



PERSPECTIVES: ECOLOGY

Seeking New Recruits

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Why does the size of some animal populations remain remarkably stable from one year to the next, whereas the size of others fluctuates by an order of magnitude or more? It has proved remarkably difficult to determine the causes of population fluctuations or to predict changes in the size of a population (1, 2). Elucidating the patterns and processes that generate changes in population size over time is essential for the conservation of rare animal species (3). In their comparative study on page 2070 of this issue, Sæther and colleagues (4) show that differences in the population dynamics of various bird species can be predicted based on variations in their life histories.

A change in population size is simply the population size at the last count plus the number of animals that have joined minus the number that have departed. But births, deaths, and dispersal can all be affected by a wide range of environmental stresses, including disease, competition (for food, territories, or mates), and catastrophic events (both natural and man-made). Despite a huge body of literature examining aspects of population abundance, there are few studies that provide the detailed data

required to accurately identify the causes of population fluctuations. These studies usually follow many individuals throughout life, collecting information on births, deaths, and breeding attempts. However, most natural animal populations do not lend themselves to this type of detailed study.

As it is difficult to obtain comprehensive data, it would be valuable to identify general trends that correlate types of population fluctuations (for example, stable or unstable) with changes in the life history of a species (5)—the number of offspring an individual

produces at each breeding attempt, the number of times it breeds each year, and its predicted longevity. Without such broad-scale generalizations, population ecology becomes reduced to a large set of specific examples.

Sæther and colleagues (4) analyzed population size data for 12 bird species that had been collected over at least 15 years. The species ranged from the cactus finch, a small, short-lived seed-eating land bird, to the south polar skua, a large, long-lived carnivorous seabird (see the figure). The authors fitted their data on population



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The short and long of it. Changes in population size of a short-lived seed-eating terrestrial bird, the cactus finch, and a long-lived carnivorous seabird, the south polar skua, over a 40-year period. The wide fluctuations in population size for the short-lived cactus finch contrast with the minimal fluctuations in population size for the long-lived skua. Such differences can in part be explained by the species' life history—how long individuals live, when they breed for the first time, and how many offspring they produce in each breeding attempt. [Data for south polar skua courtesy of Henri Weimerkirch; data for cactus finch from (9)]

dynamics to a model called the θ -logistic (6) to determine the contribution of density dependence (how the size of the population this year affects the size of the population in future years) and environmental factors. Density dependence is driven by a range of processes but is typically associated with competition between individuals for a limited resource such as food or nesting sites. Similarly, variation in the environment (environmental stochasticity) can be generated by a range of processes, such as weather, but are independent of the size of the population. The θ -logistic is a powerful tool, as different values of the parameter θ correspond to different relationships between popula-

tion size and the rate of population growth. With a large θ , density dependence is strongest when the population is close to carrying capacity (the maximum population allowed by the environment); with a small θ , density dependence is strongest when the population is further from carrying capacity.

Sæther and co-workers show that in long-lived species like the south polar skua, density dependence has the greatest influence on the dynamics of the population when the size of the population is close to carrying capacity (θ is large). In contrast, in shorter-lived birds the effect of density dependence is greater at lower relative densities (θ is small). Similarly, the impact of environmental stochasticity varied among the bird species according to their different life histories, but had the greatest effect on short-lived species.

Sæther *et al.* go on to demonstrate that in all species, both density dependence and environmental stochasticity were significantly associated with population dynamics. There are several examples of this association in single populations (7, 8), but now Sæther *et al.* describe how their relative importance varies across a range of species.

Many bird populations are regulated by the number of territories available. Among long-lived bird species, many adults return to the same breeding territory year after year. Sæther *et al.* explore associations among survival rates, recruitment rates, and population dynamics. They found that in long-lived

species where adult return rates are high (high survival), the number of new recruits into a population was negatively correlated with the return rate of adults in each year. Thus, the number of recruits into the population was highest in years when adult return rates were lowest. In contrast, in shorter lived species with relatively low survival rates, there was a positive correlation between the number of new recruits and the return rates of adults. Thus, in years when there is high survival, there is also a high turnover of adult birds within the population as many recruits have also survived.

These results help to link demography to population dynamics: They suggest that

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in short-lived bird species the population dynamics are more strongly influenced by the recruitment of new individuals into the population, whereas in long-lived birds the dynamics are more strongly influenced by the survival rates of the adults that are already present in the population. Understanding the association between population dynamics and birth, death, and dispersal rates requires that detailed data be collected from marked individuals. This knowledge is crucial for wildlife managers, as it identifies the key demographic rate that should be targeted to reverse population declines or to prevent population eruptions. The findings of

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Sæther *et al.* demonstrate that generalizations might exist. The next step will be to attempt to confirm these generalizations with more data sets from a wider range of populations and species.

Sæther *et al.* show that there are predictable differences between the population dynamics of species with different life histories. They present a benchmark study in the relatively new field of comparative population dynamics. However, the enormous potential of this field can only be realized if data sets of sufficient length and quality continue to be collected and analyzed. Achieving this goal will require international collaboration between ecologists and statisticians, as well as the goodwill of researchers who have invested many years of their careers in collecting detailed data. Our ability to make generalizations about population dynamics will facilitate conservation efforts, and so benefit future generations.

