PNAS COMMENTARY

Arrhythmia in the earth's pulse: Bird migration timing does not track advancing spring phenology

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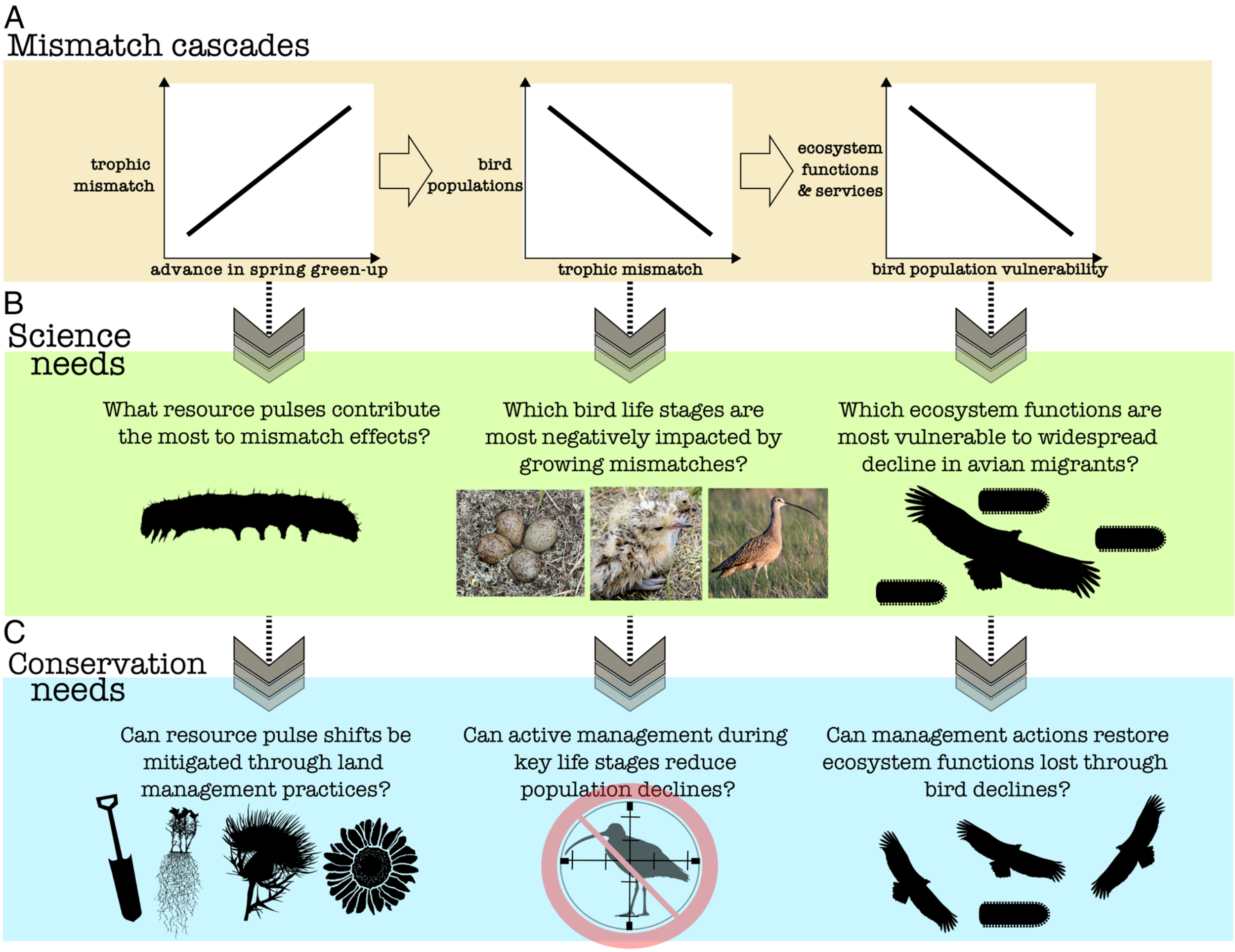

