successional or ephemeral habitat—then the benefits of escaping habitat of declining quality to find higher quality habitat more than compensates for the cost of dispersal. Thus a key factor leading to the evolution of dispersal is a spatio-temporally varying environment (Roff 1975; Johnson and Gaines 1990; McPeck and Holt 1992; Paradis 1998).

Extensive spatio-temporal environmental variation means that parents and offspring are likely to experience different environmental conditions, and thus the costs and benefits of dispersal are also likely to be distinct across generations. This should favour environmental contingency of dispersal and result in a lack of correspondence between generations in individual dispersal decisions. While some environmental contingency of dispersal is often observed (Gaines and McClenagham 1980; Hanski 1999; Ronce 2007), many studies also find a strong resemblance between parents and offspring and corresponding significant heritability of dispersal behavior (Roff and Fairbairn 2001; Hansson *et al.* 2003; Pasinelli *et al.* 2004; Sinervo *et al.* 2006; see Chapter 6 for a review). How can such constancy in dispersal behavior across generations be reconciled with selection for context-dependency of dispersal that should result from spatio-temporal environmental variation?

In this chapter, I explore the conditions that might favour both constancy and context-dependency in dispersal phenotypes across generations for species that experience spatio-temporally varying habitat. I focus on spatio-temporally varying environments because theoretical models suggest that environmental variation is the most common evolutionary cause of dispersal, and because spatial and temporal environmental variation is ubiquitous in natural systems. I first suggest that across-generation constancy in dispersal arises from consistent natural selection for close integration of dispersal with a suite of behavioral, morphological, and life-history traits that enable successful dispersal. I then explore the conditions that produce correlational selection on dispersal and other traits, and suggest that such correlational selection may ultimately lead to their genetic integration. Finally, I use western bluebirds as a model system to show how integrating ecological, quantitative genetic, and behavioral information can provide novel insights into the evolution of dispersal phenotypes.

## 7.2 Setting the stage for environment-independent expression of dispersal

If the extrinsic environment is the main factor influencing the costs and benefits of dispersal and there is temporal variation in environmental quality, then individuals should make their dispersal decision based solely on their assessment of current environmental conditions. However, in many organisms, an individual's own phenotype can also influence the costs and benefits of dispersal because individuals vary in a suite of morphological, behavioral, and

life-history traits that influence dispersal and/or colonizing ability (Gaines and McClenagham 1980; Dingemanse *et al.* 2003; Rehg and Sih 2004; Garant *et al.* 2005; Phillips *et al.* 2006, Duckworth and Badyaev 2007; Skjelseth *et al.* 2007; Chapter 12). If traits that alter the costs and benefits of dispersal are heritable, then these costs and benefits are likely to be similar across generations, and parents and offspring should make similar dispersal decisions. Assuming dispersal is also heritable, this sets the stage for evolution of genetic integration of these traits.

Interactions among traits that increase organismal fitness or performance can lead to selection for functional integration and trait co-expression (Lande 1979, 1980; Cheverud 1996). Consistent correlational selection on an evolutionary timescale can lead to the evolution of genetic correlations between traits at the level of the population (Houle 1991; Atchley *et al.* 1994; Cheverud 1996). Thus, one explanation for a significant genetic component to dispersal strategies is that consistent natural selection for close integration of dispersal with a suite of other behaviors and morphologies that enable successful dispersal has favoured across-generation constancy in the expression of dispersal.

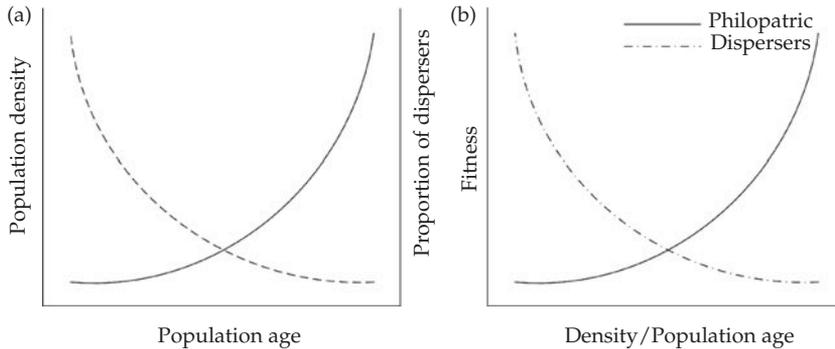
### 7.3 Correlational selection for phenotype-dependent dispersal

Dispersal polymorphisms are frequently observed in species that depend on ephemeral or successional habitat, especially when habitat patches are moderately stable allowing the persistence of multiple generations, and thus a benefit to a philopatric strategy, before the patch disappears (Harrison 1980; Crespi and Taylor 1990; Johnson and Gaines 1990; Roff 1994). These species must continually recolonize new habitat in order to survive, and older and newer habitat patches are expected to differ in density of conspecifics because new populations are typically colonized by just a few individuals, but population density often increases rapidly once a population is established (Figure 7.1A). These predictable changes in density over time mean that the earliest colonizers experience conditions that are distinct from what later generations will experience.

