

**IJEE SOAPBOX:  
ON THE USES AND ABUSES OF  
COMPARATIVE DEMOGRAPHY**



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In a foreign country, few pleasures can match being in the field with a local biologist, steeped in the reticulate details of local natural history and passionate about the task of understanding the rhythms of the natural world. My wife Lynne and I recently spent an enjoyable day with Professor Steven Piper exploring the splendor of the Drakensberg Mountains near Durban, South Africa, seeking out highly localized endemic species of birds with lovely names such as the Orange-breasted Rockjumper and Gurney's Sugarbird. Professor Piper is well-known in the ornithological community for his long-term population studies in southern Africa, and in particular for his studies of two endangered species of vulture found in these mountains, the Cape Vulture and Bearded Vulture. To monitor these birds, he and his assistants must put bands on the legs of adult and juvenile birds caught at the nest. To do that, they must first risk life and limb by clambering up cliffs, and then put up with the stomach-churning behavioral responses (I will spare you, the reader, the details) of vultures indignant at being manhandled. By tracking a number of banded individuals over time, vital statistics such as per capita birth and death rates can eventually be estimated. When carried out over a sufficiently long time period, and at a number of sites, a picture of how demographic processes vary over space and through time is gradually built up, with each hard-won datum implicitly representing many hours of human sweat and effort.

The literature of ecology, conservation, and wildlife biology is implicitly replete with stories like this. (I sometimes think that it would be very instructive for publications to have appendices, quantifying the magnitude of human effort that has gone into producing each figure and table.) Given how difficult it is to gather comparative demographic data, it is important to think very clearly about how such data can be used, and the conceptual traps that may arise when interpreting demographic patterns. One such trap goes as follows: It seems intuitive that if a hypothesized environmental factor impacting

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Robert D. Holt is our first invited *IJEE Soapbox* essayist. Bob is Professor of Zoology and Arthur R. Marshall, Jr., Chair in Ecology at the University of Florida, and is one of the foremost theoreticians in ecology and evolutionary biology. His research focuses on theoretical and conceptual issues at the population and community levels of ecological organization and on linking ecology with evolutionary biology. Bob is best known for his pioneering work on apparent competition, multispecies interactions in food webs (community modules) in time and space, and the evolution of niche conservatism.

mortality rates, say a toxin or an introduced predator or hunting pressure, is more effective at limiting population size in one region than another, this will be made manifest as a parallel increase in realized death rates.

This may be true, but it need not be. I have a particular interest in the role of predation in shaping species' ranges and community structure, so in the next few paragraphs I will sketch my argument in the context of how spatial variation in predation pressure maps onto spatial variation in realized mortality rates. To understand the potential importance of predation as a factor limiting and/or regulating prey populations, it is essential to place predation into the context of *all* the factors that influence prey population dynamics, and in particular to consider how density dependence is operating, and at which life-history stages. This is always the case in population biology, but it is particularly important to consider when studying population and community dynamics in heterogeneous landscapes, where characterizing spatial variation in demography is essential for understanding the system. I will illustrate this point with a simple graphical model (which to my knowledge stems from Williamson (1972)).

Consider the following scenario: there are two habitats A and B, each containing a particular predator-prey interaction. Each habitat is at its respective demographic equilibrium (allowing populations to fluctuate around their equilibria does not affect the conclusions below, at least with moderate fluctuations). Assume there is no movement between the two habitats. Habitat B has more predators, and as a consequence the prey population is lower in abundance there; indeed, I will assume this difference in predation is the *only* difference in the two habitats. Is it necessarily the case that the overall prey mortality rate will be higher in habitat B? If so, then careful comparative demographic studies can immediately provide valuable indirect insight into the importance of predation as a factor limiting population size. If not, then approaches that go beyond comparative demography alone are required.

The graphical models depicted in the panels of Fig. 1 suggest that whether or not the expected relationship between predation pressure and mortality rate holds will depend crucially on the nature of density dependence in the prey population. The figures show the basic demographic components of births and deaths in a prey population, with continuous overlapping generations. Per capita birth rates ( $b$ ) and death rates ( $d$ ) are shown as functions of prey density ( $N$ ) in each habitat. At each density, the mortality rate in habitat B is higher than in habitat A because of greater predation pressure in the former.

In Fig. 1A, I assume that the predator acts simply as a density-independent mortality factor, and that deaths are otherwise density-independent as well; graphically, this is represented as a horizontal line. The horizontal line describing death in habitat B is elevated by a constant amount above the death line for habitat A. The prey population experiences density entirely via births (e.g., due to exploitative competition for food), which in the figure implies a line of negative slope describing births versus density. A population will be in equilibrium when its birth rate matches its death rate, which graphically is given by the density at which the two lines cross. By inspection of the figure, it is clear that in the habitat with higher predation, at equilibrium, prey population size is reduced, and the realized per capita death rate indeed is elevated. So comparative demography here faith-

