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.

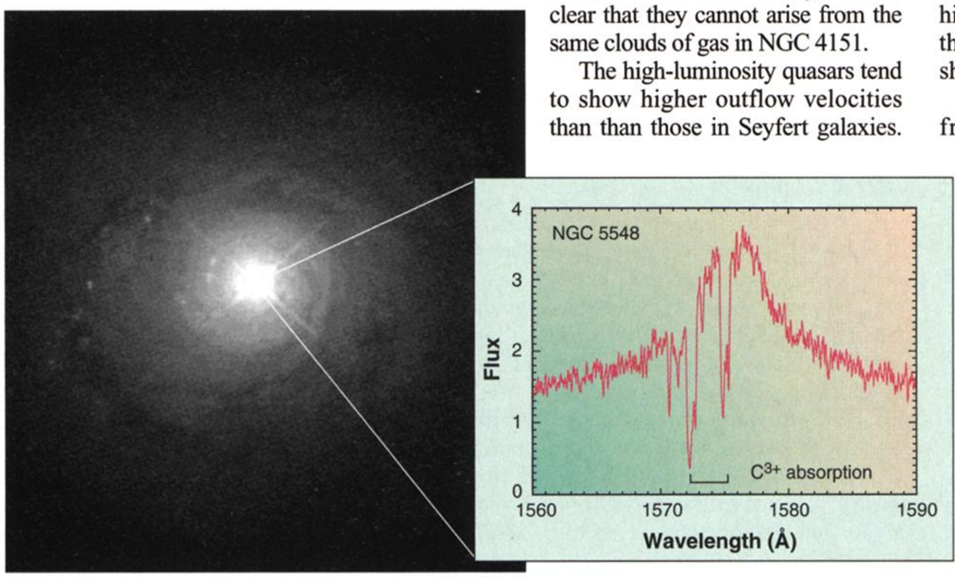
Recently, astronomers have discovered that many active galactic nuclei eject clouds of ionized gas with velocities of up to 10% of the speed of light over a wide range of angles, in contrast to the previously known collimated jets (*3*). These mass outflows are intriguing because they provide information 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

tending from the radio to the x-ray region of the electromagnetic spectrum. This continuum source is the distinguishing characteristic of active galactic nuclei. The continuum radiation yields few diagnostics, and astronomers often rely on its effects on surrounding regions for clues to the physical nature of the central engine. Much research has focused on the high-velocity (10^3 to 10^4 km s^{-1}) clouds of gas that are photoionized by extreme ultraviolet and x-ray radiation from the central engine.



Signature of an active galactic nucleus. The HST optical image shows the bright, unresolved continuum emission from the central engine in the Seyfert galaxy NGC 5548. The HST/STIS UV spectrum for the same galaxy shows the wavelength region around the broad C^{3+} emission line, superposed on the UV continuum emission. The strongest absorption lines are labeled. The blueshift of these lines, relative to the emission, indicates an outflow velocity of 340 km s^{-1}. Weaker absorption at other velocities is also evident.

CREDIT: OPTICAL IMAGE/NASA

One component of the ionized gas detected in Seyfert galaxies is the x-ray "warm absorber," which was detected in previous x-ray missions through absorption edges from highly ionized oxygen at 739 and 831 eV. The warm absorber is characterized by high temperatures (10^5 K) and high column densities (10^{21} to 10^{23} hydrogen atoms per square centimeter in the line of sight). Chandra and XMM-Newton have discovered absorption lines from these and many other highly ionized species and have shown that they are blueshifted with respect to the emission from the active nucleus, indicating outflow velocities of up to 1000 km s^{-1} (*5, 6*). Between 50 and 100% of the continuum radiation is occulted by the warm absorber, implying outflow rates of more than 0.1 solar masses per year—at least 10 times the mass accretion rates.

A related phenomenon is the appearance of intrinsic ultraviolet (UV) absorption lines in about half of all Seyfert galaxies (see figure). These lines are typically from highly ionized oxygen, nitrogen, and carbon species and show outflow velocities of up to 2500 km s^{-1}. Observations at high spectral resolution with HST/STIS and FUSE have shown that the lines split into multiple components, indicating discrete clouds at different outflow velocities. HST/STIS spectra (*7*) of the brightest Seyfert galaxy, NGC 4151, yield a huge range in density (10^{10} to 10 cm^{-3}) and distance of the UV absorbers from the central engine (0.1 to 6000 light years). The connection between the UV and x-ray absorbers is still a source of controversy, but it is clear that they cannot arise from the same clouds of gas in NGC 4151.