Because highly dispersive individuals are most likely to colonize new habitat (Hanski *et al.* 2004, Phillips *et al.* 2006) and philopatric individuals are more likely to breed in older, well-established populations, this sets the stage for correlational selection on dispersal and the traits that influence the ability to breed in different density conditions (Olivieri *et al.* 1995). Dispersers should display traits that adapt them to colonizing new areas and to breeding in low-density conditions, and philopatric individuals should display traits that adapt them to remaining near their natal site and to breeding in high-density conditions (Olivieri *et al.* 1995, Hanski 1999; Figure 7.1B). Under these conditions, correlational selection will only be detectable when comparing fitness of individuals of different dispersal strategies across populations that vary in their stage of colonization.

Some of the most dramatic examples of phenotype-dependent dispersal occur in insects where wing dimorphism is common (Harrison 1980; Roff 1986; Zera and Denno 1997). These dimorphic species depend on ephemeral habitat, and winged individuals are able to disperse over long distances to colonize new habitat patches; however, the possession of wings and the flight muscles that power them carries a significant fitness cost in terms of female fecundity (Roff 1984; Langellotto *et al.* 2000). Extensive work on wing dimorphic sand crickets by Derek Roff and Daphne Fairbairn has shown that wing morphology is genetically correlated to fecundity, muscle histolysis, and flight propensity (for an overview, see Roff and Fairbairn 2001; Roff and Fairbairn 2007).

In vertebrates, such distinct locomotor morphs within a species are rare; however, dispersal is often correlated with behavioral, physiological, or life-history traits, such as aggression, cooperative behavior or reproductive investment, rather than morphological traits (Gaines and McClenagham 1980; Dingemanse *et al.* 2003; Duckworth and Badyaev 2007; Skjelseth *et al.* 2007; Chapter 12). Thus in vertebrates, correlational selection, rather than targeting co-expression of dispersal behavior and locomotory performance, may more commonly target co-expression of dispersal and traits that influence either colonizing ability or the ability to



**Figure 7.1** Conceptual framework for understanding the link between correlational selection on dispersal and other traits in the context of species that depend on ephemeral habitat. (a) During the process of colonizing new habitat patches, density of conspecifics should increase with population age (solid line) and proportion of dispersers should decrease with population age (dashed line) because new populations are colonized solely by dispersers and the proportion of dispersive individuals in the population decreases as offspring from the initial colonizing generations are recruited into the population as breeders. This sets up a situation where dispersive and philopatric individuals experience predictable differences in population density during the process of colonization. (b) Correlational selection for distinct dispersal strategies depends on population density and age. The link between population age and density means that dispersers should evolve a strategy (a suite of integrated behavioral, life-history, and morphological traits) that enables them to have high fitness in new populations where density of conspecifics is low, and philopatric individuals should evolve a strategy that enables them to have the high fitness in high density conditions that are commonly found in older populations. Trade-offs between dispersal-related traits and fecundity (see text) should prevent individuals from performing well in all density conditions.

perform in a high- or low-density population. Lack of distinct, easily observable, dispersal morphs in vertebrates may explain why phenotype-dependent dispersal is less well-documented in these groups compared to insect taxa. Moreover, the difficulty of recognizing and measuring the behavioral and life-history traits associated with dispersal in vertebrates has made studies of the genetic basis of phenotype-dependent dispersal difficult. The most detailed examination of the ecology and genetics of distinct dispersal strategies in a wild vertebrate has been carried out in western bluebirds (*Sialia mexicana*). We have used large-scale field experiments, measures of lifetime fitness, and pedigree-based quantitative genetic studies to show that western bluebirds have evolved distinct genetically integrated dispersal strategies that enables them to colonize new habitats continually while maintaining populations in older habitat patches.

