

EVOLUTIONARY ECOLOGY

Cycles of species replacement emerge from locally induced maternal effects on offspring behavior in a passerine bird

Renée A. Duckworth,^{1*} Virginia Belloni,^{1,2} Samantha R. Anderson¹

An important question in ecology is how mechanistic processes occurring among individuals drive large-scale patterns of community formation and change. Here we show that in two species of bluebirds, cycles of replacement of one by the other emerge as an indirect consequence of maternal influence on offspring behavior in response to local resource availability. Sampling across broad temporal and spatial scales, we found that western bluebirds, the more competitive species, bias the birth order of offspring by sex in a way that influences offspring aggression and dispersal, setting the stage for rapid increases in population density that ultimately result in the replacement of their sister species. Our results provide insight into how predictable community dynamics can occur despite the contingency of local behavioral interactions.

Interactions among individuals often drive population- and community-level patterns (1, 2), and in turn, community dynamics and species interactions can affect individual variation in traits (3). Understanding these reciprocal feedbacks requires knowledge of the mechanisms underlying trait variation (4, 5). Maternal effects can link phenotypic changes and environmental conditions across generations, making them a potentially important driver of population dynamics (6–9). In particular, offspring dispersal and competitive ability often depend on conditions experienced by the mother (10, 11) and adaptively track changes in population density and resource abundance (12–15). The evolution of such adaptive responses requires a reliable link between the cue that induces the response and the environment in which the induced phenotype functions (16–18). Yet it is not clear how environmental variation can predictably trigger appropriate changes in phenotype.

Here we show that successional replacement of mountain bluebirds (*Sialia currucoides*) by their sister species, western bluebirds (*S. mexicana*), emerges as an indirect consequence of changes in competition experienced by western bluebird females and its impact on levels of aggression and dispersal in their offspring. The two species' ranges overlap in the northwestern United States, where they aggressively compete for nest cavities in successional post-fire habitat (19). Mountain bluebirds, the more dispersive species, colonize newly created habitat patches first but are eventually replaced by the slower to arrive (20–22), but more aggressive, western bluebirds (Fig. 1) (23). Differences in competitive ability and dispersal propensity produce cycles of species replacement that result in predictable changes in breeding

density and competition for nest sites (Fig. 1) (24). An important part of this cycle is changes in western bluebird behavior over time: New habitat is colonized by aggressive dispersing males, and the proportion of nonaggressive-philopatric males increases over time (24). Maternal effects adaptively influence aggression and dispersal

in western bluebirds, because the birth order of male offspring is negatively correlated with aggression and dispersal in adulthood (fig. S1) (25), and females produce a greater proportion of sons late in a clutch, when nest cavities on their territories are abundant, and a greater proportion of sons early in a clutch, when nest cavities are scarce (25). However, it is unclear how these maternal effects are induced and whether they mediate changes in aggression and dispersal during the process of colonization. To investigate this, we measured sex-biased birth order within and across populations that varied in colonization stage, experimentally manipulated nest cavity density to determine its effects on female behavior, and assessed the maternal allocation of androgens to eggs.

If maternal effects are driving changes in competitive ability and dispersal over time, then females breeding in newly colonized populations should produce a higher proportion of males later in a clutch as compared to females breeding in older populations. Comparison of sex-biased birth order (percentage of males laid in fourth to seventh position) of clutches ($N = 106$) across six populations (26) that varied in colonization stage (Fig. 2) revealed that, in populations with a low density of breeding western bluebirds, females produced more sons late in a clutch as compared to populations with a high density [Spearman's rank correlation (r_s) = -1.0,