Fig. 1. The primary finding of Roberston et al. (5), depicted in (*A*) at left as increasing trophic mismatch with increases in climate-driven phenological change in green-up. These mismatches cascade into declines in populations of avian migrants (*A*) center, which, in turn, cascade into losses of ecosystem services and functions (*A*) right. Each of these consequences of the shifting phenology of spring green-up drives new or updated science needs for understanding (*B*) key resource pulses such as caterpillar phenology (*Left*); avian demography of, for example, long-billed curlews (*Center*); and the role of migrants in ecosystem services, such as the role of vultures in controlling spread of rabies in Africa [(10) *Right*] and conservation needs (*C*) such as altered land management to mitigate shifts in resource phenology (*Left*); increasing restrictions on persecution of avian migrants (*Center*); and the need to replace ecosystem services, such as control of disease spread, provided by avian migrants.

Climate warming is altering the timing and distribution of primary production across the globe and threatening the integrity of trophic systems that are highly adapted to seasonal plant phenology (1, 2). Forecasting consequences of phenological changes in productivity depends heavily on the capacity of consumers to respond (3). In temperate ecosystems, many consumers are migrants who travel long distances to exploit the spring pulse of productivity. Consequently, there has been intense research focus on the phenological dynamics of long-distance migrant birds who breed at high northern latitudes where temperatures are rapidly warming (4). Robertson et al.

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(5) make an important advance in our understanding of these dynamics by demonstrating that nearly all groups of migrant birds in North America are not keeping pace with advances in the timing of spring green-up. Rather, their migratory phenology is decoupled from current phenological trends and is better aligned with long-term averages, which lag current conditions.

Robertson et al. make an important advance in our understanding of these dynamics by demonstrating that nearly all groups of migrant birds in North America are not keeping pace with advances in the timing of spring green up.

Interest in how avian migrants sync their departures and arrivals predates our concerns over climate warming and reaches back at least centuries. A pressing open question is whether the timing of long-distance migrations is constrained by "slow processes" such as the climatological synchrony described by Robertson et al. (5) or other quantitative genetic and social factors that constrain the rate of change in migration timing. Alternatively, migration timing might be a facultative product of "fast processes" such as behavioral or developmental plasticity and can adjust quickly across the lifetimes of individuals (6). As endpoints of a gradation of outcomes, the contrast of slow vs. fast regulation of migration is useful in generating a clear dichotomous prediction. If migration timing is regulated by slow processes, it will take generations to see proportional responses to rapid directional environmental change, whereas if fast processes govern timing, environmentally appropriate migration timing would be observed in adults within seasons or across a few years (e.g., a generation) with little time lag.

There has been consensus for decades that day-length cues trigger migratory behaviors in birds and a majority of evidence suggests that long-distance migrants have stable departure dates across years and environmental conditions (7); supporting a primary role for slow processes. In contrast, a majority of studies find that long-distance migrants arrive earlier at local breeding grounds in response to annual or climate-related variations; evidence that fast processes are primary (8). One of the most consistent observations across migratory birds is that short-distance migrants more closely match annual variation in seasonal conditions than do long-distance migrants, suggesting that migration distance may co-vary with the speed of the regulatory mechanisms. This mix of evidence has led to a sense that each species (or taxonomic group) combined some slow and fast processes in coping with the need to track both the predictable progression of the season and the annual variation in seasonal conditions.

If migration timing is primarily governed by slow processes, then the current pace of phenological change will exceed the capacity of migrants to keep up, result in a decoupling of spring green-up from migration timing, and create trophic mismatches as well as a cascade of ecological and social impacts (Fig. 1). Late arriving migrants miss the peak in seasonal productivity and fail in reproduction leading to pervasive declines in migratory populations such as those recently documented (9). Alternatively, under the control of fast processes, migration timing should match the seasonal conditions—or near-term trends—and prevent severe trophic mismatches and the demographic consequences. A major advance provided by Robertson et al. (5) is the first continental cross taxa assessment of the support for these two predictions. The finding that nearly all groups of migratory birds are decoupled from ongoing phenological change suggests that migration timing is predominantly governed by slow processes and that behavioral and developmental plasticity is not sufficient to keep pace with rapid directional change in spring green up. The inference from this result is that many migrant birds are likely susceptible or already suffering the consequences of trophic mismatches.