#### 7.4 Ecological context for evolution of distinct dispersal strategies in western bluebirds

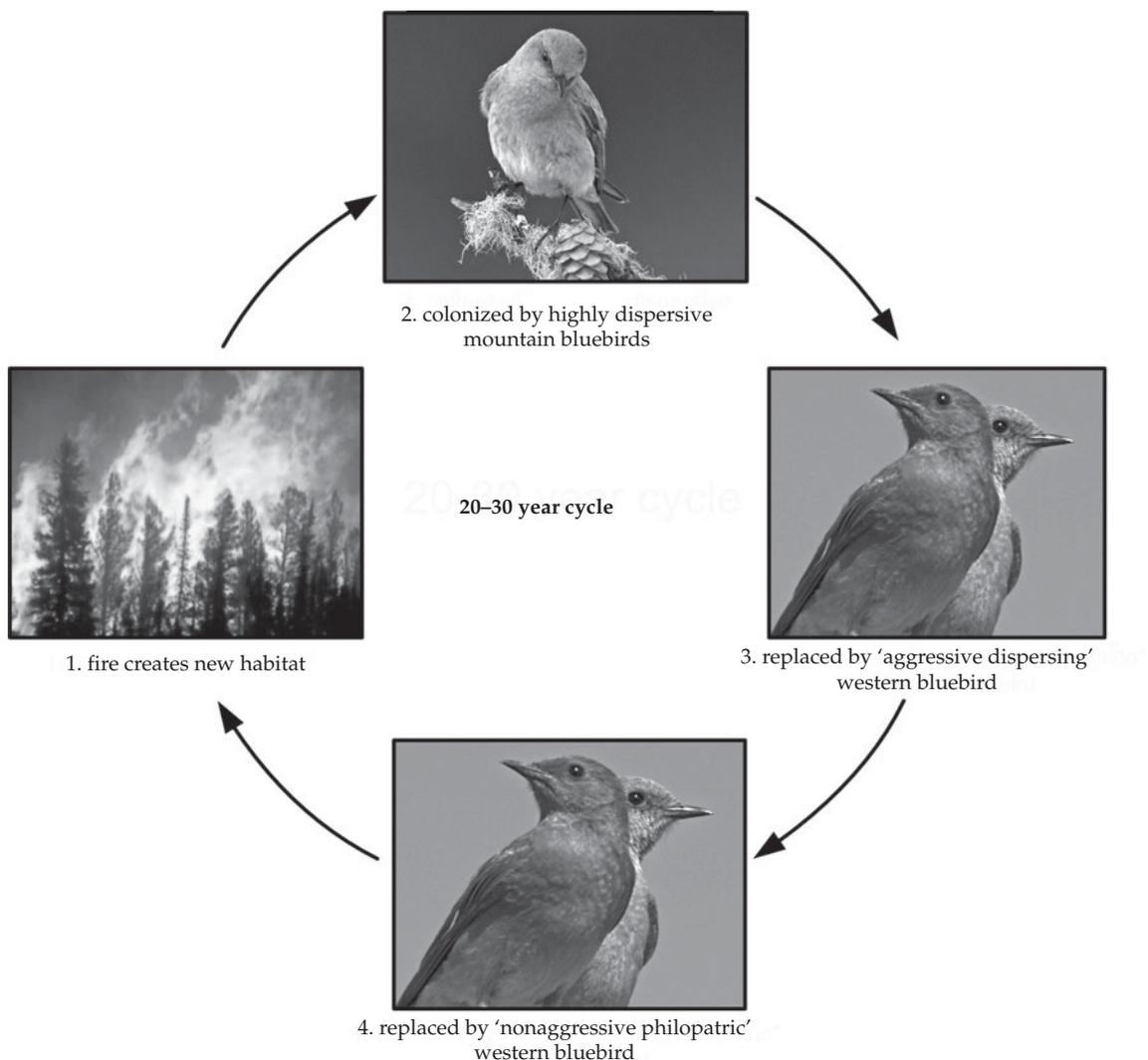
Western bluebirds depend on tree cavities to breed—a limiting resource that historically was patchily

distributed and ephemeral. Nest cavities occur at high densities following forest fire which creates suitable habitat for bluebirds by opening up understory vegetation and creating dead snags. Eventually, as the forest regrows, bluebirds are no longer able to breed in these habitat patches because snag density decreases and regrowth of the forest eliminates the open meadows bluebirds depend on to forage for insect prey (Power and Lombardo 1996; Guinan *et al.* 2000). Western bluebird's sister species, mountain bluebirds (*S. currucoides*), are frequently among the earliest colonizers following forest fires (Hutto 1995), whereas western bluebirds often show delayed patterns of colonization (Kotliar *et al.* 2007; Saab *et al.* 2007). Competition for nest cavities among these and other secondary cavity nesting species is intense and often involves aggressive displacement (Gowaty 1984, Newton 1994, Merilä and Wiggins 1995; Duckworth 2006b). Western bluebirds, while less dispersive and slower to find new habitat, are on average more aggressive than mountain bluebirds, and rapidly displace them when they colonize newly available habitat (Duckworth and Badyaev 2007).

