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Eco-evolutionary dynamics: investigating multiple causal pathways linking changes in behavior, population density and natural selection

Renée A. Duckworth¹ · Stephanie M. Aguillon^{1,2}

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Abstract Correlations between population density, natural selection and phenotypic change are widespread and may comprise an eco-evolutionary feedback loop, yet we still know very little about the causes of connections between them. Isolating the mechanistic links in eco-evolutionary feedback loops, both in terms of identifying sources of variation in traits and in terms of determining how and why natural selection varies with population density, can provide key insight into avian population dynamics. Here, we summarize more than a decade of findings in western bluebirds (*Sialia mexicana*) to illustrate the multiple and potentially interacting mechanisms that can cause simultaneous changes in traits and population density. In previous work, we discovered correlated changes in aggression, population density and natural selection during the process of colonization. Here we provide evidence that density-dependent selection, maternal effects and demographic consequences of selection on aggression may all play a role in driving feedback between phenotypic change and population density. Thus, this system provides an example of the multiple mechanistic links that can produce such feedback loops and emphasizes the importance of investigating alternative hypotheses for correlated

patterns of ecological and phenotypic change even when there is strong evidence that natural selection is acting on a trait. Ultimately, identifying these mechanisms is crucial, as eco-evolutionary feedback have the potential to explain avian population cycles, range dynamics, population persistence, and even patterns of species coexistence.

Keywords Phenotype-dependent dispersal · Maternal effects · Rapid evolution · *Sialia* · Passerine bird

Introduction

Changes in the expression of traits, particularly in behavioral traits, are often a major driver of ecological dynamics such as changes in population density, species interactions, community formation and successional changes (Duckworth et al. 2015; Miner et al. 2005; Werner 1992). For example, in territorial species, because individual variation in aggression can influence the spacing of individuals, changes in aggression at the population level can influence population density (Mougeot et al. 2003). Similarly, changes in dispersal propensity, because it influences the number of offspring recruited to a population and colonizing new areas, can also influence population density and connectivity (Hawkes 2009). When such changes in behavior are driven by density-dependent selection, a feedback loop is produced whereby natural selection leads to population-level changes in behavior, which influences population density, which in turn influences selection on that behavior. Such feedback has the potential to produce fluctuations in both population density and trait expression over time and space, and thus may be a key to explaining population cycles, range dynamics, population persistence, and even patterns of species coexistence (Thomas et al.

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✉ Renée A. Duckworth
rad3@email.arizona.edu
Stephanie M. Aguillon
sma256@cornell.edu

¹ Department of Ecology and Evolutionary Biology, University of Arizona, PO Box 210088, Tucson, AZ 85721, USA

² Department of Ecology and Evolutionary Biology, Corson Hall, Cornell University, Ithaca, NY 14853, USA

2001; Turcotte et al. 2011b; Vasseur et al. 2011; Weese et al. 2011).

Recent empirical studies have confirmed that evolutionary change in traits can occur rapidly enough to influence ecological interactions (Fussmann et al. 2007; Schoener 2011), making eco-evolutionary dynamics potentially important for understanding population processes such as changes in population density over time. Eco-evolutionary feedback loops occur when strong natural selection shifts the expression of traits, which in turn influences a species' ecology, and thereby changes the direction and/or strength of natural selection on those traits (Fig. 1a; Ezard et al. 2009; Pelletier et al. 2009). Such feedback is particularly likely to occur for traits that directly affect offspring recruitment and population density, such as dispersal, life history traits, and traits that influence competitive interactions (Agrawal et al. 2013; Dunlop et al. 2009; Hanski and Mononen 2011). When these traits are heritable, and when the direction and/or strength of natural selection on them depends on population density, it will create a feedback loop in which the phenotypic response to natural selection affects population density, and the resulting change in population density, in turn, differentially selects for particular genotypes (Fig. 1a).

