

SCIENCE'S COMPASS

tivity than is actually measured. However, the spectral weight of the quasi-particle features in the ARPES data is very small, suggesting that only a small fraction of the sample is metallic whereas the remainder is insulating. Complementary x-ray and neutron diffraction experiments (9) on the same material have provided clues to the nature of these insulating regions by revealing microscopic patches in which charge carriers are localized and form ordered arrays. The periodicity of the charge order within the arrays matches the wave vector connecting nearly flat segments of the Fermi surface determined by Chuang *et al.* It is thus plausible that the metallic and insulating states are on either side of a zero-temperature Peierls-type (10) phase transition and that $\text{La}_{1.2}\text{Sr}_{1.8}\text{Mn}_2\text{O}_7$ is in the middle of a two-phase coexistence region. The unusual line shape of the ARPES spectra [which are broad in energy but sharp in momentum space (8)], as well as some aspects of the x-ray and neutron diffraction data (9), suggest

that the coexistence may not be static and that fluctuations between nanoscale domains may persist down to 0 K. This remains a topic for future investigation.

The detailed microscopic picture obtained by Chuang *et al.* is new, but extended two-phase coexistence regimes have also been reported for a wide variety of other manganites (11). The pronounced propensity toward phase separation is at least partly due to the fact that different *d*-orbitals, with their associated lattice distortions, are available to conduction electrons in the manganites (12). This makes these materials highly susceptible to lattice strain. In the copper oxides, where these orbital degrees of freedom are largely quenched, phase separation has also been reported (13) but appears to be relatively rare. Certainly, the extremely broad ARPES spectra in the normal state of underdoped and optimally doped high-temperature superconductors cannot be attributed to phase separation. Having barely survived

in the manganese oxides, the quasi-electron is still in mortal danger in their copper-based sister materials.

References and Notes

1. S. Y. Savrasov, D. Y. Savrasov, *Phys. Rev. B* **54**, 16487 (1996).
2. T. Valla *et al.*, *Phys. Rev. Lett.* **83**, 2085 (1999).
3. A. G. Loeser *et al.*, *Science* **273**, 325 (1996).
4. M. R. Norman *et al.*, *Nature* **392**, 157 (1998).
5. P. W. Anderson, *Science* **288**, 480 (2000).
6. D. S. Dessau *et al.*, *Phys. Rev. Lett.* **81**, 192 (1998).
7. R. Joynt, *Science* **284**, 777 (1999).
8. Y. D. Chuang *et al.*, *Science* **292**, 1509 (2001); published online 26 April 2001 (10.1126/science.1059255).
9. C. P. Adams *et al.*, *Phys. Rev. Lett.* **85**, 3954 (2000).
10. As proposed theoretically by Peierls and later shown experimentally in many materials, the energy of low-dimensional metals can be reduced through a static charge or spin modulation with periodicity equal to the Fermi wave vector.
11. A. Moreo *et al.*, *Science* **283**, 2034 (1999).
12. Y. Tokura, N. Nagaosa, *Science* **288**, 462 (2000).
13. J. M. Tranquada *et al.*, *Phys. Rev. Lett.* **78**, 338 (1997).
14. I acknowledge useful discussions with D. Dessau.

Published online 26 April 2001;
 10.1126/science.1061205
 Include this information when citing this paper.

PERSPECTIVES: POPULATION ECOLOGY

Not All Sheep Are Equal

Jean-Michel Gaillard, Marco Festa-Bianchet, Nigel G. Yoccoz

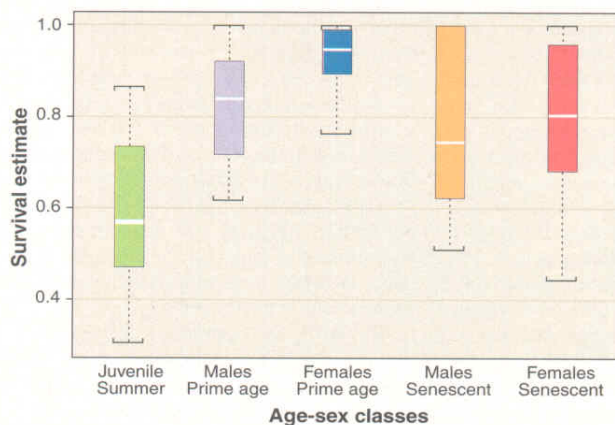
Our lives and those of large mammals are inextricably intertwined: We hunt them and spend time in zoos and wildlife parks viewing them; they feed on domestic animals, damage crops, cause traffic accidents, and may even eat the "produce" of local fisheries. Given this, it is not surprising that we are interested in ecological factors that govern the dynamics of large mammal populations (1). Whereas some large mammals are very abundant (2), others are endangered (3), spurring the need to identify the ecological factors that maintain, increase, or reduce abundance. Although many studies have tested the accuracy and precision of census methods (4), it has proved difficult to test whether yearly field counts of wild mammal populations can accurately determine the factors causing variations in population numbers (5).

