

Comment: Population homeostasis might be an evolved adaptation*

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All populations, to be viable, must possess a capacity for positive growth. How, then, can one explain long-term stability? Hamilton and Walker (2018, *Evolutionary Ecology Research*, **19**: 85–102) propose a model, developed with pre-agricultural human biology in mind, in which stochastic events lead to frequent local extinctions. They conclude that homeostasis in human populations resulted from a positive growth rate balanced by (1) natural disasters and (2) extinctions caused by local, stochastic fluctuations. In contrast, although I realize I am in the minority, I believe that population homeostasis is an evolved adaptation. And I know of no reason to suspect that human populations should differ from other animals.

First, I base my claim on the literature. Michael Gilpin's work (1975, *Group Selection in Predator–Prey Communities*. Princeton, NJ: Princeton University Press) essentially proved that predator–prey population dynamics are inherently chaotic, and that without population-level adaptations toward homeostasis, predator and prey are headed for quick extinction. In effect, he supplied a theoretical foundation for the empirical claims made by V.C. Wynne-Edwards (1962, *Animal Dispersion in Relation to Social Behaviour*. Edinburgh: Oliver & Boyd). And, using the same logistic growth model used by Hamilton and Walker's (2018) analysis, I have argued (Mitteldorf, 2006, *Evolutionary Ecology Research*, **8**: 561–574) that logistic population dynamics always operates through delayed feedback, and the delay changes fundamentally the system dynamic, leading frequently to instabilities. These instabilities, in turn, comprise a group-selective force in favour of adaptations that modulate population growth in response to environmental conditions.

I find it an enduring irony: Wynne-Edwards, the naturalist, recorded and eloquently described abundant evidence that animals actively maintain population homeostasis in diverse circumstances. But he was tarred and feathered because he couldn't articulate a

*Editor's note: Evolutionary biology has been wending its way simultaneously down two separate paths: individual fitness and group selection. A fence separating them is made of one-way glass so that those on the individual-fitness path rarely even perceive the existence, let alone the progress, of the other. Hamilton and Walker's (2018, *Evolutionary Ecology Research*, **19**: 85–102) contribution assumes the individual-fitness path, but it does so in a way that challenges someone travelling the group-selection path to respond. In his comment, Josh Mitteldorf provides that response. – M.L.R.

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deductive theory to support what he saw. A decade later, Gilpin provided a careful and rigorous theoretical model for the evolution of population homeostasis. But he was ignored because evolutionary biologists had learned the wrong lesson from Wynne-Edwards' book. They had learned that 'group selection' was an idea that could ruin your career.

As I see it, when you put Wynne-Edwards and Gilpin together, you have a basis for understanding how stable ecosystems can evolve and persist. In particular, human hunter-gatherers have a broad array of behaviours and technologies that allow them to respond to fluctuating resource availability at time scales of hours to days, much shorter than the lag times required to induce complex dynamics in time-delayed logistic models.

The fact is that animal populations, including pre-agricultural humans, seldom rise to the level where they are drawing down a major portion of their renewable food reservoirs. In my own work, I take this fact as evidence that predators are adapted for population control. I emphasize that if predator populations ever do reach a level where prey populations are substantially drawn down, they are on a slope that pulls them toward population chaos and probable extinction. I maintain that the need to avoid population chaos is a powerful group-selective force.

Our pre-agricultural ancestors maintained population homeostasis through territoriality, the same way that most mammal and bird species do. Packs or herds or tribes all do the same. They stake out territories large enough to support their population generously and sustainably over the long term, and they actively limit their populations to what can be supported, exporting founders of new population groups that are on the lookout for new or vacated territories. This is not a passive, automatic process. Occasionally, it involves battle and conquest, but far more often it involves communication and mutual respect of boundaries. Crucially, there are (typically) large migrant populations lacking a territory that don't reproduce, but buffer the population dynamics and are ready at a moment's notice to take over territories that are vacated (e.g. Stewart and Aldrich, 1951, *The Auk*, **68**: 471–482).

Are birth rates controlled by physiology and instinct in response to the perception of crowding? This is the most controversial part of the view that population sizes are controlled by group selection. It has been observed in insects (Stevens, 1989, *Evolution*, **43**: 169–179), in mice (Christian and LeMunyan, 1958, *Endocrinology*, **63**: 517–529), and in humans (Wagner *et al.*, 1985, *Journal of Genetic Psychology*, **146**: 65–78). I believe it is universal, though I know of no review making this claim. However, as to death rates (the other side of the model) my own work has established that they are indeed an evolved mechanism of population homeostasis (Mitteldorf, 2016, *Aging is a Group-Selected Adaptation*. Boca Raton, FL: CRC Press).

Why should we think that the stability of pre-agricultural human populations is a mystery distinct from other stable ecologies with even more ancient roots?

Yet the more conventional view is that stable demographics constitute a by-product of ecological interactions, including predator–prey, with no need for group-level adaptation (e.g. Rosenzweig, 1973, *Evolution*, **27**: 89–94). In Hamilton and Walker's (2018) analysis, population instability is the result of stochastic events in the environment that are independent of the fundamental interactions (in their case, logistic) that determine the population level.

How can one distinguish empirically between these two basic models? Is there a way we can know whether population instabilities are driven primarily by instabilities in the nature of the predator–prey interaction that determines carrying capacity, or, instead, primarily by

changes in the environment that are largely independent of the target population? And can we ask experimentally whether the stable ecosystems that we observe are stable 'for free' (by the nature of their interspecific dynamics), or whether stable ecosystems require evolved adaptation, i.e. reproductive restraint and genetically determined lifespans?

