evolved as a means of escape from herbivory. Others argue that it is the differences in developmental phenology, resulting from trade-offs associated with male versus female function, that cause plants to be differentially susceptible and/or responsive to herbivory. Too little work is available to discriminate between these alternatives. Studying the effects of herbivory in male versus female morphs of facultatively sex-changing species may prove useful in this regard.

Whatever the case, differences in the developmental phenology appear crucial for determining plants' overall responses to herbivory (overcompensation, compensation, undercompensation), as well as the likelihood of and pattern of response to sex-biased herbivory in dioecious plant species. Study of the evolution, maintenance and importance of patterns of developmental phenology in plants is proving to be an exciting and productive area of research, one which may give rise to predictive theories in areas formerly resistant to generalization. Already, these studies are yielding important insights into the limits of plant plasticity as an adaptive strategy and the importance of developmental constraints in regulating plants' responses to their environments.

Acknowledgements
The manuscript has benefitted from the comments of Brenda Casper, Monica Geber, Timothy Griffith, Katherine Preston and Jason Price. The development of this manuscript was funded by a grant from the National Science Foundation.

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The Keystone cops meet in Hilo

'Keystone species', a term coined by Paine[1] more than 25 years ago, has proven a powerful metaphor for the investigation of forces that organize ecological communities. Increasingly, the concept influences the thinking of managers and policy makers who must set priorities in their efforts to conserve species and habitats. The meaning of the term, however, has been blurred by overly expansive usage and for this reason, its application poses real dangers of misuse in decision making[2].

On the other hand, the term is too charismatic, too entrenched and too useful to be abandoned. Based on these concerns, Hal Mooney (Stanford University, CA, USA) and Jane Lubchenco (Oregon State University, Corvallis, USA) organized a workshop on the Keystone Species Concept on December 8–11, 1994 in rainy Hilo, Hawaii, USA, as part of the Global Biodiversity Assessment (GBA) sponsored by the United Nations Environmental Programme (UNEP). At the heart of the workshop was a belief that conservationists and managers have too few ecological tools to predict and prevent loss of biodiversity and ecosystem function, and that a refined keystone concept would be an important addition. The workshop had two goals: to seek consensus on a definition of keystone, and to explore whether potential keystone species could be identified *a priori* (before experimental confirmation, or their loss due to local extinction) by any distinguishing traits. The GBA team – Mooney, Lubchenco, Tony Janetos (NASA, Washington, DC, USA), Osvaldo Sala (Universidad de Buenos Aires, Argentina), Hall Cushman (Sonoma State University, CA, USA) and Rodolfo Dirzo (UNAM, Mexico) – met with nine ecologists who have investigated keystone species to address these and other questions about keystone species. What are keystones, how can they be identified? How many systems have them? How vulnerable are they to human impacts? What ecosystem functions and services would disappear if they were lost?

Mooney and Lubchenco launched the workshop, challenging the group to achieve consensus on a definition that followed either historical (Paine's original usage) or functional criteria (can we arrive at an expanded definition that remains clear and heuristic?) The need is immediate. According to Janetos, the Science and Technology Panel of the World Bank (a group that makes decisions about funding projects with impacts on biodiversity) has found no body of comprehensive statements in which ecologists express any consensus on such issues.

In short, ecologists need to make their science more useful for conservation and biodiversity practitioners. With this mandate, the nine workshop participants initiated discussion with brief synopses of their previous and current views on keystones. Bob Paine (University of Washington, Seattle, USA) began by reviewing his original definition. 'Keystone' in Paine[1] originally referred to a species that preferentially consumed and held in check another species that would otherwise dominate the system. This suppressed target species could be a competitive dominant (e.g. the mussels suppressed by a starfish in Paine's rocky intertidal system) or coupled to a trophic cascade (e.g. sea urchins, suppressed by sea otters[3]). The interaction had to be of sufficient strength to mediate observable indirect effects in the community. Traits suggesting a potential keystone role for a consumer were preference for prey of high competitive ability, and the ability to control this prey at all sizes (so the prey had no escape in size).