J.-M. Gaillard is at the Unité Mixte de Recherche No. 5558 "Biométrie et Biologie Evolutive," University of Lyon, Villeurbanne Cedex, France; e-mail: gaillard@biomserv.univ-lyon1.fr. M. Festa-Bianchet is in the Department of Biology, University of Sherbrooke, Sherbrooke, Québec J1K 2R1, Canada; e-mail: mbianche@courrier.usherb.ca. N. G. Yoccoz is in the Division of Arctic Ecology, Norwegian Institute for Nature Research, Polar Environmental Centre, N-9296 Tromsø, Norway; e-mail: nigel.yoccoz@ninos.ninanku.no.

Such difficulties, however, have not deterred Coulson and colleagues (6). On page 1528 of this issue, they report their 11-year field study of a Soay sheep (*Ovis aries*) population on a remote island off the coast of northwest Scotland. The merit of their study resides in the fact that they marked individual Soay sheep and tracked the dramatic annual fluctuations in the sheep population by moni-

toring the survival and reproduction of individuals of known age and sex. The authors found that age-structured models—which take into account the different ages and numbers of males and females in the sheep population—provided the most accurate predictions of population fluctuations in response to ecological stresses such as adverse weather patterns or increasing population density. Their study is the first to show that large mammal populations of equal size can have markedly different dynamics depending on their sex and age structure. This is not surprising—individual susceptibility to changing environmental conditions is known to differ between males and females and young and old animals—but has been difficult to demonstrate unequivocally.

In feral sheep and in other ungulates, young and old individuals are affected more severely by adverse weather conditions and increases in population density than are adults of prime reproductive age (7), and males often tend to be more affected than females (8). Similar sex and age differences exist for susceptibility to parasites and disease, the probability of dispersal, and vulnerability to predation or harvesting



The rise and fall of large mammals. Variations over 15 years (1985 to 1999) in the age- and sex-dependent survival (box-plot of yearly estimates) of a roe deer population (*Capreolus capreolus*) in eastern France. As with the Scottish island population of Soay sheep (6), females of prime reproductive age had the best survival rates and juveniles (during their first summer) the worst.

by humans. Because the sex and age structure of the Soay sheep population fluctuates over time, independently of population density, Coulson and colleagues had to take into account changes in both the sex and age structure and the population density to explain the cyclical variations in sheep abundance (6).

The overwhelming importance of age structure in determining the fluctuations in the Soay sheep population is also likely to be true for other large mammals. Like the Soay sheep, many populations of large mammals have a relatively low growth rate with wide overlap between generations, resulting in a slow turnover of reproducing individuals (9). In populations that are not hunted, reproducing females typically belong to 10 or more cohorts (all animals born in the same year belong to the same cohort), that is, they span 10 years or more in age. Each cohort may be permanently affected by weather patterns and population density during its first year of existence (10). One of the most obvious (and quantifiable) sources of heterogeneity among cohorts is age (11).

The life cycle of long-lived mammals is composed of three distinct age classes that differ greatly in average fitness (survival and reproduction) and in variations of fitness with ecological stresses (12) (see the figure). From birth to 1 year of age is the time when large mammals are the most susceptible to ecological changes. Consequently, the number of new adults added to a population can vary substantially from year to year, but is usually a small proportion of the total number of breeders. Prime-aged adults, especially females, are buffered against most ecological changes and, with few exceptions, show remarkably constant fecundity and survival over time. As they grow old, however, individuals once again become susceptible to ecological fluctuations.

If the relative proportions of these three age classes vary with time—as Coulson *et al.* report for Soay sheep (6)—then populations of the same overall size may show different responses to ecological stresses. For example, the proportion of aged females should increase as the population density increases. The reason for this is that a high population density reduces fecundity and boosts juvenile mortality resulting in a decrease in recruitment of young breeders (12, 13), whereas the survival of prime-aged adults is independent of population density (7, 12). The average age of the female population affects survival and reproduction. Consequently, counting all adult females together (regardless of age) will bias estimates of the effects of ecological stresses on population fluctuations. The few studies of large mammals claiming that adult survival decreased at high population densities (13) failed

to account for density-dependent changes in age structure. It is now clear that increased adult mortality may appear to correlate with population density because of changes in the proportions of the three age classes.