While theoretical studies and lab experiments have demonstrated that such eco-evolutionary feedback loops could be important for understanding and predicting ecological and evolutionary dynamics (Hairston et al. 2005;

Hanski 2012; Turcotte et al. 2011a), their prevalence in natural systems is an open question (Kokko and Lopez-Sepulcre 2007; Luo and Koelle 2013; Reznick 2013; Schoener 2011). This is, in part, because it is rarely possible to verify the causal links between trait change and ecological dynamics, since large-scale manipulation of species ecology and evolution is difficult in wild populations. At the same time, isolating the mechanistic links in feedback loops, both in terms of identifying sources of variation in traits and determining how and why phenotypic change influences ecological dynamics, is crucial for understanding the consequences of eco-evolutionary feedback loops in natural systems (Luo and Koelle 2013).

Although rapid evolutionary change in traits has received the most attention lately, any mechanism that causes a shift in the distribution or expression of ecologically important traits could have major consequences for ecological dynamics (Rossiter 1991; Svendsen 1974; Werner 1992). Alternative mechanisms include within-individual flexibility, transgenerational plasticity, phenotype-dependent dispersal, and even founder effects. Most importantly, the short- and long-term consequences of shifts in phenotype are predicted to vary strongly depending on which of these underlying mechanisms prevails. For example, trait responses due to phenotypic plasticity (Fig. 1b), because they can occur rapidly, may in fact have more profound and immediate effects on ecological and evolutionary dynamics than genetic shifts, whereas genetic changes in trait distribution might persist longer than

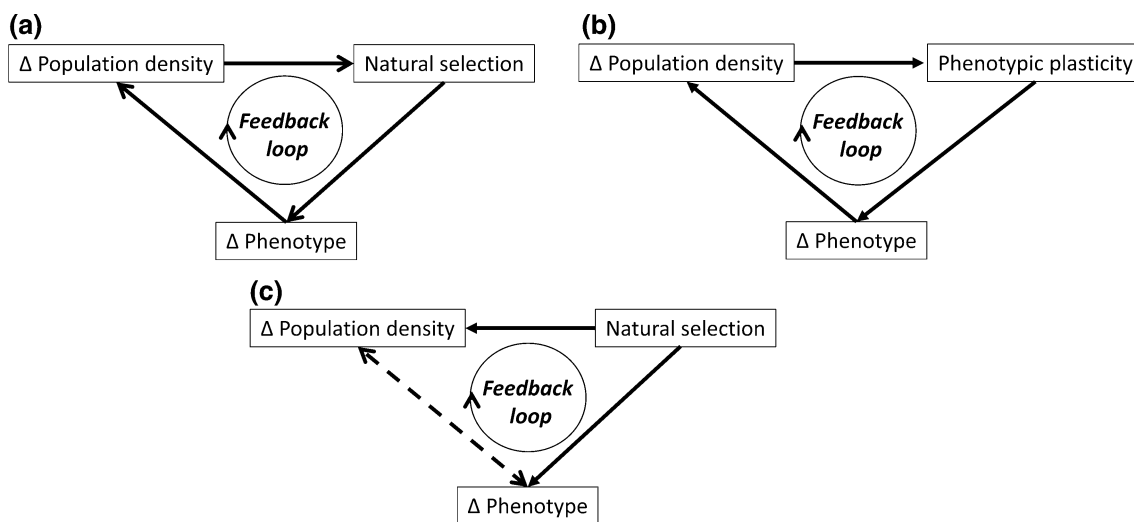


Fig. 1 Multiple pathways can produce correlations between changes in traits, natural selection and population density. *Solid arrows* show causal connections and direction. *Dashed lines and double-headed arrows* indicates correlation. **a** An eco-evolutionary feedback loop where changes in population density cause changes in natural selection, which causes phenotypic change, which in turn directly alters population density. **b** Environmental induction (e.g. through

maternal effects phenotypic flexibility or developmental plasticity) might lead to more rapid shifts in both traits and population density. **c** Natural selection can indirectly produce a correlation between population density and phenotypic change through its effects on offspring survival and recruitment, even when the trait in question has no direct impact on population density

purely phenotypic changes (Badyaev 2011; Duckworth 2009b; West-Eberhard 2003). The magnitude of differences in timing of trait shifts will ultimately depend on the type of plasticity underlying trait variation (Piersma and Drent 2003). For example, maternal effects, by generating delayed density dependence, may be an important driver of population cycles (Ginzburg 1998; Ginzburg and Colyvan 2004; Townsend et al. 2011), particularly if the environmental factor that induces the maternal effect is population density, whereas within-individual flexibility is likely to lead to more rapid fluctuations in both phenotypic change and ecological dynamics. Finally, because natural selection itself can impact population density by altering the survival or recruitment of subsets of individuals, it can produce correlations between phenotypic change and changes in population density without any functional link between them (Fig. 1c; Kokko and Lopez-Sepulcre 2007; Pelletier et al. 2007).

