CHAPTER 10.

THE FRUGIVORE COMMUNITY AND THE FRUITING PLANT FLORA IN A NEW GUINEA RAINFOREST: IDENTIFYING KEYSTONE FRUGIVORES

ANDREW L. MACK, DEBRA D. WRIGHT

Abstract

The flora at Crater Mountain Biological Research Station in Papua New Guinea is very diverse: 228 tree species (≥10 cm DBH) on a single hectare. However, the vertebrate fauna (169 bird and 31 mammal species) is less diverse than many tropical sites. At least 47% of bird species and 29% of mammal species are partially frugivorous. Using data on relative abundance, mass, and degree of frugivory for all frugivorous vertebrates at Crater, we generated a crude "index of importance" for each species. Using the fruit size and mass data from 400 plant species, we exclude fruits either too large or too heavy for each frugivore to disperse, yielding a "possible diet" for each species. Four species (a cassowary, a hornbill, a fruit pigeon and a flying fox) stand out as being crucial dispersers for a large subset of the plant community. The frugivore with the highest importance ranking, *Casuarius bennetti*, is highly effective as a disperser. Cassowaries appear to be a keystone frugivore, especially for large-fruited plant species (67 species > 50 g at our study site). The method employed is fairly simple and quickly identifies candidates for keystone frugivore status. However, further life history studies are recommended for confirmation of importance when using this method.

Key words: Cassowary, frugivory, keystone resources, New Guinea, phenology, tropical forests

INTRODUCTION

The concept of a keystone species (Paine, 1969) has been widely applied in ecological studies. Although Paine's initial keystone species was a predator, the term keystone has since been widely applied (e.g., to prey, herbivores, pollinators, resources, hosts, plants, modifiers, etc.; Power et al., 1996) with a concomitant obfuscation of just what constitutes a keystone (Mills, Soule, & Doak, 1993). Generally the term is applied to species (or resources) that somehow help to maintain structure and complexity in a community or ecosystem so that removal of

J. Lawrence Dew and Jean Philippe Boubli (eds.), Tropical Fruits and Frugivores: The Search for Strong Interactors 184 – 203.
© 2005 *Springer. Printed in The Netherlands.*

the species would result in an inordinate modification of that community or ecosystem. However defined, keystones have become candidates for concentrated conservation activity and monitoring because their extinction could have cascading effects and impact many other species (Simberloff, 1998). Given the limited resources for conservation, the issue of how to define and identify keystone species is more than an exercise in semantics among academics. Rather than broadly re-examine the entire keystone concept (e.g. Power et al., 1996; Simberloff, 1998; Zacharias & Roff, 2001), we focus on one particular relationship where the keystone species concept has been applied (frugivorous seed dispersers) from one understudied region (Papuan rainforests).

Although it has been long recognized that seed dispersal is important to rainforest systems (e.g. Ridley, 1930), it was not until the formulation of the "Janzen-Connell hypothesis" (Janzen, 1970; Connell, 1971) that an explicit mechanism was stated wherein seed dispersers directly affected plant diversity in rainforests. Janzen-Connell stimulated a continuing surge in seed dispersal studies. Many studies have highlighted keystone fruit resources in the maintenance of frugivore communities (e.g. Howe, 1977; Kannan & James, 1999; Shanahan, So, Compton, & Corlett, 2001; van Schaik, Terborgh, & Wright, 1993) and others in this volume). In this paper we focus on the converse, the keystone frugivores that are potentially important in the maintenance of plant communities.

Identifying potential keystone frugivores first requires clarification of criteria. Minimally, we need to identify the community of plants, the community of frugivores, and to characterize the interactions between these two groups in order to determine the degree of "reliance" of each plant species on each frugivore. By reliance we mean the projected impact on a plant population by the removal of a frugivore. This is the key criterion of the keystone species concept and the rationale for making keystones a conservation priority (Mills et al., 1993).