Ramifications of trophic mismatches of migratory consumers are far-reaching and alarming for many reasons. A clear initial expectation is that an ongoing decrease in migratory bird populations will continue or accelerate. There are manifold mechanisms through which the delay in spring migration contributes to declines in bird populations. These include 1) adult survival during migration being vulnerable to fluxes in food resources that fuel their migration (11); 2) increased stress of surviving individuals creating carry-over effects that reduce breeding performance; 3) for adults who manage to arrive earlier (i.e., on-time) and advance egg-laying date, there are likely cumulative effects of shifting in egg-laying date on adult fitness; and 4) late-arriving breeders who miss the peak of food abundance will produce offspring with decreased survival or fitness. Considering Roberston et al.'s (5) sweeping finding, it now becomes imperative to assess which of these (and other) potential mechanisms of decline are most pervasive and attempt to enact conservation measures that would buy time for the most imperiled migrant bird populations.

Beyond the consequences for specific bird populations and particular mechanisms creating trophic mismatches, widespread declines in migratory bird populations will have strong implications for trophic systems and the ecosystem services that benefit humans (12, 13). Migratory birds participate in trophic systems as keystone herbivores, omnivores, or predators, and prey for other birds or mammals. Birds are also critical to many ecosystem services and are culturally and economically important for humans (14). There are examples of migratory birds of prey and insectivore having a strong influence on trophic cascades as they consume granivorous rodents and herbivorous insects, respectively (15). Since birds also transfer energy and nutrients within and among ecosystems, their loss or major change in distribution or species could drastically degrade ecosystem resilience, functions, and services (12). Seed dispersal and plant pollination are underappreciated functions of birds (16), and birds are natural pest control for important crops (13). As humans continue to increase habitat disturbance globally, intact bird communities may also provide resilience to disturbance and invasive species (17). Highly efficient scavenging species like vultures that reduce disease transmission are estimated to move a thousand tons of organic matter per year (18). Additionally, the movement of migratory birds each year also brings traveling birders that spend money on equipment, hotels, and food. In 2022, over 96 million people spent time bird watching, a major component of all wildlife-watching recreation which has an economic impact estimated at over $89 billion (19).

Robertson et al.'s (5) results further motivate the urgent need for advances in both our understanding of the impacts of phenological mismatches and for planning to mitigating or adapting to the known impacts of ongoing trophic mismatches. There is sufficient general concern over the State of the World's Migratory Species that a UN commission's recent report outlined the major threats for migratory species and identifies major areas of action for conservation (20). The recommendations are not novel but reinforce the urgency of conservation actions that reduce overexploitation, preserve key habitats, encourage safe and connected migratory corridors, restore ecosystems, and reduce light pollution. Acting on these recommendations would go a long way toward mitigating the immediate impacts of phenological decoupling and provide extra time for slow processes to catch up to current environmental conditions.

It is notable that Robertson et al.'s findings were only possible through power of open access, publicly funded (e.g., Moderate Resolution Imaging Spectroradiometery (MODIS)) and community science platforms (e.g., eBird) that have transformed understanding migratory phenology at continental scales in the past decade (21, 22). Our ability to generate new knowledge that keeps pace with the rate of environmental change depends on both support for these data platforms but also increasing their accessibility to researchers globally (23). Creating equitable access to public data is a critical need for creating a functional and rapid feedback loop where cogenerated knowledge informs conservation actions and conservation needs drive inclusive research designs. Setting priorities in science and conservation are complex socio-environmental issues in which efforts to change social expectations and individual human behavior are often the most difficult objectives. Bridging these gaps isn't impossible, but it does require a clear-eyed assessment of the consequences of continuing along the current path, which Roberston et al.'s (5) findings suggest would lead to further arrythmia between spring pulses of productivity and consumers. Widening this gap would likely exacerbate cascading consequences (Fig. 1) and be disastrous for migratory bird populations as well as many people who rely on these same ecosystems.