Here, we illustrate the potential involvement of multiple alternative mechanisms underlying population processes with a case study in western bluebirds (*Sialia mexicana*). First, we give an overview of competition and species replacement cycles that are driven by dependence on successional habitat in order to show that changes in behavior, natural selection and population density are correlated in this system. We combine new evidence with previously published work to show that eco-evolutionary dynamics might be driving these changes, but also show evidence for alternative explanations, including maternal effects and the joint effects of natural selection on population density and phenotypic change. Finally, we conclude with a discussion of the implications of these findings for future work on eco-evolutionary dynamics.

Repeated cycles of colonization and competition in bluebirds

Distinguishing between alternative mechanisms linking phenotypic and ecological change is difficult because it requires combining long-term measures of individual fitness with estimates of genetic variation in ecologically relevant traits in a system with discrete populations where changes in breeding density is easy to quantify.

The western bluebird is a secondary cavity-nesting-species that, in the northwestern United States, depends on post-fire forest (Hutto 1995). The successional and relatively isolated nature of post-fire habitat patches produces recurring colonization cycles which provide a unique opportunity to investigate the causal links between population density, natural selection and phenotypic change. These cycles are characterized by predictable changes in western bluebird breeding density and aggression over time (Duckworth et al.

2015), providing a unique opportunity to compare their interaction during distinct stages of colonization.

Natural cavities are limited, and aggressive competition among cavity-nesting birds is often intense (Brawn and Balda 1988; Duckworth 2014; Gustafsson 1986; Newton 1994). Western bluebirds' main competitor is its sister species, mountain bluebirds (*S. currucooides*). These two species have evolved distinct strategies for colonizing new habitat patches: mountain bluebirds are more dispersive (Guinan et al. 2000; Power and Lombardo 1996) and are frequently among the earliest colonizers following forest fires (Hutto 1995; Schieck and Song 2006), whereas western bluebirds show delayed patterns of colonization (Duckworth et al. 2015; Kotliar et al. 2007; Saab et al. 2007). However, western bluebirds, while less dispersive and slower to find new habitat, on average are more aggressive than mountain bluebirds and rapidly displace them (Duckworth and Badyaev 2007). These differences in competitive and dispersal behavior produce cycles of species replacement that result in predictable changes in population density and competitive dynamics.

To investigate the fitness consequences and evolution of aggressive behavior in western bluebirds, we have established a network of populations across a 150,000-km² area in northwestern Montana (Duckworth et al. 2015). New habitat patches are created by placing nest boxes in open meadows where no bluebirds are currently breeding because there are no natural nest cavities. Thus we know the exact time of habitat creation and, hence, stage in the colonization cycle, for all of the populations we study. We combine these across-populations comparisons with longitudinal data in a long-term study population where we closely track changes in aggression, population density, adult survival and offspring recruitment over time (Fig. 2). All adults and nestlings in this population have been banded since 2001, and nests are monitored regularly during the breeding season to record pair affiliations and fledging success, which is used to construct a pedigree for genetic analyses and to estimate the strength of selection on aggression (Duckworth and Kruuk 2009).