Empirically evaluating these criteria is exceptionally difficult, particularly in diverse and complex tropical rainforests. For example, how do we define a frugivore among the continuum of animals from those that only rarely feed upon fruit to those that feed almost exclusively upon fruit? How do you define plant "reliance" when they have their seeds dispersed by many frugivores depending on phenology, age, location, etc.? Will the removal of one frugivore only result in more fruit for another? How many plant species must "rely" on the frugivore for the frugivore to be considered a keystone? How does one account for differences in space and time; what might be a keystone in one place or time might not be in another? Clarifying such questions is simple. But obtaining answers requires knowledge of the frugivores and detailed knowledge of their surrounding flora and ecological relationships-- "inspired natural history" is required to identify keystone species (Paine, 1995).

Here we analyze some of the main criteria for identifying keystone frugivores. We use data gathered from one site in Papua New Guinea where we have a fair knowledge of both the frugivore and plant communities. New Guinea is a conservation priority because it has some of the last remaining large blocks of intact rainforest (Mittermeier, Myers, Thomsen, Fonseca, & Olivieri, 1998; Olson &

Dinerstein, 1998). Furthermore, New Guinea has an independent evolutionary history from the rest of earth's tropical forests, so studies there can test generalizations derived from the better-studied neotropics (Westoby, 1988). Our goal is to use straightforward natural history to empirically suggest candidates for keystone frugivore status in New Guinea.

METHODS

Study Site

Field data were collected from the Crater Mountain Wildlife Management Area (CMWMA), a 2700 km^2 conservation project in Papua New Guinea (PNG). The bulk of the area, and a much larger expanse bordering it, is essentially undisturbed primary forest. The low human population impacts some valleys with swidden gardens and adjacent areas through hunting, but there is no evidence of any local extirpation of vertebrate species, nor of introduced vertebrates other than pigs. Most data was collected at the Crater Mountain Biological Research Station (CMBRS) between 1989 and 1993. The CMBRS (145^o 05' 34.5"E, 6^o 43" 26.2" S) study area spans 800-1350 m elevation from hill to lower montane forest in a region characterized as the middle elevational high rainfall zone (Hyndman & Menzies, 1990) found along the southern scarp of New Guinea's central cordillera. The study area receives 6.5-7.5 m of rainfall per annum which falls relatively uniformly all year; there is no predictable dry season. The biota of the CMBRS is representative for the portion of southern New Guinea residing on the Australian craton, which is a major biogeographic province (Heads, 2001).

Floristic data

We collected floristic data from 5 ha of vegetation and phenology plots (Wright, 1998; Wright, Jessen, Burke, & Garza, 1997) and adventitiously throughout a roughly 250 ha study area from 1989-1993. We collected and identified specimens of any plant found to bear a fleshy, endozoochorous diaspore. Although it is likely that we did not sample some species of plants that produce fleshy diaspores, particularly small-fruited epiphytes, we are confident that those species missed would comprise a small percentage of the overall available fruit biomass.

For the above species we measured greatest fruit length, greatest fruit width, greatest fruit depth and fresh fruit wet mass. Linear measurements were made to the nearest 0.1 mm with Vernier calipers and masses to the nearest 0.1 g with a triple beam balance. In order to approximate the volume of a cylindrical ellipse (see Wright, 1998), fruit volume was calculated as:

$$4/3\ \pi (\text{fruit length}/2)*(\text{fruit width}/2) * (\text{fruit depth}/2)$$

Frugivore data

We censused the birds and mammals of the CMBRS using a variety of techniques--visual observation, spot-lighting, mist-netting and live trapping (Sherman, Elliot, and Tomahawk traps for mammals). We have conducted field surveys at elevations above (1450 m) and below (550 m) in the study area to identify species that could occur in the margins of the study area.

Birds have been intensively observed over several years to determine species composition in the study area along with their diets (Mack & Wright, 1996). Extensive observations and regular mist-netting have continued at the site for twelve years. The species accumulation curves for all combined methods of observation are nearly level for birds and for mammals. We are confident that we have observed nearly all of the species that regularly occur in the CMBRS study area.