1. T. L. Root *et al.*, Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60 (2003).
2. C. Both, M. E. Visser, Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* **411**, 296–298 (2001).
3. H. M. Kharouba, E. Wolkovich, Lack of evidence for the match-mismatch hypothesis across terrestrial trophic interactions. *Ecol. Lett.* **26**, 955–964 (2023).
4. J. T. Morisette *et al.*, Tracking the rhythm of the seasons in the face of global change: Phenological research in the 21st century. *Front. Ecol. Environ.* **7**, 253–260 (2009).
5. E. P. Robertson *et al.*, Decoupling of bird migration from the changing phenology of spring green-up. *Proc. Natl. Acad. Sci. U.S.A.* **121**, e2308433121 (2024).
6. M. A. Verhoeven *et al.*, Age-dependent timing and routes demonstrate developmental plasticity in a long-distance migratory bird. *J. Anim. Ecol.* **91**, 566–579 (2022).
7. B. Helm, M. Liedvogel, Avian migration clocks in a changing world. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.*, 10.1007/s00359-023-01688-w (2024).
8. J. C. Wingfield, Organization of vertebrate annual cycles: Implications for control mechanisms. *Philos. Trans. R. Soc. B* **363**, 425–441 (2008).
9. K. V. Rosenberg *et al.*, Decline of the North American avifauna. *Science* **366**, 120–124 (2019).
10. L. van den Heever *et al.*, Reviewing the role of vultures at the human-wildlife-livestock disease interface: An African perspective. *J. Raptor. Res.* **55**, 311–327 (2021).
11. A. J. Baker *et al.*, Rapid population decline in red knots: Fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proc. R. Soc. Lond. B Biol. Sci.* **271**, 875–882 (2004).
12. J. R. Ali, B. W. Blonder, A. L. Pigot, J. A. Tobias, Bird extinctions threaten to cause disproportionate reductions of functional diversity and uniqueness. *Funct. Ecol.* **37**, 162–175 (2023).
13. K. J. Gaston *et al.*, Population abundance and ecosystem service provision: The case of birds. *Bioscience* **68**, 264–272 (2018).
14. C. Sekercioglu, Increasing awareness of avian ecological function. *Trends Ecol. Evol.* **21**, 464–471 (2006).
15. W. T. Bridgeland, P. Beier, T. Kolb, T. G. Whitham, A conditional trophic cascade: Birds benefit faster growing trees with strong links between predators and plants. *Ecology* **91**, 73–84 (2010).
16. T. D. Meehan, H. M. Lease, B. O. Wolf, Negative indirect effects of an avian insectivore on the fruit set of an insect-pollinated herb. *Oikos* **109**, 297–304 (2005).
17. F. Marcolin, P. Segurado, D. Chamberlain, L. Reino, Testing the links between bird diversity, alien species and disturbance within a human-modified landscape. *Ecography* **2024**, e06886 (2024).
18. M. G. Grilli, K. L. Bildstein, S. A. Lambertucci, Nature's clean-up crew: Quantifying ecosystem services offered by a migratory avian scavenger on a continental scale. *Ecosyst. Serv.* **39**, 100990 (2019).
19. U.S. Department of the Interior, "2022 National survey of fishing, hunting, and wildlife-associated recreation" (Report number 15, U.S. Fish and Wildlife Service, Washington, DC, 2022).
20. UNEP-WCMC, "State of the World's migratory species" (UNEP-WCMC, Cambridge, UK, 2024).
21. J. F. Kelly, K. G. Horton, Toward a predictive macrosystems framework for migration ecology. *Glob. Ecol. Biogeogr.* **25**, 1159–1165 (2016), 10.1111/geb.12473.
22. J. F. Kelly *et al.*, Novel measures of continental-scale avian migration phenology related to proximate environmental cues. *Ecosphere* **7**, e01434 (2016).
23. M. D. Wilkinson *et al.*, The FAIR Guiding Principles for scientific data management and stewardship. *Sci. Data* **3**, 160018 (2016).