The high-luminosity quasars tend to show higher outflow velocities than than those in Seyfert galaxies. Ten percent of quasars show broad absorption lines that extend to velocities as high as 30,000 km s^{-1}. About 25% of quasars show narrow absorption lines, similar to those seen in Seyfert galaxies but extending to higher velocities. The correlation between luminosity and velocity suggests that in both types of objects, cloud acceleration is driven by radiation (particularly bound-bound transitions in highly ionized species). Recent x-ray, UV, and optical observations found unusually large column densities (10^{24} cm^{-2} hydrogen atoms per square centimeter) for broad absorption line quasars (*8, 9*).

The emission spectra of active galactic nuclei paint yet another picture. They reveal more compact clouds of ionized gas, traditionally divided into a broad-line region (velocity = 10^4 km s^{-1}, distance = 0.01 to 0.1 light years) and a narrow-line region (10^3 km s^{-1}, 1 to 1000 light years).

The velocity flow patterns in the broad-line region are still controversial, but recent work on the narrow-line region supports outflow. This result comes from the ability of HST to obtain radial velocities at much higher resolution than ground-based telescopes. Early results show that the narrow-line–region clouds are accelerated outward from the nucleus to a distance of a few hundred light years and are subsequently decelerated over the next few hundred light years (*10*). The latter result was unexpected and is presumably the result of collision with an ambient medium. In the bright Seyfert galaxy NGC 1068, the evidence for collision includes enhanced heating and high-velocity dispersions (~1000 km s^{-1}) at the velocity turnovers, presumably due to shocks at the locations of impact.

A greater understanding of mass outflow from active galactic nuclei will come through comparison between observations and dynamical models, which have grown in sophistication over the past few years. In the most popular models, radiation drives material from the accretion disk to form a clumpy wind (*11*). The disk wind models can generate streams of material with column densities, velocities, and covering factors similar to those observed in broad absorption line quasars. Whether these models are generally applicable to absorption and emission line regions in Seyfert galaxies remains to be established. Competing models, such as those that accelerate clouds along magnetic field lines (*12*), cannot yet be ruled out.

It also remains to be shown how matter reaches the active nucleus in order to fuel the central engine. The UV and x-ray observations have found no evidence for infalling matter (*13*). If the infalling matter is cold, then infrared or radio observations at high spatial and spectral resolutions may be needed to detect it. Establishing the geometry of both infall and outflow will provide a great step toward understanding the nature, origin, and evolution of active galactic nuclei.

References and Notes

1. Named after Carl Seyfert on the basis of his pioneering work on these objects (*14*).
2. J. Kormendy, *Science* **289**, 1484 (2000).
3. D. L. Meier, S. Koide, Y. Uchida, *Science* **291**, 84 (2001).
4. "Mass Outflow in AGN: New Perspectives," Catholic University of America, Washington, DC, 8 to 10 March 2001.
5. J. S. Kaastra *et al.*, *Astron. Astrophys.* **354**, L83 (2000).
6. S. Kaspi *et al.*, *Astrophys. J.* **535**, L17 (2000).
7. S. B. Kraemer *et al.*, *Astrophys. J.*, in press.
8. S. Mathur *et al.*, *Astrophys. J.* **533**, L79 (2000).
9. N. Arav *et al.*, *Astrophys. J.* **524**, 566 (1999).
10. D. M. Crenshaw *et al.*, *Astron. J.* **120**, 1731 (2000).
11. D. Proga, J. M. Stone, T. R. Kallman, *Astrophys. J.* **543**, 686 (2000).
12. M. Bottorff *et al.*, *Astrophys. J.* **537**, 134 (2000).
13. There is one claim of infalling gas in the x-ray spectra of NGC 3516 [K. Nandra *et al.*, *Astrophys. J.* **523**, L17 (1999)], which needs to be verified.
14. C. K. Seyfert, *Astrophys. J.* **97**, 28 (1943).