Data on avian diets were obtained through direct observation (Mack & Wright, 1996) and collected from the literature (e.g. Baptista, 1990; Beehler, 198x, 1983; Beehler & Dumbacher, 1996; Bell, 1983; Coates, 1985, 1990; Frith, Crome, & Wolfe, 1976; Hicks, 1988; Hicks & Hicks, 1988a, 1988b; Hopkins, 1988, 1992; Lamothe, 1979; Peckover, 1985; Pratt, 1984; Pratt & Stiles, 1985; Terborgh & Diamond, 1970; Wahlberg, 1992). Data on mammalian diets were also derived from direct observation and from the literature (e.g. Bonaccorso, 1998; Bonaccorso & Gush, 1987; Hopkins & Hiaso, 1994; Woolley & Allison, 1982).

Weights and dimensions of birds and mammals were taken from our unpublished field survey data, from many of the sources cited in the previous paragraph, and from specimens at the PNG National Museum and Art Gallery.

Possible fruit diet determined by frugivore size

Fruits weighing more than 15% or 30% of the mass of each bird and mammal species, respectively, were categorized as too large to be dispersed from the parent tree by that species. The percentage is lower for birds because of stronger aerodynamic constraints (e.g., bats can carry larger payloads than birds). We estimated the maximum fruit diameter each bird or mammal species could swallow or carry given its bill/mouth size as a gape/handling constraint (Wheelwright, 1985). We used these mass and diameter constraints to calculate what proportion of the fleshy-fruited plant species (n = 400) in our study area each frugivore species could hypothetically disperse and called these its potential diet.

"Index of importance"

The potential importance of a frugivore as a seed disperser is defined by several parameters. We created a unit-less index of relative importance. Species with higher ranks (closer to unity) have greater importance. We expect that anything considered a "keystone" frugivore would be an outlier to the distribution of species indices. We used three parameters to generate the index:

Abundance-- an abundant but poor disperser could be more "important" than a rare but efficient disperser. For each species, abundance (*a*) was ranked 1-6 based on census data at the CMBRS with 1 being least common and 6 most common.

Degree of frugivory-- this is a composite of the proportion of fruit in the diet along with an estimate of whether the seeds of those fruits are potentially dispersed; e.g., seed predators rate low even though they may consume many fruits. For each species, degree of frugivory (*f*) was ranked as a percentage of total diet (0-100%) based on our literature search and personal observations.

Amount consumed-- this is a direct scale to body size, given the same degree of frugivory, the larger the animal the more it will consume to meet basic energetic needs (ignoring the few exceptions of taxa with similar body sizes and very different metabolic rates). For each species we used the data on body mass (*m*) collected by trapping at CMBRS and from literature and museum specimens. No animal weighed less than 1 gram.

These three parameters were combined and standardized to sum to unity with the following formula:

$$\text{Index} = \frac{\left[\left(\frac{a}{\sum a}\right)+\left(\frac{f}{\sum f}\right)+\left(\frac{\sqrt[3]{m}}{\sum \sqrt[3]{m}}\right)\right]}{3}$$

Analyses

Statistical analyses were performed using two computer software programs: SPSS version 10.0 and Excel 2002.

RESULTS

Diversity

Frugivorous birds and mammals are an important component of the New Guinea and Crater Mountain fauna in terms of numbers of species. Roughly 40% of bird and 30% of mammal species consume some fruit and roughly 8% of each of these taxa consume mostly fruit (Figure 1). These percentages hold whether looking at the island as a whole, at the smaller Wildlife Management Area, or at the even smaller study area.