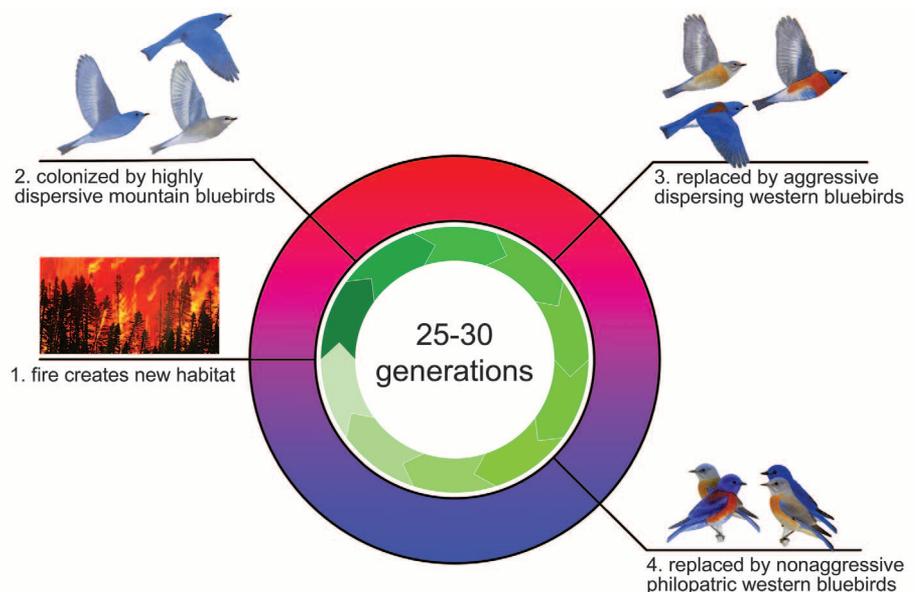


Fig. 1. Cycles of bluebird species replacement in post-fire habitat. New habitat is produced by fire (1) and colonized first by mountain bluebirds (2). Mountain bluebirds are replaced by aggressive dispersing western bluebirds (3), which in turn are replaced by nonaggressive philopatric individuals (4). Shading from red to purple indicates changes from high (early stages) to low (late stages) western bluebird aggression that are associated with increases in breeding density (24). The inner green ring indicates the predictable decrease in nest cavity availability as breeding density increases; darker arrows indicate greater resource availability. Post-fire forests provide habitat for up to 30 years. These cycles can be experimentally induced by creating new habitat, using nest boxes placed in open meadows where there are no natural nest cavities (24).

¹Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA. ²Department of Tropical Medicine, School of Public Health and Tropical Medicine, Tulane University, New Orleans, LA 70112, USA.

*Corresponding author. E-mail: rad3@email.arizona.edu

$P < 0.01$; Fig. 3A]. Across populations, the breeding density of western bluebirds was negatively correlated with the proportion of breeding mountain bluebird pairs ($r_s = -0.83$, $P = 0.04$), leading to a positive correlation between sex-biased birth order and mountain bluebird presence ($r_s = 0.82$, $P < 0.02$; Fig. 3A).

From among-population patterns, the cue that induces females to modify sex-biased birth

order is unclear because multiple factors vary with population age. To disentangle these factors, we measured sex-biased birth order over 10 years in a population from which mountain bluebirds had already been excluded (26). At this site, the typical association of nest cavity availability and breeding density was reversed through the addition of nest boxes (fig. S2). Whereas under natural conditions the number of available nest

cavities decreases as western bluebird population density increases, we increased nest cavity availability as western bluebird density increased (fig. S2). In contrast to the among-population pattern, in years of high conspecific density, females produced a higher proportion of sons late in a clutch [$F = 8.54$, standardized regression coefficient (b_{ST}) = 0.72, $P = 0.01$, $n = 10$ years, 190 nests]. However, this correlation was driven by an association of nest box density and sex-biased birth order ($F = 24.59$, $b_{ST} = 0.89$, $P = 0.001$; Fig. 3B): In years of high nest box density, females produced more sons late in a clutch, making nest box density a better predictor of sex-biased birth order ($t = 5.21$, $b_{ST} = 1.25$, $P = 0.001$) than conspecific density [t statistic (t) = -1.54, $b_{ST} = -0.36$, $P = 0.17$]. These patterns suggest that cues related to nest cavity availability, rather than the number of bluebirds in an area, induce the maternal effect.

How could the simple presence of unoccupied nest cavities trigger the adaptive adjustment of offspring phenotype? Western and mountain bluebirds defend exclusive territories, and the majority of competitive interactions among bluebirds occur in March and April, well before the onset of oogenesis, making them rare during the period when effects on sex-biased birth order are most likely (fig. S3). However, bluebirds defend their primary cavity throughout the breeding period from other species, and the peak of these non-bluebird intrusions overlaps with oogenesis (fig. S3). Thus, we hypothesized that females on territories with extra nest cavities experience differential competition from non-bluebird nest site competitors.

We tested this by experimentally creating territories of high and low nest cavity availability and recording female behavior during oogenesis (26). Females breeding on territories where nest cavity abundance was increased experienced fewer attempted takeovers of their primary nest cavity by competitors (0.65 ± 0.11 /hour) than females