To measure aggression, we have established a standardized and reliable assay in which we simulate territorial intrusions by presenting birds with a live tree swallow (*Tachycineta bicolor*), a heterospecific nest site competitor. Using a heterospecific species to elicit aggression avoids infanticide that can occur when a conspecific is presented, and standardizes measurement of aggressive response between males and females (Duckworth 2006b). The swallow is placed in a wire cage on the nest box, and the number of times an individual attacks, flies by, or hovers near the model within a 2-min period is recorded. This measure of aggression is highly repeatable within and between contexts and years, is strongly positively

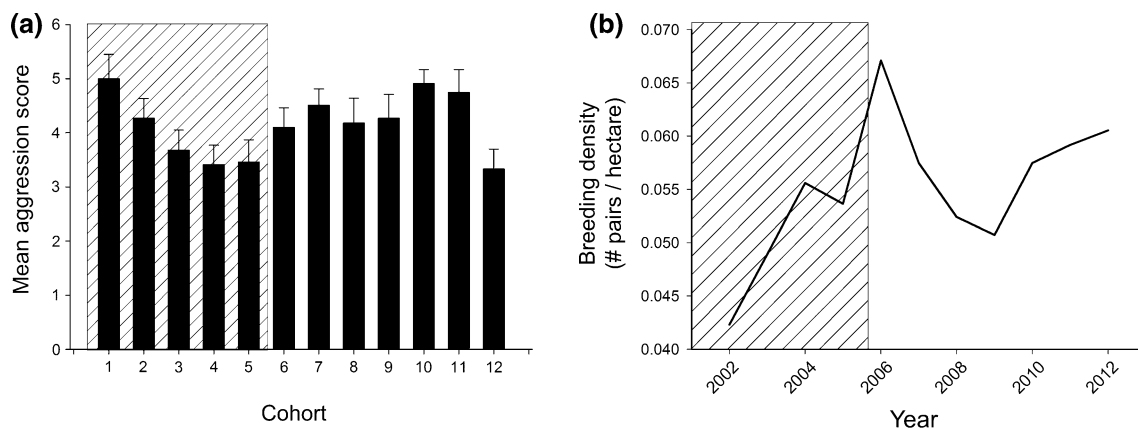


Fig. 2 Changes in **a** aggression of males and **b** population density across 12 cohorts at the long-term study site. *Shaded boxes* in each figure indicate the colonization period, characterized by rapid

population growth, which is followed by a post-colonization phase in which both density and aggression fluctuate

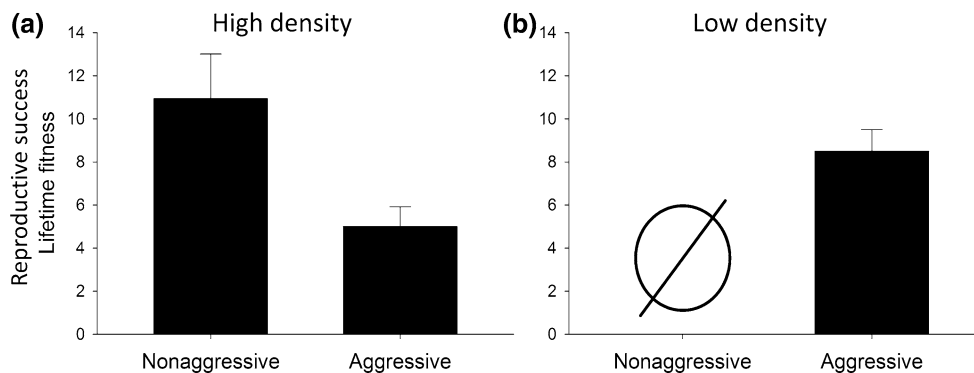


Fig. 3 Fitness consequences of aggression across **a** high- and **b** low-density populations (summarized from four populations, $N = 154$ males). Low-density populations were created experimentally by placing nest boxes in open habitat where there were no natural nest cavities and, therefore, no bluebirds breeding before the addition of nest boxes. Nonaggressive males perform best in higher-density

populations, where they are able to acquire territories by cooperating with relatives. Aggressive males perform significantly better in low-density, newly colonized populations, compared to aggressive males breeding in older, high-density populations. Nonaggressive males were not observed in these newly created low-density populations. Adapted from Duckworth (2008)

correlated with aggression toward conspecifics, and in both experimental and observational studies has been shown to be functionally linked to territory size and quality (Duckworth 2006b, 2014; Duckworth and Sockman 2012).