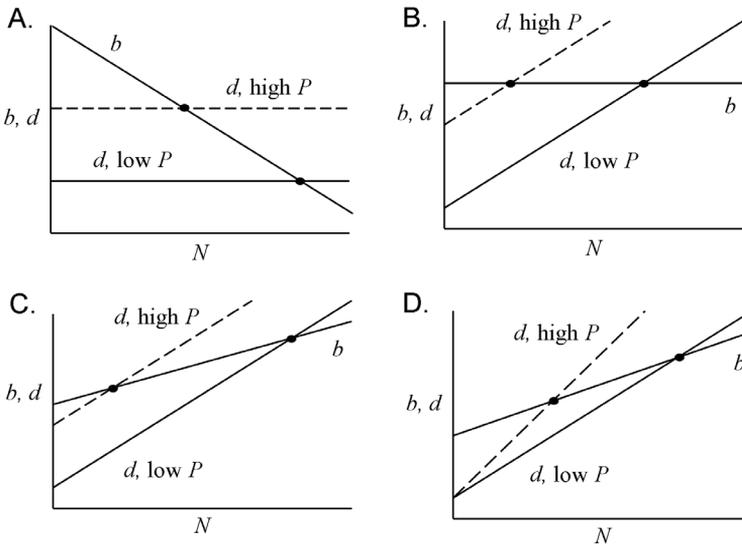


Fig. 1. Per capita birth and death rates as a function of density, for two habitats (or species) differing in predation pressure. The dots indicate equilibrium (the population size at which births equal deaths). A. Births are density-dependent, and deaths are density-independent. B. Births are density-independent. Intrinsic mortality is density-dependent, but predation acts in a density-independent manner, with a constant difference between the two habitats. C. As in B, but births are now weakly positively density-dependent. D. Predation is density-dependent, and intrinsic mortality is equal in the two habitats. Births are weakly positively density-dependent. In all cases, greater predation leads to lower equilibrium prey density. However, whether or not this is reflected in realized per capita mortality rates depends upon the nature of density dependence in the system. ( $P$  denotes predator abundance.)

fully reflects the spatial pattern of predation pressure; the realized per capita mortality rate at equilibrium is indeed higher in the habitat with higher overall predation.

Now consider Fig. 1B. Here, I assume that births are density-independent, over the range of densities of interest (so the birth lines are horizontal), and that density dependence occurs entirely via deaths. I also assume that there is positive density dependence in deaths, for reasons other than predation (e.g., intraspecific aggressive behaviors). Again, we assume that the predator itself acts as a density-independent mortality factor, and that mortality factors are additive. The line relating death rates to density thus differs by a constant amount across habitats (the two death lines are parallel). Again, the habitat with higher predation does have lower prey abundance. However, at equilibrium the death rates in the two habitats are *identical*. An exhaustive field study of comparative demography showing no difference in mortality rates would misleadingly suggest that differences in predation were not responsible for the observed difference in abundance between the two habitats.

To make life even more complicated, now consider Fig. 1C. I have now assumed that over the range of densities near carrying capacity there is *positive* density dependence in births. There are many mechanisms that can lead to Allee effects in reproduction, ranging from unbalanced sex ratios at low population size, to specific social adaptations fostering reproduction that are more efficient at higher numbers, to the simple difficulty in sexual species of finding mates at low abundance. To keep the population from exploding indefinitely, one must then have density dependence in deaths that is stronger than density-dependence in births. Graphically, the death-lines must have a steeper slope than the birth-lines. Again, I assume that predation acts as a density-independent mortality source, so the death rate as a function of density of habitat B is elevated by a constant amount across all densities above that of habitat A. As one can see by inspection of the figure, now the habitat in which prey abundance is lower because of predation, actually exhibits a *lower* rate of mortality when the population is at demographic equilibrium! A straightforward interpretation of comparative demographic data in this case might give a totally misleading picture of the importance of predation in explaining differences in abundance between habitats.

Finally, assume that density dependence arises because of predation, and that predators ignore very rare prey (so that the mortality rate at very low  $N$  is equal in the two habitats) (as in Fig. 1D). In habitat B, the death line should have a slope greater than that in habitat A, but the two lines should converge at low  $N$ . Given an Allee effect in reproduction, not only is the realized mortality rate lower at equilibrium in the habitat with higher predation pressure (habitat B), but even the percentage of mortality that can be ascribed to predation is also lower, in the habitat where predation is more important!

A final twist (not shown) would be to make density-dependence nonlinear. If negative density dependence in births is weak at low densities, but strong at high densities, then when predation is strong, small differences in mortality rates lead to large differences in equilibrium abundances. By contrast, when predation is weak, so numbers are high, equivalent differences in mortality rates may have negligible effects on equilibrium numbers.

The bottom line of this simple model is that to understand the role of predation in generating spatial pattern in prey abundance requires much more than is provided by a correlation between predator abundances or attack rates, or by measuring the net ambient mortality due to predation (or other causes). For comparative demographic data to be of greatest utility, one should embed such data in plausible models of how density-dependence is operating in the populations under study.

The graphical model of Fig. 1 could also apply to different species in the same community experiencing different levels of predation (e.g., because of body size). A species which persists at low numbers because of predation, may not have any higher realized mortality rates than an abundant species that enjoys immunity from such predation. It would be useful to repeat this exercise, paying attention to age- and size-structure effects explicitly, and factors such as nonequilibrium dynamics. Moreover, I do not want any reader to go away with the idea that comparative demographic data is useless. A sudden increase in predation pressure should in the short run be indicated reliably in elevated

mortality rates, and examining temporal trends in demography is clearly a valuable and indeed essential tool when monitoring populations trending towards extinction—as in the beleaguered vultures of the Drakensberg.

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#### REFERENCE

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