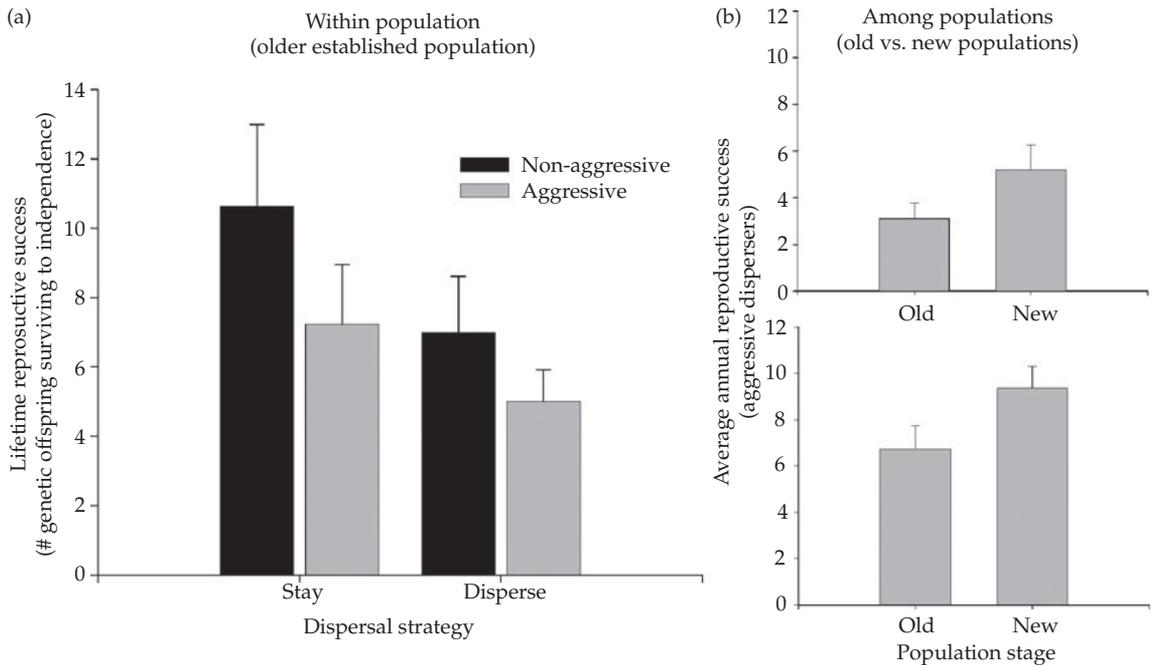
The maintenance of these cycles of species replacement (Figure 7.2) depends at least partly on the evolution of two distinct dispersal strategies in

western bluebirds where highly aggressive males tend to leave their natal populations and disperse to new areas to breed; whereas, non-aggressive males tend to remain in their natal population and eventually acquire a territory near relatives (Duckworth and Badyaev 2007; Duckworth 2008). Aggression and dispersal are functionally integrated because

colonization of new populations by dispersing males requires the ability to outcompete earlier arriving heterospecific competitors for nesting sites and territories. Yet there is a trade-off between aggression and investment in parental care that results in a fecundity cost (Duckworth 2006b). Because of this trade-off, an individual's



**Figure 7.2** Ephemeral habitat and the evolution of both inter- and intra-specific differences in dispersal strategy produce cycles of species replacement. New habitat is created by fire (1), and is colonized first by highly dispersive mountain bluebirds (2). Mountain bluebirds are eventually replaced by aggressive dispersing type of western bluebird (3). In turn, aggressive dispersing western bluebirds are eventually replaced by non-aggressive philopatric type (4). Eventually, forest succession resets the cycle (steps 4 to 1). Burned forests can provide habitat for bluebirds for up to 30 years, approximately 20 bluebird generations.

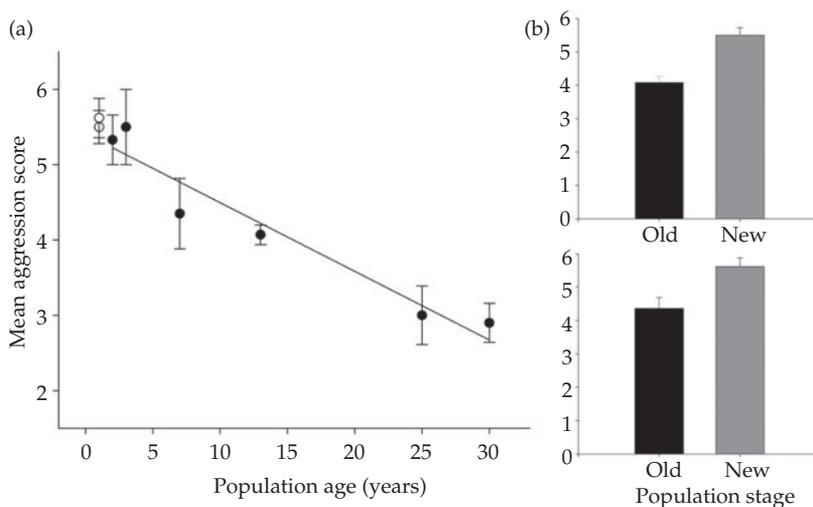


**Figure 7.3** Correlational selection on aggression and dispersal is detectable when comparing populations of differing colonization stages. (a) Within an older, well-established population non-aggressive males that were born in the population and stay there to breed have the highest fitness (measured as lifetime genetically verified reproductive success); whereas aggressive dispersing males have the lowest fitness in this context. (b) When comparing fitness of aggressive dispersers across populations of differing colonization stage, they have higher fitness (measured as average annual reproductive success) when colonizing new areas. Data show replicated results where a new population was experimentally created within a few kilometers of an older well-established population in two geographically distinct regions. Only aggressive dispersers colonize new populations, so this is the only strategy compared in this population level comparison. Figure modified from Duckworth 2008.