Using both within- and among-population data, we documented rapid shifts in western bluebird aggression during the process of colonization, such that newly colonized populations consisted solely of highly aggressive males, whereas older, well-established populations contained both aggressive and nonaggressive males and were thus less aggressive overall (Duckworth 2012). Changes in aggression across the cycle are correlated with changes in both natural selection on aggression and population density (Duckworth and Badyaev 2007). New populations start out with a low density of western bluebirds and show a rapid increase in density over a few generations (Duckworth et al. 2015). In high-density populations, nonaggressive males have higher fitness than aggressive males (Fig. 3;

Duckworth 2008). The lower fitness of aggressive males is due to a tradeoff between aggression and investment in parental care (Duckworth 2006b). This deficit largely disappears when aggressive males colonize new populations where density of conspecifics is low (Fig. 3; Duckworth 2008), suggesting that selection on aggression is density-dependent: positive or neutral in low-density populations and negative once populations become established.

Evidence of selection on genetic variation in aggression

Demonstrating eco-evolutionary feedback requires showing that natural selection produces genetic change over time. In western bluebirds, there is evidence that natural selection on aggression is at least partly involved in producing the shifts in phenotype that are observed during

population colonization. Changes in aggression within populations were not due to within-individual flexibility, as there is no substantial change in aggression in individuals across their lifespan (Duckworth 2006b; Duckworth and Sockman 2012). Observed changes in aggression occur across consecutive generations (Duckworth and Badyaev 2007), and experimental manipulations have shown that individuals do not modify their aggressive phenotype in response to changes in the competitive environment (Duckworth 2006a). Instead, data from our long-term population, where aggression and fitness were measured during rapid population growth and establishment, showed negative selection on breeding values (estimate of the genetic merit of the trait; Kruuk 2004) for male aggression ($F = 9.05$, $b_{ST} = -0.33$, $P < 0.01$, $N = 76$). Moreover, there was a tendency toward a decrease in breeding values for aggression across generations ($F = 3.24$, $P = 0.07$, $N = 82$ individuals, 6 generations) in concordance with phenotypic shifts in this population. However, given the non-significance of this result and the fact that estimated breeding values often greatly overestimate the significance of changes over time (Hadfield et al. 2010), further analysis is needed to verify a role for selection in producing genetically based changes in aggression. Moreover, the observed shifts in aggression were too rapid to be produced by selection alone (Fig. 4; Duckworth and Badyaev 2007), suggesting that other mechanisms are also important in driving changes in behavior in this system.

Alternative mechanisms for rapid phenotypic change

Many studies have found changes in phenotype that are concordant with natural selection, and have concluded that selection is driving these changes (see Reznick et al. 2004

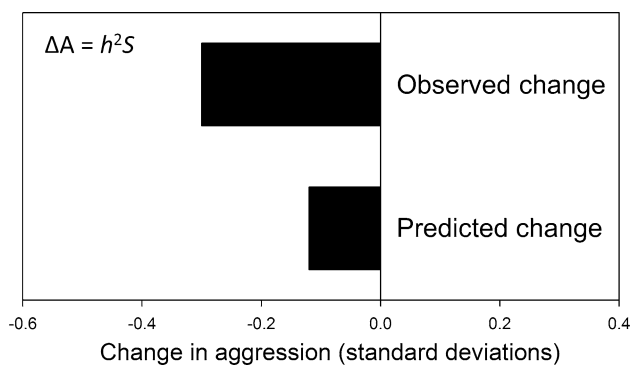


Fig. 4 Comparison of observed and predicted changes in aggression measured in standard deviations based on the breeder's equation, where ΔA is the estimated change in aggression, h^2 is the heritability, and S is the standardized selection gradient (from Duckworth and Badyaev 2007)

for review). However, theory suggests that long-term fluctuating selection should ultimately lead to the evolution of adaptive plasticity (Gomulkiewicz and Kirkpatrick 1992; Kawecki and Stearns 1993; McNamara 1998; Sultan and Spencer 2002). Therefore, observed current selection on traits could be more important in maintaining adaptive plasticity than in driving trait changes. In particular, the environmental variation that is the source of variable natural selection may affect the phenotypic distribution of a population more directly through individual or transgenerational plasticity, and this can similarly generate a feedback loop between phenotypic change and population density (Donohue 2005; Duckworth 2009b; Miner et al. 2005). Such direct feedback due to adaptive plasticity may be more prevalent for species such as western bluebirds that have experienced predictable environmental variation over an extended evolutionary period, whereas feedback due to eco-evolutionary dynamics may be more prevalent for species experiencing novel environmental variation.