David Tilman (University of Minnesota, Minneapolis, USA) defined keystone in terms of the effect of a change in one species on some characteristic of its community or ecosystem, such as species richness, productivity or nutrient availability. He stressed that the measure should reflect per capita or per unit biomass effects of the species, and the total, not the partial, derivative of the change in the community, characteristic with change in the species, because the total derivative reflects indirect as well as direct effects. The change should be measured after all important feedbacks have had time to occur. These feedbacks may be more rapid in aquatic systems, but can take longer in terrestrial systems such as the deserts in which Jim Brown and colleagues found more unexpected results as the experiment aged[4]. Tilman also argued that the term keystone should not be restricted to animals or a particular trophic level, although consumers at higher trophic levels would, *a priori*, seem more likely to have larger per capita effects than plants, which commonly have larger biomass.

Jim Estes (University of California, Santa Cruz, USA) drew upon his classic studies of sea otters and their role in trophic cascades that can completely alter the structure of subtidal and even adjacent intertidal communities. These studies have led to three questions of broad relevance to other systems containing keystones: (1) How general are the direct and indirect interactions? (2) What is the breadth of effects on other members of the community? (3) What are the evolutionary consequences? Since the vast majority of systems in nature either have not been or cannot be studied in comparable detail, it is important to evaluate whether or not keystone species and interactions can be predicted *a priori* based on some aspect of the predator, prey or ecosystem. In the sea otter–kelp forest system, the keystone predator is much larger and more mobile than its primary prey. Estes argued for increased use of 'natural experiments' and 'adaptive management' in evaluating the potential importance of other large, mobile consumers. His comparative surveys of otter–urchin interactions throughout the northeast Pacific have shown that prey properties (e.g. whether urchins graze attached or drift kelp) can also influence the strength of these interactions and the breadth of the cascading effects that they generate.

The theme of prey influence on keystones was continued by Juan Carlos Castilla (Pontificia Universidad Católica de Chile, Santiago, Chile), who reviewed his studies of the keystone carnivorous gastropod, *Concholepas*, on the rocky shores of Chile. In his studies, the snail's keystone status depended on whether its prey could be both eaten and bulldozed off the substrate. Mussels and barnacles were susceptible, hence *Concholepas* plays a keystone role where these prey are dominants. Other intertidal communities are dominated by a tunicate, which cannot be bulldozed, and in these, the snail is not a keystone. Castilla also reviewed results from studies of *Homo sapiens*, which feeds heavily on *Concholepas*, with consequences that ripple through the intertidal food web.

Mary Power (University of California, Berkeley, USA) emphasized that keystones have been distinguished from other types of strong interactors by having effects that are much greater than would be expected from their relative abundance. She also pointed out that the original metaphor has had a second useful connotation: keystone species, if experimentally perturbed, can be keys to understanding the forces that organize communities. Although it would be useful to discover traits that identify keystones *a priori*, she was skeptical that a 'field guide to strong interactors', as Steve Carpenter (pers. commun.) has called it, could be compiled until we have a better understanding of the context dependencies of interaction strength. She illustrated this point by reviewing her studies in northern California rivers, in which the keystone role of fish as top predators depends on whether or not scouring floods have occurred.

Bruce Menge (Oregon State University, Corvallis, USA) supported the argument that keystone species are context dependent, citing a variety of studies from marine habitats including his own recent work. He further noted that detecting keystone species can be difficult, particularly when several similar species are candidates for potentially controlling a system. Removing a single suspected keystone from a multispecies group of consumers could lead to no change in the community for one of three reasons: (1) the removed species had no impact; (2) control was imposed not by a single species but by the entire group, the remaining members of which compensated for the absent species; or (3) none of the consumers had an effect. To distinguish among these, Menge advocated, where feasible and appropriate, a combination of experiments that would estimate both the collective trophic impact of all consumers, and the isolated impacts of single species (or individual trophic groups). As yet, no species or system traits reliably distinguish keystones from nonkeystones. Examples from a wide variety of habitats are available, however, which could be mined for comparative guidelines in efforts to identify the most likely strong interactors in unstudied systems or systems being considered for management.