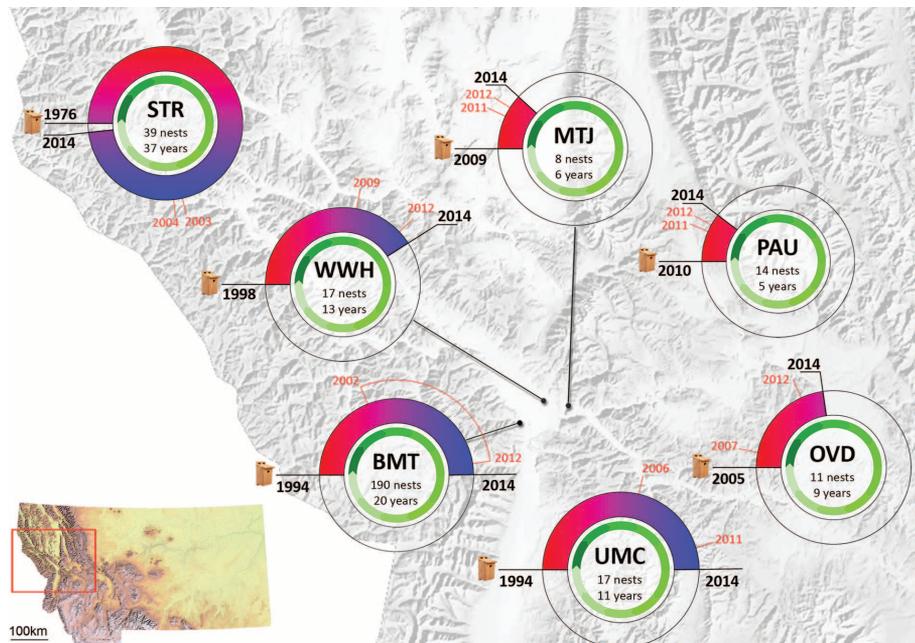


Fig. 2. Colonization stages of study populations in western Montana. The shading of the outer circle shows the start of new habitat (nest box symbol) and the population's current cycle stage (Fig. 1). Red lines transecting the outer ring indicate sampling time. The text in a circle shows population name (OVD, UMC, PAU, WWH, MTJ, and STR), sample size, and time since western bluebirds' colonization.

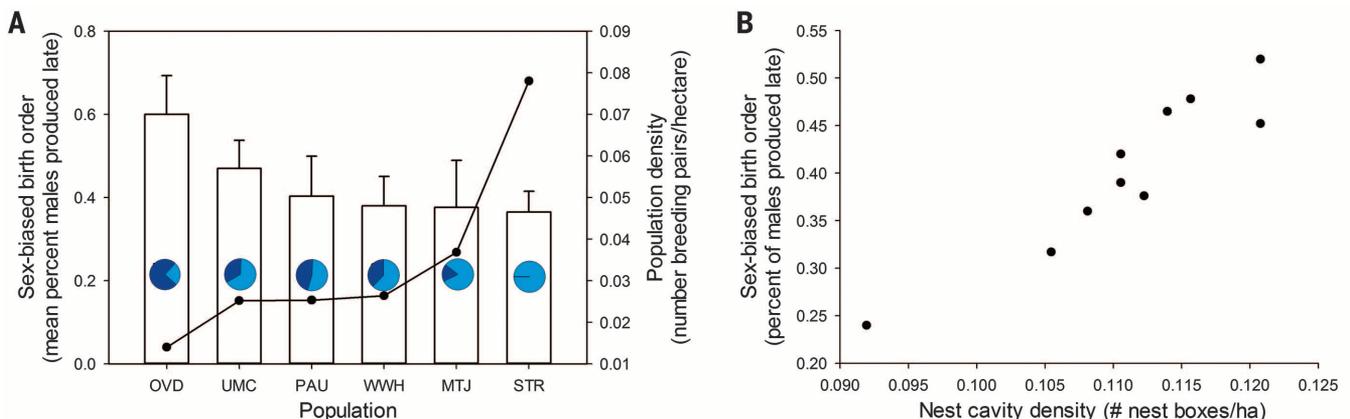


Fig. 3. Among- and within-population variation in sex-biased birth order. (A) Sex-biased birth order (bars with standard errors) was negatively correlated with conspecific density (dotted line) and positively correlated with the presence of mountain bluebirds (pie charts). Dark and light blue indicate the percent of territories occupied by mountain and western bluebirds, respectively. (B) In years of high nest cavity density, in which nest sites were abundant, females produced sons later in the clutch as compared to years of low nest cavity density ($n = 10$ years).