performance in a particular population depends on both their aggressive phenotype and population stage (Duckworth 2006a, 2008). Non-aggressive males, despite being poor competitors, benefit from remaining in their natal population where they can gain a territory by cooperating with relatives. These males have higher fitness than aggressive males in older, well-established populations but rarely, if ever, are observed colonizing new populations (Figure 7.3A; Duckworth 2008); whereas aggressive males have the highest fitness when dispersing to new populations where density of conspecifics is low (Figure 7.3B; Duckworth 2008). The exact mechanism for higher fitness of aggressive males breeding in new populations is not known; however, they are likely to perform better in these populations because they acquire territories that are twice larger than in the older, highly dense, populations and

thus have access to more resources (Duckworth 2008). In addition, the higher density of conspecifics in older populations means that aggressive males have more opportunities for agonistic encounters and thus may invest more in aggressive interactions at the expense of parental care in this context. The ecological importance of integration of these behaviors is emphasized by their role in facilitating the recent expansion of western bluebirds' range across the northwestern United States over the last 40 years (Duckworth and Badyaev 2007).

In concordance with these fitness costs and benefits, aggression and dispersal of western bluebird populations shift rapidly during the process of colonization (Duckworth 2008). Newly colonized populations comprise highly aggressive dispersers, and older well-established populations comprise less aggressive philopatric individuals (Figure 7.4).



**Figure 7.4** Newly colonized western bluebird populations were more aggressive than older, well-established populations. (a) In populations that were colonized naturally across a recent range expansion (black circles), younger populations were more aggressive than older populations. The new experimental populations in (a) (white circles) did not differ in aggression from newly colonized populations at the edge of the range. (b) Paired replicates of older, well-established, and newly created experimental populations show that new populations were more aggressive. Figure modified from Duckworth 2008.

These shifts are due to the non-random settlement of new populations by highly aggressive individuals followed by rapid decreases within these populations to lower levels of aggressive behavior (Duckworth and Badyaev 2007). Changes in aggression within populations are not due to flexibility in the expression of aggression as it does not systematically decrease with age and is not influenced by the current competitive environment (Duckworth 2006b; Duckworth and Badyaev 2007). Rapid phenotypic changes across populations are most likely due to a combination of nonrandom sorting of individuals during the initial stages of colonization in conjunction with natural selection favouring non-aggressive individuals once populations are established. Thus, these observations are concordant with the metapopulation model prediction that dispersal ability should shift rapidly as populations age (Olivieri *et al.* 1995; Hanski *et al.* 2004).

### 7.5 Proximate basis of distinct dispersal strategies: reconciling genetic variation and maternal effects

Consistent natural selection for co-expression of traits should lead to developmental and genetic

integration of their components. Thus, if selection for co-expression of aggression and dispersal has been consistent for many generations, then quantitative genetic models predict that this should lead to the evolution of genetic integration of aggression and dispersal (Houle 1991; Atchley *et al.* 1994; Cheverud 1996).

To determine whether aggression and dispersal were genetically integrated in western bluebirds, we used a complex multi-generational pedigree of individually marked western bluebirds to assess heritability of dispersal and aggression, and to determine whether the link between these traits is the result of their common dependence on genetic or environmental factors. The pedigree contained 873 individuals, spanned six generations, and contained both maternal and paternal half-sibs (due to both extra-pair paternity and divorce), as well as full and half-sibs reared in different nests (within and across breeding seasons), enabling estimates of heritability as well as genetic and environmental correlations. Analysis indicated that there was significant genetic variation for these behaviors and that they are positively genetically correlated (Duckworth and Kruuk 2009; Table 7.1), such that dispersive fathers were more likely to produce

**Table 7.1** Components of variance ( $V_A$ , additive genetic variance and  $V_R$ , residual variance), heritability ( $h^2$ ), and the phenotypic ( $r_p$ ), genetic ( $r_G$ ), and environmental correlations ( $r_E$ ) for aggression and dispersal using a bivariate restricted maximum likelihood model. Standard errors are in parentheses. (\* $P < 0.05$ , \*\* $P < 0.01$ ,  $P$  values estimated from likelihood ratio tests). Dispersal was considered a 'threshold trait' which assumes that it is underlain by a continuous distribution. Modified from Duckworth and Kruuk 2009.

