

their assumption that memory capacity is fixed throughout would be false. Memory capacity could be a plastic variable.

In conclusion, Brodin and Clark¹² present a summary of how they currently believe energy is balanced between fat reserves and hoards in a winter population of parids. By presenting their ideas in the form of a model, they are able to make concrete, testable predictions of the type of patterns one should be able to observe in the wild. In the model, increasing capacity and longevity of memory does not contribute much to the fitness of the individual at the end of winter. This is a direct consequence of the fact that even forgotten seeds still contribute to the food supply, since they are hoarded in the bird's own foraging niche. This in turn suggests that it may be time to reconsider the function of spatial memory in food-hoarding in the Paridae.

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Craning for a better view: the Canopy Crane Network

Interest in the canopies of trees has increased dramatically in the past five years^{1–4}. Until recently, the study of this important biological stratum has been hindered by a lack of safe and adequate access⁵. One novel method, the canopy crane, seems to have found utility and acceptance for a wide range of researchers. By 1998 there will be at least seven canopy cranes in use at forest sites in Panama, USA, Venezuela, Japan, Australia and Malaysia.

The first international canopy crane symposium was held in Panama in March of this year to discuss how the research of the increasing number of canopy crane researchers can be integrated to best effect. A canopy crane network was established and agreements made on site protocols and minimum datasets to ensure that the resulting data will be compatible and will allow global comparisons. The symposium brought together scientists involved in canopy research, conservationists, global change specialists and those involved in the management of forests. Representatives from the Secretariats of the Conventions on Biological Diversity, Climate Change and the Ozone

Layer and other key international statutes indicated how they saw the canopy cranes being used to answer critical global questions. The results of this symposium will be published by the United Nations Environment Program (UNEP) in a format suitable for policy-makers, scientists and environmental change managers.

Why do so many research groups see cranes as being such a useful tool for canopy research? Until now most studies of the rainforest biota and ecosystem processes have been carried out at ground level or from those few points in the canopy made accessible by towers and canopy walkways, and yet it is the canopy – where the atmosphere meets the biosphere – where many of the critical ecological processes take place. Cranes provide rapid, easy and non-destructive access to many parts of the canopy for small teams of researchers. It takes just seconds from stepping into the three-person gondola on the ground to be lifted up to the top of any tree. The gondolas can carry live power or battery power and other equipment so that direct measurements and readings can be taken. This

allows researchers to have both hands free to manipulate leaves and branches. Although pseudo-replication is potentially a problem for experimental science using the canopy crane, in practice the reach of the boom permits multiple individuals of many trees to be accessed and manipulative experiments, such as shading of branches or raising CO₂ levels for individual branches, are highly feasible. For example, more than 29 tree species with three or more individuals exist at the Parque Metropolitan site in Panama. Some of the cranes are operated by full-time drivers who are expert at returning to a large number of site locations within the canopy with pin-point accuracy. Using smaller narrower one-person gondolas allows the researcher to drop below the upper canopy level to look at sub-canopy levels. Equipment can be left in the canopy and monitored at regular intervals.

The first construction crane used for tropical rainforest research was established by the Smithsonian Tropical Research Institute (STRI) and the UNEP at the Parque Natural Metropolitan in tropical dry forest on the outskirts of Panama City⁶ (8°59'N, 79°32'W). This crane is situated within sight of the Pacific Ocean and in forest which has an annual rainfall of 1740 mm with a distinct dry season. The remarkable success of this project can be judged by the breadth and novelty of the science that it has facilitated. In the six years since this crane was erected, 75

investigators from 16 countries have carried out collaborative research in a range of scientific disciplines.

Research here has focussed on seasonality, plant phenology and ecophysiological relations between plants and the atmosphere^{4,7,8}. Recent investigation of the relationship between leaves and the upper canopy environment indicates that the opening and closing of stomates may have minimal effect on transpiration in species that maintain a humid boundary layer, effectively buffering the leaf from the dry canopy atmosphere⁹. The photosynthetic rate of leaves in the canopy of *Ficus insipida* has been found to be higher than that of any wild species yet recorded, although researchers suspect that similar high photosynthetic rates will be found repeatedly as leaves of other species are analysed in the upper canopy¹⁰. Perhaps one of the most remarkable discoveries is seasonal changes in the morphology of new leaves produced in single tree crowns. These strong seasonal changes adjust plant allocation to photosynthesis to seasonal changes in the availability of light and water in surprising ways¹¹. Other groundbreaking research has led to the discovery of strong species and season-dependent emissions of volatile hydrocarbons by tree canopies (M. Lerdau and M. Keller, pers. commun.). Collectively, these results have worldwide implications that will contribute to the parameterization of global climate models⁴. None of these studies would have been possible without the access provided by the canopy crane.