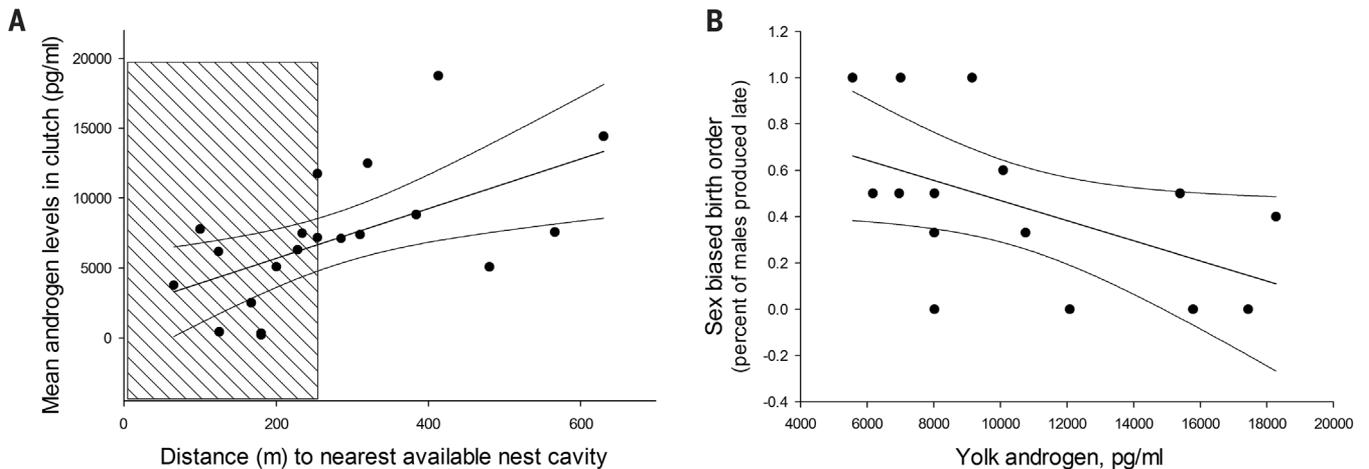


Fig. 4. Androgen allocation to a clutch is a key link between sex-biased birth order and resource availability. (A) Mean androgen levels were positively related to the distance to the nearest unoccupied nest cavity. The hatched area indicates distances within a typical bluebird territory. (B) Clutches in which females produced sons late in the birth order contained less androgen than did clutches in which females produced sons early. Shown are 95% confidence intervals.

on control territories, which had only a single nest cavity ($1.75 \pm 0.42/\text{hour}$; $t_{52} = -2.50$, $P < 0.02$). Intrusion rates of competitor species and female aggressive response rates were correlated ($r = 0.90$, $P < 0.0001$), so that females on multicavity territories engaged in fewer aggressive interactions ($0.73 \pm 0.15/\text{hour}$) than did females on single-cavity territories ($1.70 \pm 0.42/\text{hour}$; $t_{52} = -2.17$, $P < 0.05$). In vertebrates, engaging in aggressive interactions influences physiology, such as the concentration of circulating steroid hormones (27, 28), which can influence both sex-biased birth order and maternal allocation of hormones to eggs (29, 30).

To determine whether variation in the local competitive environment influenced females' deposition of hormones in eggs, we used enzyme immunoassays to measure yolk androgens (26)—which are known to have both short- and long-term effects on offspring competitive behavior (31, 32)—from 20 clutches of eggs collected from a population in which nest cavity density was highly variable. Androgen allocation to eggs differed significantly among clutches (fig S4), and females with extra nest cavities allocated less androgen to their clutches than did females without extra nest cavities on their territories ($F = 9.04$, $b_{ST} = 0.58$, $P < 0.01$; Fig. 4A). To determine whether androgen variation among clutches was linked to sex-biased birth order, we biopsied yolk samples from 15 additional clutches, allowed offspring to develop normally, and determined their sex (26). Clutches with a higher percentage of males early had higher androgen levels than clutches with a higher percentage of males in later positions ($r_s = -0.54$, $P < 0.05$, $n = 15$ clutches; Fig. 4B). These results suggest that hormone allocation to egg yolk is a key link between resource abundance, sex-biased birth order, and changes in offspring behavior.

Maternally induced variation in western bluebird behavior ultimately results in the displace-

ment of mountain bluebirds, as females from crowded populations produce aggressive sons that colonize new areas. However, the cue that induces the maternal effect has no direct connection to this larger-scale pattern. Instead, the process of colonization itself sets the stage for rapid changes in aggression over time. By dominating mountain bluebirds and acquiring large resource-rich territories (19), the colonizing generation creates the environment that induces rapid changes in offspring aggression and population growth. As habitat patches become crowded, females then produce aggressive sons, which disperse and colonize new areas, restarting the cycle. The extreme limitation of nest cavities for secondary cavity-nesting species means that there will always be competitor species intruding on bluebird territories, making competitive interactions over nest sites a reliable cue of the availability of parental resources. Thus, our results provide insight into how predictable community dynamics can occur despite the contingent nature of local-scale behavioral interactions.

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