Scott Mills (University of Idaho, Moscow, USA) raised the question of whether keystone characteristics are dichotomous (some species are keystones, the rest are wimps), or whether the effects of species on their communities were in fact more continuously distributed. Presumably, a community with keystone species would have 'community importance' or interaction strength values distributed very differently from communities that are traditionally modeled. He warned of the dangers of the lack of an operational, repeatable criterion for designating keystone status if this term is to be used by decision makers. He stressed, however, that the keystone phenomenon is real and the need for application is great, so that

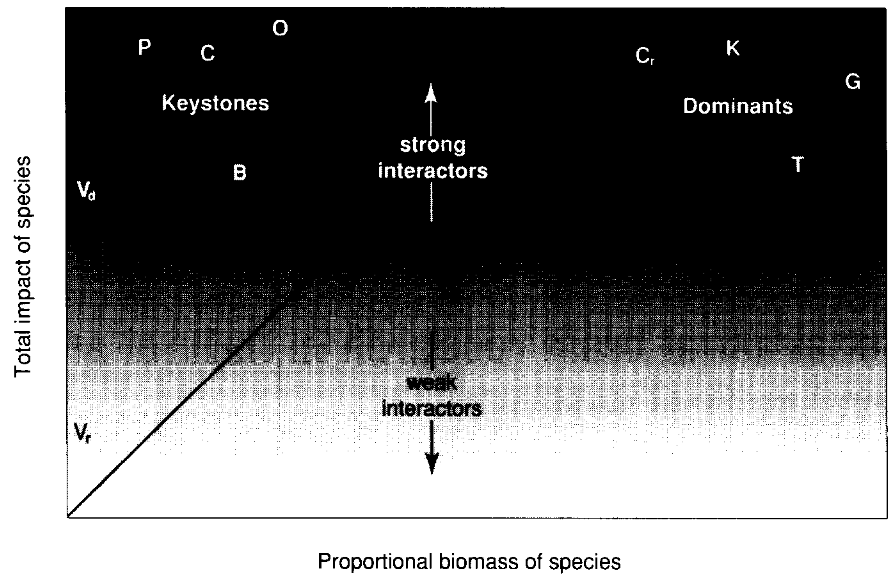

Fig. 1. Total (collective) impact of species versus its proportional abundance. A point representing a species whose total impact is proportional to its abundance would fall along the diagonal line $x = y$. Keystones have effects that exceed their proportional abundances by some large factor. They also have a total effect whose magnitude exceeds some absolute threshold. Therefore, although a rhinovirus that made wildebeests sneeze (V_r) might have a total effect that far exceeded that expected from its very low biomass, it would not be a keystone if the total effect fell below the threshold. On the other hand, a distemper virus (V_d) that killed lions or wild dogs might have a collective effect of sufficient magnitude for keystone designation. *Pisaster* (P), sea otters (O), the predatory snail *Concholepas* (C) and freshwater bass (B) have disproportionately large impacts on their communities. Trees (T), giant kelp (K), prairie grasses (G) and reef-building corals (C_r), which dominate community biomass, have total impacts that are large, but not disproportionate to their biomass. Quantitative values that should be prescribed for thresholds of absolute total collective impact (vertical position) and factors by which keystone effects should exceed a species' proportional abundance (distance left of the line $x = y$ required for keystone status) may vary with the community trait (e.g. species richness, biomass of other species or guilds, primary productivity, nutrient or soil retention, albedo) under consideration. In addition, interaction strengths, and therefore status as keystones or dominants, may change for given species under different environmental circumstances. Impacts of succession, changes in productivity, or deletions of other species on the status of a species could be represented by families of points representing the same species in different contexts.

steps towards a clearer operational definition would be welcome.

Gretchen Daily (University of California, Berkeley, USA) described how determining the consequences of a species deletion requires overcoming some of the greatest challenges in ecology: starting with a flash of naturalists' intuition; bridging across spatial scales to detect the influence of individual behavior on characteristics of communities and ecosystems; working over potentially formidable timescales and with a daunting diversity of taxa; and all the while persevering with knowledge that similar consequences may not manifest themselves in seemingly similar systems. She argued that, nonetheless, it is imperative to incorporate the potentially dramatic role of subtle, indirect species interactions when depicting communities in conservation and management models.