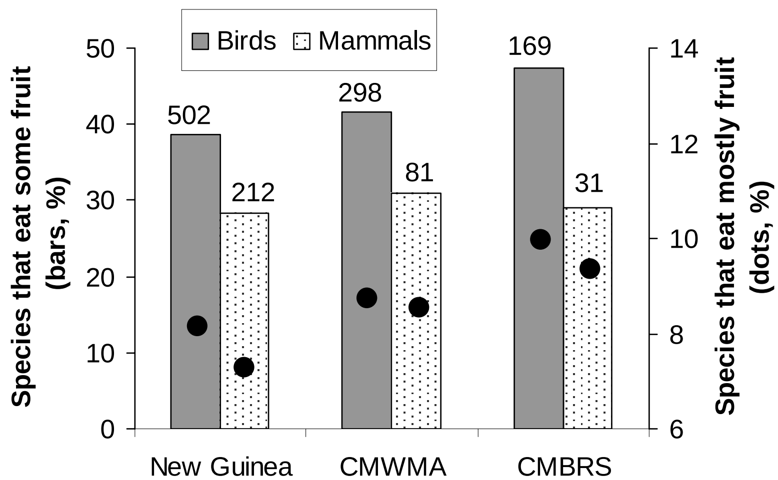

Figure 1. *The percentage of bird and mammal species from New Guinea, from the Crater Mountain Wildlife Management Area (CMWMA) and from the Crater Mountain Biological Research Station study area (CMBRS) that consume some fruit (bars) and the percentage that consume almost only fruits (solid dots). Total species sample size is given above each bar. No matter which grain scale we examine, the percentages remain very similar within birds and within mammals.*

Degree of frugivory

Most species that consume fruits also consume other food items (e.g., insects, nectar, vertebrates, seeds, and other plant matter). Forty seven percent and 29% of the bird and mammal species, respectively, in our study area were at least partially frugivorous. But only 10% of each were highly frugivorous (Figure 2). Some bat species eat only fruit, but some marsupials and murids (including tree kangaroos, wallabies, bandicoots, cuscus and some rodents) live partly on fruit matter and may disperse seeds (Appendix 1). Cassowaries, fruit pigeons, hornbills, some parrots, berrypeckers and some birds of paradise eat mostly fruit, but some pigeons, megapodes, parrots, honeyeaters, birds of paradise, and other passerines consume fruit along with other important dietary components (Appendix 1).

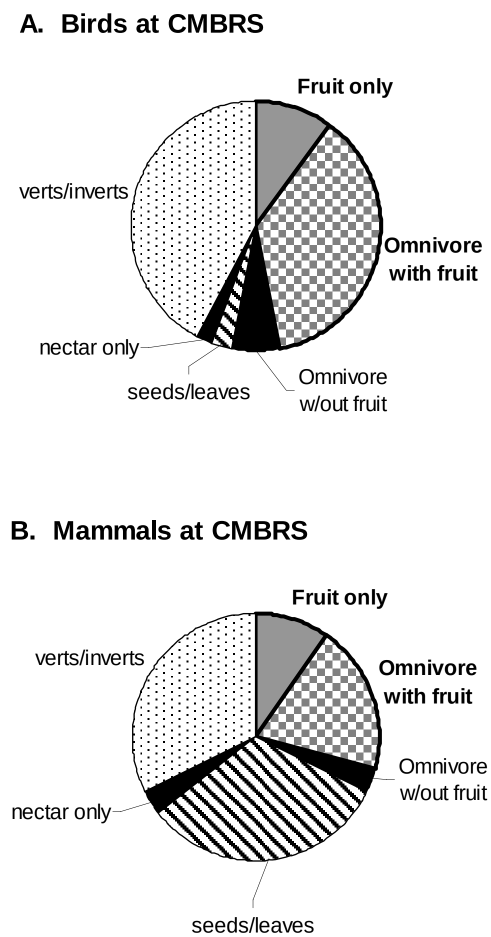

Figure 2. *The proportion of bird (A) and mammal (B) species known to inhabit the Crater Mountain Biological Research Station that fall within each dietary category.*

Sizes of fleshy fruits

We collected linear measurements and mass of fleshy fruits from 114 plant species. Using these species we found a tight correlation of fruit mass to fruit volume ($r^2 = 0.981$, $P < 0.0001$) and obtained the linear regression formula: fruit mass = (0.9574 * fruit volume) + 1.25. We used this formula to estimate fruit mass for an additional

286 fruit species where we had recorded linear measurements, but not mass, to yield a total sample of 400 plant species for the study area.
Mean fruit mass was 31.7 g (SD = 82.0). Most species (45%) had small fruits (< 5 g), but 17% had fruits over 50 g and 31 plant species (8%) had fruits over 100 g (Figure 3).