Trait	Mean	$V_A$	$V_R$	$h^2$	$r_p$	$r_G$	$r_E$
<b>Aggression</b>	4.02 (0.09)	0.89** (0.32)	0.82 (0.28)	0.52 (0.17)**	0.22 (0.09) *	0.55 (0.24)*	-0.21 (0.29)
<b>Dispersal</b>	0.57 (0.04)	0.13** (0.05)	0.08 (0.04)	0.60 (0.20)**			

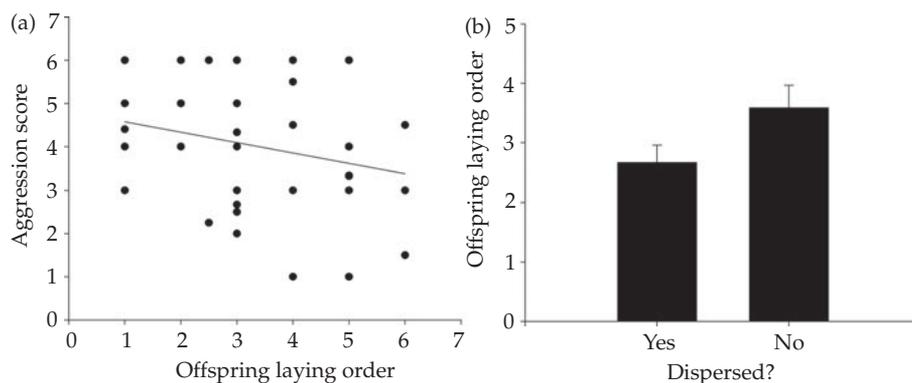
aggressive offspring and philopatric fathers were more likely to produce non-aggressive offspring. This result is consistent with the idea that long-term functional integration of these traits has led to their genetic integration.

Genetic integration of aggression and dispersal makes sense in the context of long-term selection due to functional integration of these traits; however, because the local availability of nest cavities is dynamic across years, environmental contingency in the expression of dispersal should also be favoured. For example, as density of bluebirds in newly colonized areas increases over time, resource availability decreases which means that the conditions that aggressive colonizers experience are different from the conditions experienced by later generations. Thus, even though there is selection for co-expression of aggression and dispersal which favours across-generation constancy in the link between these behaviors, there should be some environmental contingency in the specific strategy an individual pursues. Yet previous work has shown that expression of aggression in adulthood is not influenced by changes in resource availability (Duckworth 2006a). Moreover, the decision to disperse occurs during the juvenile period in the first few months of an individual's life. These observations point toward a possible role for maternal effects in the expression of dispersal strategies because if environmentally contingent expression occurs, it should have an effect early in ontogeny.

Maternal effects can enable breeding females to influence offspring phenotype in response to changes in current environmental conditions, and may be particularly important in species that experience temporal or spatial environmental variation (e.g. Sutherland 1969; Donohue 1999; Galloway 2005; Duckworth 2009). Pedigree-based quantitative genetic analysis did not detect a significant

maternal effect on aggression or dispersal; however, in subsequent analyses, we showed that this was due to a significant effect of offspring laying order that increases variance in dispersal strategy among siblings of the same nest such that males from early-laid eggs were more aggressive and dispersive in adulthood compared to males from later-laid eggs (Duckworth 2009; Figure 7.5). In quantitative genetic models, maternal effects are typically estimated by looking for a greater similarity among offspring of the same mother over and above what one would expect from their genetic relatedness (Kruuk 2004). As a consequence, maternal effects that increase variance among offspring cannot be detected using an animal model approach.

The mechanism underlying the correlation between laying order and aggression is currently not known; however, other studies suggest that hormones or other substances deposited in the egg are likely to be important. In birds, breeding females lay one egg a day and changes in female behavior and physiology during oogenesis can lead to a gradient in hormones, carotenoids and morphogens among sequentially laid eggs in a clutch (Schwabl 1993; Lipar *et al.* 1999; Reed and Vleck 2001; Badyaev *et al.* 2006; 2008) which in turn has the potential to affect oocyte sex determination (Rutkowska and Badyaev 2008) and offspring phenotype (Schwabl 1996; Forstmeier *et al.* 2004; Groothuis *et al.* 2004; Badyaev 2005; Amdan *et al.* 2006). Most importantly, it is thought that changing environmental conditions can influence fluctuations in hormone levels that occur when females are transitioning between oogenesis and egg laying, and can lead to differential allocation of maternal resources to oocytes of different ovulation order (Schwabl 1993; Groothuis and Schwabl 2002; Müller *et al.* 2002; Badyaev *et al.* 2006; Rutkowska and Badyaev 2008).