Canopy cranes also provide a means of more accurately identifying and understanding arthropod diversity in the canopy. One critical study of the host-specificity of herbivorous beetles to canopy trees has revealed that there is a distinct beetle fauna associated with lianas of the family Bignoniaceae in Panama. Through continuous observation of herbivorous beetles feeding in the canopy, F. Odegaard (pers. commun.) has found 49 undescribed species of bariidine weevils adapted to hold on to the tendrils of the twelve species of bignoniaceous lianas at the Panama crane site by means of a groove on the thorax and abdomen.

The prototype crane has been so successful that STRI and UNEP have established a second crane at the 'wet' end of the Panama Canal some seventy kilometres to the north (9°17'N, 79°55'W). Here the forest is evergreen and rainfall exceeds 3400 mm annually and monthly rainfall averages less than 60 mm for just two months. Research has just started at this site and with so many plant species shared between the two sites it will be interesting to see how they and their associated biota respond to the different rainfall regimes.

The United Nations Environment Program, in supporting the STRI canopy crane program, recognized the value of canopy cranes as tools for scientists to help address many of the critical science questions posed by a number of the international conventions that UNEP administers. For example, the scientific and technological committees for each of the Conventions on Biological Diversity, Climate Change and the Ozone Layer have all set research priorities. Many of these involve studies of forests and in particular processes which take place in the canopy of trees or between the biosphere (the canopy) and the atmosphere.

Two other canopy cranes are currently operational in Venezuela and the USA. The Venezuelan crane, located in lowland rainforest near La Esmeralda in Southern Venezuela (3°10'N, 64°40'W), is different from the others in that it is mounted on a 150 m length of rail to provide access to a larger area of forest. This facility, established in 1996, supports research in plant phenology, ant-plant interactions, forest energy balance, avian community structure and frog and orthopteran communication.

The only established temperate rainforest crane is the Wind River crane located in the Douglas fir forests of Washington State (45°49'N, 121°57'W). With a height of 85 m and a jib length of 75 m it is the largest crane so far established for canopy research, providing access to 320 individual tree crowns over 2.3 hectares of forest. Although the diversity here is considerably less than at the tropical forest sites, studies of other similar forest in north-west America indicate that this still has a rich arthropod fauna requiring further investigation¹². This crane facility, established in 1995, has already supported about 45 projects which have been completed, are ongoing or are planned for the future. In line with work conducted on the other canopy cranes much of this research aims to focus on canopy tree ecophysiology. Another crane is proposed for establishment in temperate forests in 1998 at the Tomakomai Forest Station of Hokkaido University, Japan.

The tropical rainforests of Australia occupy less than 0.2% of this continent's land mass and yet have a very high proportion of its terrestrial biota; as noted in the successful application for World Heritage listing in 1988, 30% of the marsupials, 60% of the bats, 30% of the frogs, 23% of the reptiles and 63% of the butterflies of Australia are found within this region. By the end of 1997 a canopy crane will be established in an area of exceptional biotic diversity and endemism in this World Heritage forest. Many of the plants in this area are gondwanan relics¹³, and the crane will provide unparalleled access for stud-

ies of the biology of these unusual plants and the organisms associated with them.

Little is understood of the biology of the giant dipterocarp forests typical of lowland rainforest in Borneo and elsewhere in south-east Asia west of the Wallace line. For example, until recently dipterocarps were thought to be pollinated by thrips¹⁴. Several recent studies in Thailand, Sri Lanka, and Malaysia¹⁵⁻¹⁷ now indicate that bees and many other insects are involved. T. Inoue and colleagues from Kyoto University, Japan, who previously have been studying the biology of some 500 species of trees in dipterocarp forest in the Lambir Hills National Park in north Sarawak using an extensive canopy walkway system, will be installing a crane of similar size to the Wind River crane in 1998. This multi-access canopy system will provide an unparalleled opportunity to study an area of forest with over 1200 species of trees.