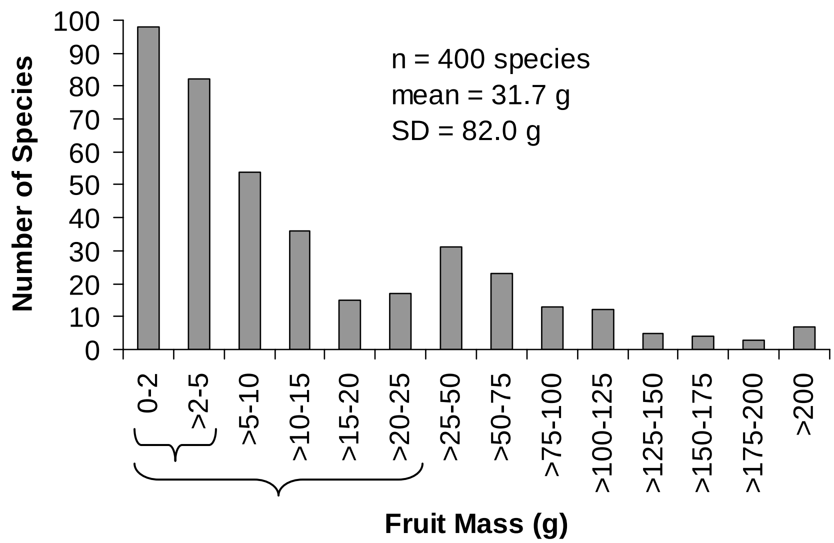

Figure 3. *Size histogram for plant species with fleshy fruits at the CMBRS.*

Potential diet

Of all of the bird and mammal species that eat some fruit in our study area, 82% were too small (body mass or gape limitations) to handle 30% of the fruit species. Furthermore, 18% of the flora could only possibly be moved by seven frugivore species (*Casuarius bennetti*, *Rhyticeros plicatus*, *Dobsonia magna*, *Uromys caudimaculatus*, *Phalanger gymnotis*, *Spilocuscus maculatus* and *Dorcopsulus macleayi*, Appendix 1).

Index of importance

The distribution for the Relative Importance Indices did not differ from normal (K-S test, Z = 0.632, P = 0.82, n = 88), and only three species stood out as being exceptionally important frugivores (more than two standard deviations from the mean-- *C. bennetti*, *R. plicatus* and *Ducula zoeae*; Figure 4).