In western bluebirds, there is evidence that maternal effects play a key role in generating population-level changes in aggression in response to variation in population density. Specifically, the order in which breeding females produce male and female offspring (hereafter, sex-biased birth order) strongly influences aggressive behavior in male offspring, as male progeny from clutches where males are produced late are less aggressive (Duckworth 2009a). Moreover, sex-biased birth order is correlated with population density (Duckworth et al. 2015). In low-density populations where resources are abundant, females produced a higher proportion of sons late in the laying order, and in high-density populations where resources were scarce, females produced a higher proportion of sons early. This pattern is adaptive—females are producing aggressive sons under conditions that favor a highly competitive phenotype (high-density populations) and less aggressive sons under conditions where sons can acquire territories locally (in low-density populations; Aguillon and Duckworth 2015; Duckworth et al. 2015). These findings suggest that observed rapid changes in aggression may be due to maternal effects. Because maternal effects cause a much quicker response to environmental variation than natural selection, they may reconcile the discrepancy between observed and predicted responses to selection on aggression (Fig. 3).

Linking changes in traits to ecological dynamics

Eco-evolutionary feedback requires that changes in traits affect ecological dynamics (Ellner et al. 2011), yet in the case of aggression, there are both direct and indirect mechanisms that can link the two. For example, changes in

aggression may directly influence population density if variation in aggression influences territory size. More aggressive individuals often acquire larger territories, and thus population-level increases in aggression should result in reduced population density (Adams 2001; Moss et al. 1994; Watson et al. 1994). Alternatively, changes in phenotype could be indirectly linked to changes in population density through natural selection. Natural selection influences survival and recruitment of subsets of individuals in the population depending on their phenotype, and therefore can simultaneously cause changes in phenotype and alter population growth trajectories, leading to correlations between the two (Horvitz et al. 2010; Pelletier et al. 2007). Finally, western bluebirds show phenotype-dependent dispersal: more aggressive males are more likely to disperse than less aggressive males (Duckworth and Badyaev 2007). Therefore, dispersal can simultaneously influence the relative proportion of aggressive and nonaggressive phenotypes and population density through its effects on immigration and emigration.

The relative importance of each of these direct and indirect mechanisms for producing correlations between phenotypic change and population density in western bluebirds is not known. Prior research has shown that more aggressive males acquire larger territories than nonaggressive males (Duckworth 2014); however, this relationship is complicated by colonization dynamics. Aggressive males are often breeding in newly colonized populations of very low density. Therefore, it is not clear whether the association between aggression and territory size is a direct consequence of the greater competitive ability of aggressive males or is simply a result of the dynamics of colonization which produces an immediate association between aggression and population density. If the link between the two is direct, it would follow that even outside the window of colonization, population-level aggression should be negatively correlated with breeding density in the same year, yet we found no relationship between them ($F = 0.27$, $P = 0.62$, $N = 11$ years). This suggests that aggression does not directly influence population density through its effect on territory size.

There is also evidence that aggression is linked to lifetime recruitment of offspring, as less aggressive males recruit more offspring into the population than aggressive males (Spearman's rank correlation $r_s = -0.18$, $P = 0.048$, $N = 114$). There are three different mechanisms by which this pattern could be produced. First, it could arise if nonaggressive males have higher survival than aggressive males. Such a difference would mean that nonaggressive males produce more offspring than aggressive males over their lifetime simply because they live longer. There is support for this idea, as recruitment was significantly higher in males that bred in multiple seasons

compared to males that bred in only one season ($Z = 3.51$, $P < 0.001$, $N = 114$, Fig. 5a), and males that bred in multiple seasons were less aggressive than males breeding in only a single season (Wilcoxon rank-sum $Z = -2.67$, $P < 0.01$, $N = 130$, Fig. 5b). Western bluebirds have high breeding site fidelity and are unlikely to disperse to another breeding site after their first breeding season (Guinan et al. 2000; RAD pers obs). Thus, overwinter mortality is more likely than post-breeding dispersal to account for a male's failure to return to the study site for subsequent breeding seasons, suggesting that the lower probability of aggressive males to return to the study site is due to a survival cost to aggression. If such survival costs of aggression are passed on from aggressive father to aggressive son, then differential overwinter survival of aggressive and nonaggressive sons could also contribute to observed differences in offspring recruitment.