This point was emphasized by William Bond (University of Cape Town, Cape Town, South Africa), who decried the lack of contribution by ecologists of protocols that would allow conservation priorities to be set on the basis of interactions. Keystone, he pointed out, was the only single name widely associated with interactions that can conform to database formats ('species *i* is a keystone, and it's here'). A keystone can be pragmatically defined as a species whose loss from or addition to a system would change community composition, structure or function enough to arouse concern. Keystones are best demonstrated by experiments, which, unfortunately, are slow, particularly in terrestrial systems. Consequently, we do not yet know whether deletions of possible keystone mutualists (pollinators, seed dispersers) would in fact alter population dynamics to produce large effects on the rest of their communities. In general, we lack and need a protocol for evaluating probable keystone interactions for biodiversity conservation, so that we can flag those species involved and the species or key processes that would be vulnerable to their loss.

During the subsequent days, the group hammered out a verbal, and a potentially operational, definition of keystone. The verbal definition, which expands the original definition to include interactions other than trophic ones, was: '*A keystone species is a species whose impacts on its community or ecosystem are large, and much larger than would be expected from its abundance*'. This verbal definition distinguishes keystones from other strong interactors whose effects are due to their dominance of ecosystem biomass. The potentially operational definition takes a step towards quantifying 'large, and larger than expected' by formally defining the community importance of a species, deriving from this species' total (collective) impact, and relating this impact to its proportional biomass in the community (Fig. 1). This definition distinguishes keystones from dominants and other species. Its potential for examining the context dependence of species interaction strengths and keystone status (for example, how these change with the gain or loss of other members of interaction webs, or over the course of succession) will be explored in a paper by this group in preparation for *BioScience*.

By developing a more operational definition, the workshop participants hope to refocus the term keystone for ecological research, and to make it more useful for policy makers concerned with preserving biodiversity. All agreed that it was premature to prescribe 'magic numbers' (specified quantitative thresholds above which species would be designated as keystones). Nevertheless, there was growing excitement over research questions that emerged or were clarified during discussion, and a general optimism that the keystone concept was evolving towards a form that could take an important place in the conservation biologist's tool box.

Acknowledgements
We thank Adrian Sun for help in preparing Fig. 1.

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Behavioural brain research in natural and semi-natural settings

In the 'decade of the brain', the goals of neuroscience have become very ambitious. Why should we not find the genes of memory, describe the neural basis of consciousness or of reason? These goals, however, demand explicit solutions, and it is not at all clear whether we are prepared for such reduction. In general, scientists agree that a reductionist approach is merely a convenient way to design feasible experimental studies. But in this case, the main problem is defining relevant functions within an evolutionary perspective, whether at the cognitive or the cellular and infracellular levels. Moreover, linking different levels of description requires exceptional research competence as well as effective communication among scientists in different fields.

The first aim of Enrico Alleva (Istituto Superiore di Sanita, Rome, Italy), Hans-Peter Lipp (Anatomy Institute, University of Zürich, Switzerland) and Lynn Nadel (University of Arizona at Tucson, USA) – the organizers of a recent NATO ASI workshop in Maratea, Italy – was therefore to bring together behavioural ecologists and neurobiologists. Presentations and discussions were aimed at understanding the evolution of the nervous system as an adaptive process in relation to specific ecological niches. Four very active discussion groups were concerned with the major underlying theoretical issues, that is, (1) the conditions in which a reductionist study of brain structures might be acceptable, (2) the process of assessing the adaptive value of behavioural or cognitive abilities, (3) the limit and complementarity of laboratory and field approaches, and (4) the functions of the hippocampus. Neuroanatomy methods were taught by specialists with the aim of helping researchers to do in one week what might take a year in the absence of supervision. Behavioural techniques were demonstrated, from homing pigeon (Fig. 1) tracking with sophisticated radiotelemetry devices, to bat detection or satellite tracking. In general, there was an ideal complementarity between theoretical and practical topics.

The definite neodarwinian bias of the meeting, '*le comportement moteur de l'évolution*'[1], was introduced in the opening lecture on microphrenology, in which Lipp discussed the mechanisms by which mutations are more likely to be buffered or to appear as behavioural traits that have been submitted to natural selection. Changes in brain structure in the course of evolution were related to specialized digit capacity (Randolph Nudo, University of Texas, Houston, USA) or to nutritional regime (Gerd Rehkamper, Heinrich Heine