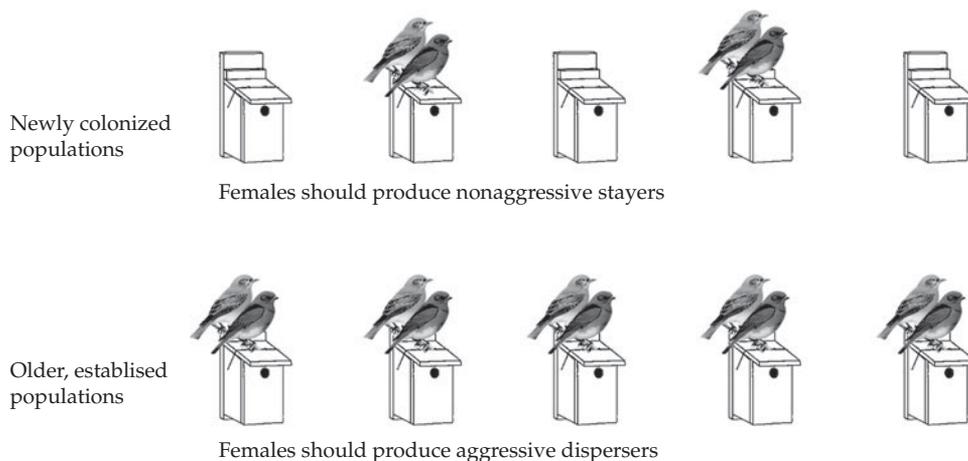
**Figure 7.5** Maternal effect on expression of offspring dispersal ability. (a) Male aggression in adulthood is significantly correlated to his laying order, and (b) Males from earlier laid eggs were more likely to disperse away from their natal territory compared to males from later laid eggs. Figure modified from Duckworth 2009.

These observations raised the possibility that early ontogeny maternal effects on offspring dispersal strategy might be adaptive in the context of the dynamic process of population colonization. To test this idea, we carried out a series of field experiments to mimic different stages of colonization within a single population (Figure 7.6). In newly colonized populations, density of conspecifics is low and there are many open territories where non-aggressive individuals can acquire a territory near their parents. Under these conditions, producing male offspring that are non-aggressive and remain in their natal population is adaptive. In contrast, in older, well-established populations, density of bluebirds is saturated and there are few, if any, territories available for male offspring to acquire near their parents. Under these conditions, producing aggressive male offspring that are good at colonizing new areas is adaptive. From the mother's perspective, the difference between these two colonization stages is the local availability of nest cavities. Thus to determine whether the link between aggression and laying order was adaptive, we experimentally mimicked these different colonization stages by manipulating the local availability of nest boxes. For one group of birds, we increased the number of nest boxes on their territory, and for the other group, we left only a single nest box.

Results of this experiment showed that females adaptively adjusted their son's dispersal phenotype

depending on the local availability of resources (Duckworth 2009). Females breeding under conditions of low nest cavity availability produced sons early in the laying order (i.e. they produced aggressive dispersers), whereas females breeding under conditions of high nest cavity availability produced sons later in the laying order (i.e. they produced non-aggressive stayers; Figure 7.7A). We also acquired data from a population in which nest cavity availability varied naturally and found the same pattern of female adjustment of offspring laying order in relation to the number of nest cavities on their territories (Figure 7.7B). The results of these studies suggested that maternal effects act as a bridge that enables the parental generation of colonizers to produce offspring that are less aggressive and more likely to remain philopatric and take advantage of the surplus of resources acquired by their parents. At the same time, by over-producing aggressive males when conditions are crowded or declining in quality, females ensure that their sons are prepared to leave their natal population, and search for and colonize a new habitat patch. Thus, maternal effects on male dispersal phenotype, by enabling close tracking of resource availability, are likely to have played a key role, not only in this species' recent range expansion, but also in this species' persistence.

Our long-term studies of western bluebirds show that the expression of dispersal strategies is