A second potential mechanism linking aggression and offspring recruitment is phenotype-dependent dispersal. Aggression and dispersal are genetically correlated in western bluebirds (Duckworth and Kruuk 2009); therefore

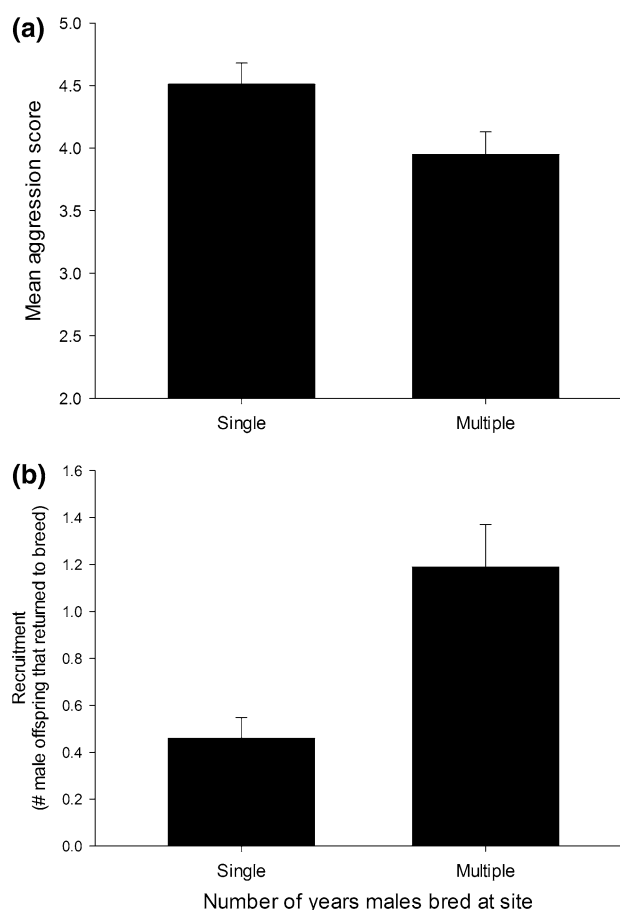


Fig. 5 Males that bred at the site for multiple years differed from males that bred at the site for only a single year in both **a** aggression and **b** recruitment of offspring

Table 1 Influence of mean population aggression (year t), offspring recruitment (year $t + 1$) and their interaction on population density in year $t + 1$ over 10 years

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

aggressive males may recruit fewer offspring to the population not just because they have lower survival, but also because their offspring inherit a higher propensity to disperse and may be less likely to return to their natal population. Finally, aggressive and nonaggressive males could differ in the number of offspring they recruit into the population if they produce different numbers of offspring in the first place. The overall number of male offspring fledged (the sex most likely to return to the natal population) was significantly negatively correlated with father aggression ($r_S = -0.331$, $P = 0.0003$, $N = 117$), as was the total number of offspring fledged ($r_S = -0.199$, $P = 0.023$, $N = 130$). Therefore, to determine whether there was a difference in recruitment among fledged offspring, we also compared the percentage of offspring recruited (the number of male offspring recruited divided by the total number male offspring fledged) and found that the correlation between aggression and recruitment was still negative, albeit not significant ($r_S = -0.22$, $P = 0.22$, $N = 114$). However, because density differed between early and late colonization stages, and because we know that dispersal behavior can be influenced by population density (Aguillon and Duckworth 2015), we also compared the relationship between recruitment and aggression within each of these stages separately, and found that the percentage of male offspring recruited into the population was significantly negatively correlated with father aggression during the post-colonization phase when density was high ($r_S = -0.285$, $P < 0.01$, $N = 82$), but not during the colonization phase when density was low ($r_S = 0.032$, $P = 0.863$, $N = 32$). At low density, individuals acquire territories that are double the size of those for individuals settling in a high-density population (Duckworth 2008), and this difference in territory size can influence offspring settlement patterns, as larger territories often have more nest cavities, thus increasing the likelihood that male offspring will settle nearby (Aguillon and Duckworth 2015).

