

Understanding conditions for long-period cycles in biological populations

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Population cycles have long been documented in natural systems, though most research has focused on insects, small mammals, or systems with tightly coupled consumer-resource interactions. Evidence for long-period cycles also exists for large-bodied, long-lived species, but the data are typically qualitative, in some cases deriving mainly from the knowledge of indigenous people. Density-dependent vital rates—potential contributors to population cycling—are known from long term ecological studies of Soay sheep (*Ovis aries*) and Alaskan muskoxen (*Ovibos moschatus*). Likewise, studies of bighorn sheep (*Ovis canadensis*) and roe deer (*Capreolus capreolus*) have documented so-called “cohort effects” in which birth conditions have lasting influences on fecundity and survival through accumulated body condition. However, the implications of these demographic feedbacks on the potential for periodic population dynamics have not been explored mathematically. Here, we present a synthetic model of barren-ground caribou (*Rangifer tarandus groenlandicus*), an ungulate species for which extensive knowledge from Indigenous communities suggests the existence of decades-long fluctuations in abundance that may constitute population cycling. Caribou are further theorized to be subject to both cohort effects and density dependent vital rates. Our model links these endogenous demographic factors with exogenous forcing in the form of non-periodic stochastic environmental drivers. We couple applied harmonic analysis via wavelets with global sensitivity analyses via Sobol’ indices to clarify the conditions for and characteristics of population cycles. We find that cohort effects mediating demographic rates—particularly survivorship—can induce long-period cycles across considerable regions of parameter space. Periodicity is possible under a wide

range of environmental regimes and can even arise in the absence of environmental forcing, driven entirely by cohort effects and population structure. These findings support a subset of the theories of large-scale periodic fluctuations in caribou abundance. Furthermore, our model is generalizable to other long-lived, large-bodied mammals with complex demographic structure that may be subject to cohort effects. This work represents a novel step in broadening the scope of inquiry into proximal drivers of periodic population dynamics.

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