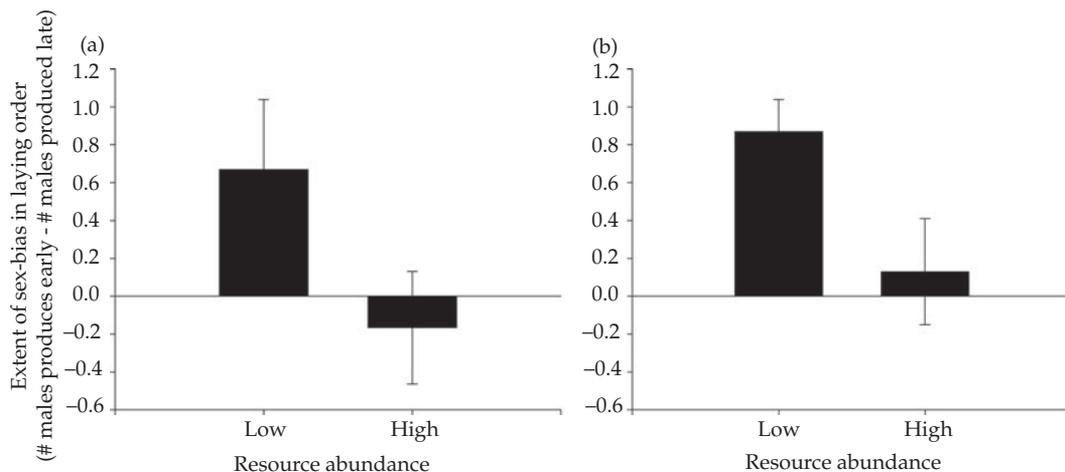


**Figure 7.6** Experimental rationale for mimicking different colonization stages. Each box represents a territory and boxes with birds on them represent occupied territories. In newly colonized populations, density of bluebirds is low and there are many open territories—in this situation females would benefit by producing nonaggressive sons that can acquire a territory nearby. In older, established populations, density is high and territories are saturated—in this situation, females should produce aggressive sons that disperse.

influenced by genetic variation, but is also contingent on local environmental conditions. Such simultaneous across-generation stability and contingency of expression suggests that while the general propensity to disperse and be aggressive may be set by genetic variation, there is some flexibility of expression such that maternal effects can act to shift offspring toward one strategy or another depending on current environmental conditions. Thus genetic integration of the strategies ensures that the link between the appropriate combination of expression is maintained across generations while maternal effects fine-tune the expression of strategies to match environmental context.

To what extent can these findings inform our understanding of the evolution of dispersal strategies in other vertebrate taxa? The link between dispersal and aggression in this system is analogous in several ways to distinct dispersal polymorphisms described in many insect and plant species (Sorensen 1978; Harrison 1980; Venable and Levin 1985; Zera and Denno 1997). In these other taxa, dispersal is linked to traits that increase either mobility or colonization ability and is not just integrated with functional traits (e.g. winged versus non-winged insect morphs), but because of a trade-off between disper-

sal-related traits and fecundity (Roff 1984) is also linked to distinct life-history strategies. In western bluebirds, aggression is costly in terms of fecundity because highly aggressive males invest less in parental care (Duckworth 2006b) suggesting that the link between aggression and dispersal is but one axis of a suite of interrelated behaviors that have evolved as a consequence of the fundamental life-history trade-offs associated with dispersal. Finally, similar to our findings in western bluebirds, species that display distinct dispersal morphologies often depend on ephemeral habitat and variation in dispersal strategy is maintained in these systems through spatial and temporal variation in habitat availability (Roff 1986; Johnson and Gaines 1990; McPeck and Holt 1992). Such spatio-temporal variation in selection pressures can not only maintain variation in these dispersal-related traits, but on a regional scale can also produce correlational selection for their co-expression (Olivieri *et al.* 1995). The similarities between distinct behavioral strategies of western bluebirds and dispersal dimorphisms of insect taxa suggest that the evolution of phenotype-dependent dispersal is a common solution to the life-history trade-offs associated with dispersal in species that depend on ephemeral habitat.



**Figure 7.7** Evidence for adaptive adjustment of offspring dispersal ability. In both (a) experimental, and (b) naturally varying populations, the order in which females produced males depended on local nest cavity availability. When nest cavity availability was low, females produced males earlier, and when nest cavity availability was high, females produced males later. This sex-biased adjustment of offspring laying order was adaptive because earlier laid males are adapted to disperse; whereas, later-laid males are adapted to remain in their natal population. Figure modified from Duckworth 2009.

## 7.6 Concluding remarks

In this chapter, I suggest that the key to understanding both across generation constancy and contingency in dispersal is the recognition that individuals vary in an array of traits that influence dispersal ability and thus often express phenotype-dependent dispersal. Because an individual's own phenotype can influence the costs and benefits of dispersal, over the long term, this may favour genetic integration of dispersal and other traits.

The widespread occurrence of phenotype-dependent dispersal brings up the question of whether dispersal is a trait in its own right or whether it is an emergent property of individuals matching their phenotypes to the environmental contexts where they will perform best. In the latter scenario, the dispersal decision is reliably transmitted across generations because inheritance of particular traits makes offspring assessment of current environmental conditions similar to their parents' assessment. If this is true, then measures of genetic variation for dispersal behavior might reflect genetic variation for the suite of traits that influence dispersal rather than dispersal behavior *per se*. This is an important distinction because it determines how

we investigate the proximate basis of variation in dispersal; i.e. whether we focus on the propensity of individuals to undertake directed movements, or focus on how behavioral, morphological and life-history traits interact to lead to a particular dispersal decision. Regardless, it is important to recognize that like most traits, dispersal tendency comprises multiple components, and thus understanding the developmental, functional, and genetic integration among these components is crucial to understanding its evolution.

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