References

1. G. M. Mace, R. Lande, *Conserv. Biol.* **5**, 148 (1991).
2. N. Owen-Smith, *J. Anim. Ecol.* **59**, 893 (1990).
3. T. Coulson *et al.*, *Science* **292**, 1528 (2001).
4. B.-E. Sæther, S. Engen, E. Matthysen, *Science* **295**, 2070 (2002).
5. S. C. Stearns, *The Evolution of Life Histories* (Oxford Univ. Press, Oxford, 1992).
6. B. E. Sæther *et al.*, *Proc. R. Soc. London Ser. B* **267**, 621 (2000).
7. H. Leirs *et al.*, *Nature* **389**, 176 (1997).
8. M. Lima, J. E. Keymer, F. M. Jaksic, *Am. Nat.* **153**, 467 (1999).
9. B. R. Grant, P. R. Grant, *Proc. R. Soc. London Ser. B* **251**, 111 (1993).

PERSPECTIVES: ENVIRONMENTAL CHEMISTRY

Tracking Hexavalent Cr in Groundwater

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Throughout the world, groundwater is used extensively as a source of drinking water. In the United States, 56% of the population rely on groundwater for their drinking water (1). Much of the groundwater extracted in North America and elsewhere is supplied by shallow aquifers, which are susceptible to the release of contaminants from industrial, agricultural, and domestic activities.

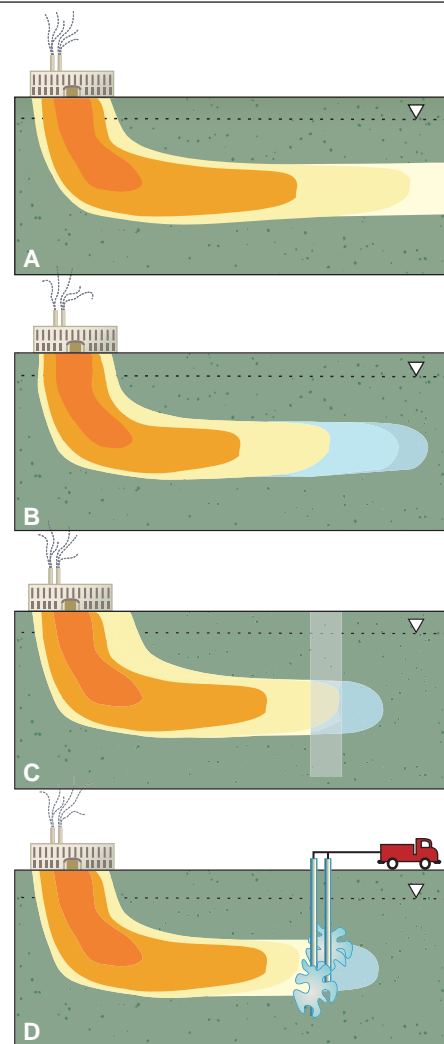
A common groundwater contaminant is chromium, which is widely used for electroplating, leather tanning, and corrosion protection (2). Chromium is the second most abundant inorganic groundwater contaminant at hazardous waste sites (3). On page 2060 of this issue, Ellis *et al.* present a technique for determining the abundance ratio of stable chromium isotopes and apply it to samples from chromium-contaminated sites (4). The technique provides an important tool for assessing the migration of chromium from contaminant sources and evaluating the effectiveness of chromium removal systems.

The oxidized, hexavalent state of Cr, Cr(VI), forms chromate (CrO_4^{2-}) or bichromate (HCrO_4^-). Chromate-containing minerals are very soluble and, because the chromate ion has a negative charge, chromate adsorption on aquifer minerals is

limited (2). As a result, chromate may be present at concentrations well above water quality guidelines and may move with the flowing groundwater in aquifers. In contrast, the reduced state, Cr(III), forms insoluble precipitates under slightly acidic and neutral conditions, limiting Cr(III) to very low concentrations in most aquifers (2). The reduction of Cr(VI) to Cr(III) thus limits both the concentration and mobility of dissolved chromium. This difference is very important because chromate is toxic and carcinogenic (5–7), whereas Cr(III) is a nutrient at trace levels.

Variations in the isotopic ratios of light elements are sensitive indicators of chemical processes that occur in natural systems. For example, the $^{34}\text{S}/^{32}\text{S}$ ratio in dissolved sulfate increases when bacteria reduce sulfate to sulfide. Ellis *et al.* (4) now show that the $^{53}\text{Cr}/^{52}\text{Cr}$ ratio also changes during reduction of Cr(VI) to Cr(III). They show that abiotic reduction of Cr(VI) resulting from reaction with the mineral magnetite, estuarine sediments, and freshwater sediments leads to a consistent $^{53}\text{Cr}/^{52}\text{Cr}$ shift. This observation indicates that $^{53}\text{Cr}/^{52}\text{Cr}$ ratios increase systematically with progressive Cr(VI) reduction in groundwater.

The conventional approach to groundwater remediation is to install a series of pumping wells, extract the water from the aquifer, and treat it with techniques previously developed for surface waters. A series of studies in the late 1980s and early



Groundwater remediation strategies. (A) No attenuation. (B) Contaminant removal by natural attenuation processes. (C) Contaminant removal using a permeable reactive barrier. (D) Injection of a reductant to attenuate the contaminant.

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