So little is known about the canopy that there remain many unanswered questions from basic inventory as to what is there to the processes that go on there. Erwin once called the canopy 'the last biotic frontier', suggesting that two-thirds of all insects are found there¹⁸. However, recent research on beetles at one intensively studied site in Indonesia indicates that most species are more closely associated with the ground than the canopy¹⁹. Vines remain virtually unexplored in tropical forests in spite of the fact that they may constitute 30% of the canopy. We currently do not have a complete understanding of water transport in tall vines which often have large vessel diameters making the generation of highly negative potentials very difficult. One of the more interesting physiological questions is whether or not water potentials at the tops of tall trees are sufficiently negative to oppose the force of gravity^{20,21} and studies are now under way at the Panama and Wind River sites to answer this question. The new network of canopy crane facilities will catalyse research programs at these sites. A preliminary cross-site experiment will explore top-down control of ecosystem function, excluding birds and other large animals from canopy and understory sites to explore the responses of arthropods, levels of herbivory on leaves and plant reproductive structures, and ultimately plant production. With the continued backing of UNEP, the network will facilitate exchanges of ideas and investigators and encourage research in all disciplines.

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Patterns and processes in the vertebrate digestive system

In his famous treaty on biological diversity, G.E. Hutchinson¹ noted that 'In any study of evolutionary ecology, food relations appear as one of the most important aspects of the system of animate nature. There is quite obviously more to living communities than the raw dictum "eat or be eaten" but in order to understand the higher intricacies of any ecological system, it is most easy to start from this crudely simple point of view.' Accordingly, studies of food relations and the underlying dynamic flow of energy and nutrients between organisms have been centrally important for our understanding of ecology at the individual, population, community and ecosystem levels and for our understanding of the evolution of ecological systems.

Another important raw dictum 'we are what we do not defecate' reminds us, however, that organisms do not assimilate all the available resources in their food. This inefficiency can result from apparent phylogenetic constraints (e.g. passerines in the Sturnidae–Muscicapidae taxon lacking the enzyme to digest sucrose²) or from compounds in the food (e.g. fiber or toxins

in plants) that retard or inhibit the breakdown and absorption of ingested nutrients. In April, a group of comparative physiologists and anatomists from across the globe gathered in Rauschholzhausen, Germany, to discuss recent advances in the study of the vertebrate digestive system and their ecological and evolutionary implications. The workshop, organized and hosted by P. Langer and R. Snipes (both of Justus-Liebig-Universität, Giessen, Germany), and J.M. Starck (Universität Tübingen, Germany), was a sequel to one held five years earlier in Cambridge, UK, which focused on the theme of food, form and function in the digestive system of mammals³. Both workshops promoted interdisciplinary investigations into the patterns and processes of the digestive system; however, the most recent workshop was expanded to include interdisciplinary research on mammals, birds and reptiles.

Three contemporary themes in the study of the vertebrate digestive system were explored: comparative anatomy and the evolution of the digestive system, form and function of the digestive system in relation to dietary niche and nutrition, and

ecological and evolutionary implications of phenotypic plasticity in the digestive system.

The first step in the analysis of any biological system is often the description of morphology and its apparent function, and the workshop included exciting presentations about the digestive system of vertebrate groups for which very little is known. N. Zhukova (Institute of Zoology, Kiev, Ukraine) used characters of the digestive system to suggest a close phylogenetic relationship between the Insectivora (e.g. moles, shrews, hedgehogs), Chiroptera (bats), and certain lower primates (the Tupaiidae). M. Olsen and S. Mathiesen (University Tromsø, Norway) discussed the functional morphology of the whale's digestive system. Their studies of the forestomach of bowhead, grey, fin and minke whales revealed remarkable functional similarities to the rumen of ruminants: slightly acidic pH (5.3–6.8), high concentrations of anaerobic bacteria (some can digest the chitinous exoskeleton of their invertebrate prey) and the presence of volatile fatty acids.

Complementing the presentations on the digestive system of less studied vertebrates were two very informative reviews of large-scale patterns in gut form and function. R. Snipes, H. Hornicke and G. Bjornhag (Swedish University of Agricultural Sciences, Uppsala, Sweden), presented an exhaustive review of the