Counting the total numbers of animals in a population, even when very accurate, is of limited use for interpreting or predicting variations in the size of populations of large mammals. Information on the sex and age structure of the population is essential for planning appropriate conservation or harvesting measures. For example, populations of large mammals that are harvested (such as herds of deer during the hunting season) include a higher proportion of juveniles and young adults than do populations that are not harvested and so may be more adversely affected by ecological changes.

Besides age and sex, there are many other factors that contribute to demographic heterogeneity. Future research should assess the impact of additional sources of heterogeneity on the population dynamics of long-lived mammals. Tagging individual large mammals and monitoring them over the long-term should contribute much to

our understanding of variations in population size. The next step is to determine the extent to which the findings for the island population of Soay sheep (6) apply to other long-lived mammals that face changes in predation, dispersal, and harvesting.

References

1. C. W. Fowler, T. D. Smith, Eds., *Dynamics of Large Mammal Populations* (Wiley, New York, 1981).
2. W. J. McShea, H. B. Underwood, J. H. Rappole, Eds., *The Science of Overabundance: Deer Ecology and Population Management* (Smithsonian Institution Press, Washington, DC, 1997).
3. G. Ceballos, J. H. Brown, *Conserv. Biol.* **9**, 559 (1995).
4. G. A. F. Seber, *The Estimation of Animal Abundance and Related Parameters* (MacMillan, New York, 1982).
5. O. N. Bjørnstad *et al.*, *Nature* **409**, 1001 (2001).
6. T. Coulson *et al.*, *Science* **292**, 1528 (2001).
7. J.-M. Gaillard, M. Festa-Bianchet, N. G. Yoccoz, *Trends Ecol. Evol.* **13**, 58 (1998).
8. T. H. Clutton-Brock, F. E. Guinness, S. D. Albon, *Red Deer Behaviour and Ecology of Two Sexes* (Edinburgh Univ. Press, Edinburgh, 1982).
9. S. C. Stearns, *The Evolution of Life Histories* (Oxford University Press, Oxford, 1992).
10. J. Lindström, *Trends Ecol. Evol.* **14**, 343 (1999).
11. B. Charlesworth, *The Evolution in Age-Structured Populations* (Cambridge Univ. Press, Cambridge, 1994).
12. J.-M. Gaillard *et al.*, *Annu. Rev. Ecol. Syst.* **31**, 367 (2000).
13. C. W. Fowler, in *Current Mammalogy*, H. Genoways, Ed. (1987), vol. 1, pp. 401–441.

PERSPECTIVES: ASTROPHYSICS

Mass Outflow in Active Galactic Nuclei

D. Michael Crenshaw

Active galactic nuclei are found in the central gravitational wells of galaxies and are powered by accretion onto supermassive black holes with masses 10^6 to 10^9 times that of the Sun. The most luminous active nuclei produce more radiation than their surrounding galaxies and are found in only 1% of nearby galaxies called Seyfert galaxies (1). Distant and even more luminous active galactic nuclei are called quasars. Inactive supermassive black holes are now known to exist in nearly all nearby galaxies (2), and research on Seyfert galaxies and quasars gives astronomers the opportunity to explore what happens when accreting matter is supplied to these enigmatic objects.

Recently, astronomers have discovered that many active galactic nuclei eject clouds of ionized gas with velocities of up to 10% of the speed of light over a wide range of angles, in contrast to the previously known

collimated jets (3). These mass outflows are intriguing because they provide information about the dynamical forces (such as radiation and wind pressure) near an active supermassive black hole.

The discovery of mass outflow in active galactic nuclei was made possible by a new generation of space-based telescopes—the Chandra X-ray Observatory (Chandra), the X-ray Multi-Mirror Satellite (XMM-Newton), the Far Ultraviolet Spectroscopic Explorer (FUSE), and the Hubble Space Telescope/Space Telescope Imaging Spectrograph (HST/STIS). These new tools have enabled astronomers to characterize the spectral features of the ejected gas with unprecedented sensitivity and spectral/spatial resolution over a broad energy range. The new observations and their implications were explored in a recent workshop (4).

The supermassive black hole in an active galactic nucleus is likely surrounded by an accretion disk and a hot x-ray corona. Together, these are often referred to as the “central engine,” a tiny region only light hours in size that is responsible for a rapidly time-variable continuum source ex-

The author is at the Catholic University of America and the NASA Goddard Space Flight Center, Code 681, Greenbelt, MD 20771, USA. E-mail: crenshaw@buckeye.gsfc.nasa.gov