Given that aggressive males have lower survival and recruitment than nonaggressive males, we would expect that years in which aggression is high should be followed by lower population density and that years when aggression is low should be followed by higher population density. We did find an overall effect of population-level aggression in year t on density in year $t + 1$, but only when recruitment and the interaction with recruitment were taken into account (Table 1;

overall model, GLM: $F = 18.89$, $P = 0.002$, $N = 10$ years). As predicted, density decreased following high-aggression years and increased following low-aggression years; however, these results should be treated with caution given the low sample size of this analysis. Interestingly, while recruitment is often expected to positively influence population density, we found the opposite—in years of low recruitment, density was higher, and in years of high recruitment, it was lower. This suggests that other factors such as adult survival and immigration rates must interact with offspring recruitment and need to be taken into account to better understand how aggression and population density are linked.

Overall, our long-term data suggest three potential mechanisms underlying feedback loops in this system. The links between changes in aggression and breeding density could be due to a true eco-evolutionary feedback loop, in which case natural selection on aggression is density-dependent, leading to changes in aggression, which in turn directly influence population density. While we have strong evidence of density-dependent selection in this system, evidence for the direct effects of aggression on population density is weak. Alternatively, maternal effects on aggression, which are induced by changes in population density (Duckworth et al. 2015), could produce feedback between changes in aggression and population density. In this case, natural selection may be more important in maintaining the link between population density and phenotype than in driving the changes in phenotype. Finally, natural selection might simultaneously produce phenotypic change and changes in population density, without any direct impact of aggression on density per se, through its effects on adult survival and offspring recruitment. Most likely, all three mechanisms play a role in driving the population dynamics of this system. As such, this system provides an example of the multiple mechanistic links that are possible in the generation of feedback loops and emphasizes the importance of investigating alternative hypotheses even when there is strong evidence that natural selection is acting on a trait.

Conclusions

Correlations between population density, natural selection and phenotypic change are widespread (Chitty 1967; Mueller 1988; Slatkin 1979; Sokolowski et al. 1997), yet we still know very little about their causes. We suggest that evidence of

natural selection and phenotypic change are not enough to conclude that eco-evolutionary processes are driving population dynamics. Instead, natural selection may be important in maintaining adaptive trait variation, and over the long term, a fluctuating environment may lead to the evolution of adaptive plasticity (Slatkin 1979), which should ultimately produce a more direct interplay between phenotypic and ecological changes. Moreover, the majority of cases of rapid evolution involve colonization events (Reznick and Ghalambor 2001; Reznick et al. 2004), raising the possibility that eco-evolutionary dynamics are most evident when species encounter novel environmental variation. Thus, it remains an open question whether eco-evolutionary feedback loops are important for understanding the dynamics of stable populations and communities. However, even if we find that true eco-evolutionary feedback in natural populations is rare, identification of the mechanisms underlying the links between natural selection, phenotypic change and population density still holds broad relevance for understanding ecological dynamics across a wide variety of systems in which population growth and individual variation in traits are correlated. In fact, we may find that in populations that experience predictably varying environments, adaptive plasticity is the most common cause of feedback dynamics.

Identifying causal links underlying these dynamics in natural populations is a tall order, yet avian systems are uniquely positioned to lead the way in advancing this field. Perhaps more than any other vertebrate taxa, birds have been the focus of long-term studies of individually marked populations for decades. Most birds are diurnal and easy to observe, making it possible to assess the behavior of marked individuals in order to discern the impact of behavioral changes on population dynamics. Moreover, because it is possible to follow individuals and family groups of many species throughout their lives, avian systems have a long history of quantitative genetic research and thus provide a unique opportunity to gain a better understanding of how trait variation contributes to population growth.

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