

PERSPECTIVES

ECOLOGY

Mothers shape ecological communities

Individual hormonal responses affect the distributions and abundances of bird species

By Ben Dantzer

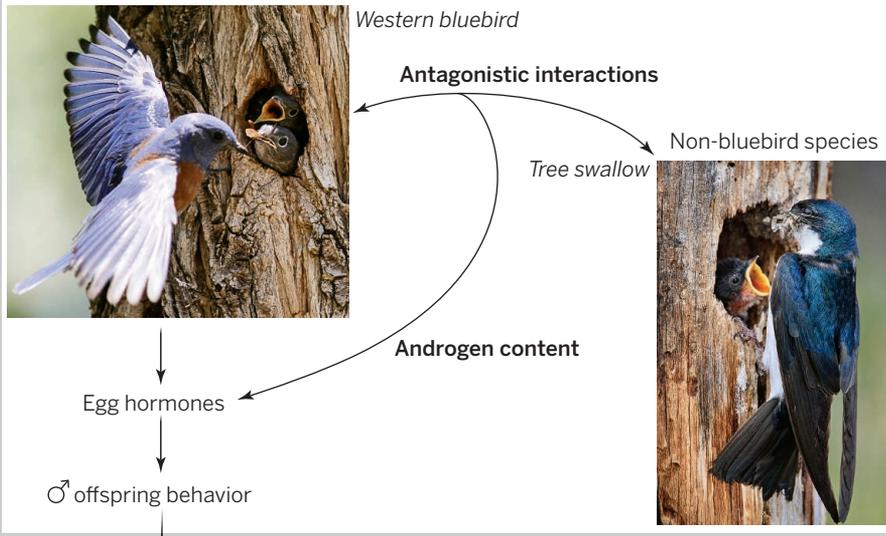
The species assemblages that make up ecological communities change over time (1), in part as a result of interactions among species such as predation and competition. However, it is often not clear how interactions among individuals scale up to affect broader ecological processes such as changes in species assemblages (2, 3). On page 875 of this issue, Duckworth *et al.* (4) provide field evidence for how individual competition between members of different bird species leads to changes in community composition. The key to these observations lies in maternal hormone changes that affect their sons' behavioral characteristics.

In western North America, forest fires create new habitat for passerine birds. Mountain bluebirds colonize these post-fire habitats before their sister species, the western bluebirds (see the photo) (5–7). These two bluebird species and other bird species compete for access to nest cavities that they need for reproduction but that are created by other species. Duckworth *et al.* use long-term data from multiple post-fire habitats in Montana to show that there is a predictable pattern of bluebird species replacement in post-fire habitats. Mountain bluebirds first colonize post-fire habitats but are eventually replaced by more aggressive western bluebirds that arrive from areas with high western bluebird densities. These more aggressive western bluebirds are eventually joined and then replaced by less aggressive and less dispersive western bluebirds. As western bluebird densities increase in the newly colonized areas, the cycle of species succession resets, and more aggressive dispersive males are again produced.



A male western bluebird at his nest.

Older post-fire habitats



Newer post-fire habitats



Disperse and displace

From individual to large-scale effects. Duckworth *et al.* (4) show that female western bluebirds experiencing increased conflict with individuals from non-bluebird species have more androgens in their eggs and produce sons that hatch early. These males are more aggressive and disperse to newer post-fire habitats, where they displace mountain bluebirds. Non-bluebird species thus indirectly affect (13) the distribution of mountain bluebirds. This hormone-mediated maternal effect on the behavior of individual male offspring in turn affects higher ecological scales by influencing the distribution and abundance of bluebird species in these communities.

Could maternal effects explain this cycle of bluebird succession? Mothers can induce pronounced changes in offspring characteristics (8). Previous work in wild animals has shown that such maternal effects can promote beneficial changes in offspring characteristics in anticipation of competitive environments and alter the evolutionary response to natural selection (8–10). Maternal effects can also affect population dynamics in laboratory studies (11), but evidence that they can influence ecological processes in natural populations has remained elusive.

Duckworth *et al.* now show that maternal effects can indeed have important ecological consequences in the wild (see the figure). In western bluebirds, eggs hatch

asynchronously. Males that hatch early tend to be more aggressive and are more likely to disperse to post-fire habitats occupied by mountain bluebirds (5–7). The aggressive male western bluebirds that first disperse to these habitats acquire large territories by outcompeting mountain bluebirds (5–7). In Duckworth *et al.*'s study, western bluebird mothers in older populations with high western bluebird densities produced sons earlier in the hatching order, and these sons were more aggressive and likely to disperse.

Same-species population density is often thought to be a cue that induces such maternal effects (10). However, in natural populations, limited resources and population density often covary, necessitating experimental manipulations (10). Duckworth *et al.* decoupled the relationship between western bluebird density and nest cavity availability by experimentally increasing

nest cavity availability for some females but not others. Females in high-density populations that had extra nest cavities on their territory produced fewer males that hatched early. This suggests that nest cavity availability (rather than population density itself) induces this maternal effect.

How do changes in nest cavity availability experienced by the mother translate into alterations in male offspring behavior? Ecological cues affecting maternal physiology can induce adaptive changes in offspring characteristics in preparation for competitive environments (8, 10). As Duckworth *et al.* show, females that experienced more antagonistic interactions produced clutches of eggs containing higher androgen hormone levels; males in these clutches tended to hatch earlier.

Maternal effects are often thought to be induced by competition with members of the same species over limited resources (8, 10). Surprisingly, antagonism from a non-bluebird species appears to trigger this maternal effect in female western bluebirds. The level of conflict with non-bluebird species was highest during egg production, whereas conflict experienced from members of the same species peaks several months prior when nests were being built (4). This is important because androgens in bird eggs accumulate during oogenesis (12). Non-bluebird species thus have indirect effects (13) on bluebird communities by influencing the hormone levels of eggs produced by western bluebird mothers.

The results show how interactions among individuals at a small spatial scale affect the organization of ecological communities at broader spatial scales through the influence of mothers on offspring behavior. The experiments by Duckworth *et al.* (4) and others (8–11) indicate that the influence of mothers on offspring characteristics likely transcends generations and ecological scales. ■

REFERENCES AND NOTES

1. H. C. Cowles, *Bot. Gaz.* **27**, 95 (1899).
2. S. A. Levin, *Ecology* **73**, 1943 (1992).
3. G. A. Wellborn *et al.*, *Annu. Rev. Ecol. Syst.* **27**, 337 (1996).
4. R. A. Duckworth *et al.*, *Science* **347**, 875 (2015).
5. R. A. Duckworth, A. V. Badyaev, *Proc. Natl. Acad. Sci. U.S.A.* **104**, 15017 (2007).
6. R. A. Duckworth, *Am. Nat.* **172** (suppl. 1), S4 (2008).
7. R. A. Duckworth, *Philos. Trans. R. Soc. B* **364**, 1075 (2009).
8. T. A. Mousseau, C. A. Fox, Eds., *Maternal Effects as Adaptations* (Oxford Univ. Press, Oxford, 1998).
9. A. G. McAdam, S. Boutin, *Philos. Trans. R. Soc. B* **271**, 75 (2004).
10. B. Dantzer *et al.*, *Science* **340**, 1215 (2013).
11. S. J. Plaiستow, T. G. Benton, *Philos. Trans. R. Soc. B* **364**, 1049 (2009).
12. T. G. G. Groothuis, H. Schwabl, *Philos. Trans. R. Soc. B* **363**, 1647 (2008).
13. E. E. Werner, S. D. Peacor, *Ecology* **84**, 1083 (2003).

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