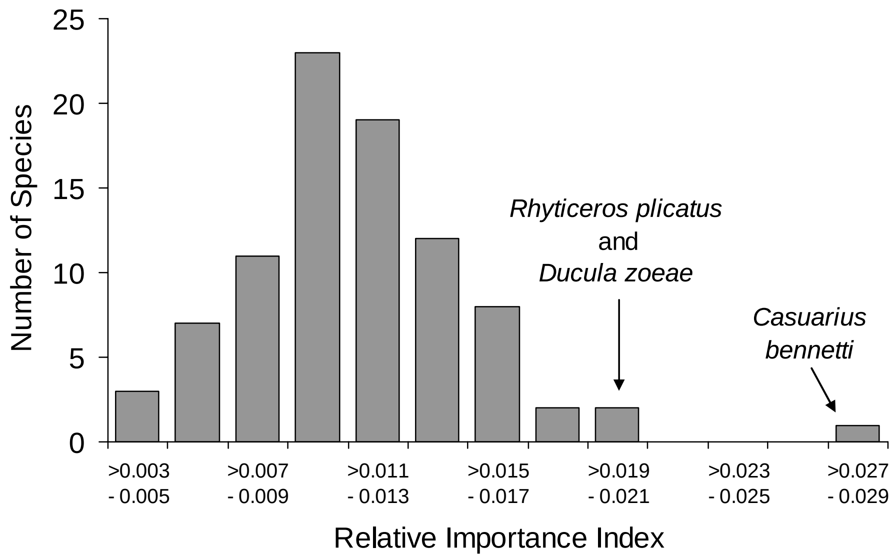

Figure 4. *The Relative Importance Index, which combines measures of frugivore abundance, degree of frugivory, and amount of fruit consumed, follows a normal distribution with few outliers. Only three species are over two standard deviations from the mean.*

Identifying the keystone frugivores

The most important frugivores, as defined by the number of fruit species that could potentially be dispersed, were not congruent with the most important frugivores as defined by the index (Appendix 1). When you consider both simultaneously, one species unambiguously emerges as the top candidate for keystone frugivore: *C. bennetti* (Figure 5). After the cassowary, several other species in the upper right side of the graph are also likely keystone candidates, including the hornbill *R. plicatus*, the flying fox *D. magna* and one of the fruit pigeons *D. zoeae*.

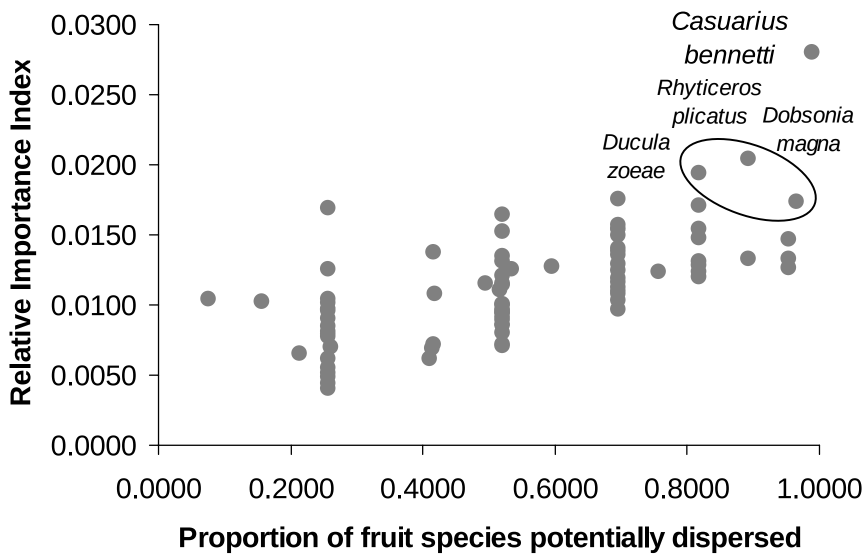

Figure 5. Casuarius bennetti *stands out as a keystone frugivore by the Relative Importance Index and by the proportion of fruit species it can disperse. Three other species also deserve attention as possible keystone frugivores.*

DISCUSSION

Diversity

The flora of the Crater Mountain study area is diverse (Takeuchi, 1999; Wright et al., 1997) and appears to be representative of a broad region along the southern scarp of the central cordillera of New Guinea (Hyndman & Menzies, 1990). The study area avifauna is also diverse and contains 34% of the bird species found across the island of New Guinea. The mammalian fauna at the study area is relatively less diverse, with only 15% of all New Guinea mammals represented. This is partially a sampling artifact as nocturnal mammals are harder to verify than plants and birds, but it is also indicative of the patchy distributions of many New Guinea mammals. Although the data are collected from a fairly limited area in the vast forests of southern New Guinea, the diversity at this locale suggests it could be representative of a broader area.

Although the flora is diverse and is comparable to the diversity of tropical rainforest locations worldwide, the frugivore fauna is not as rich on the global scale. Many sites in the Neotropics have many more species per site than the CMBRS study area. For example, the avian diversity of eastern Andean study sites of comparable size (e.g., Manu, Tambopato, Rio Napo) are roughly equivalent to the diversity of all forest birds in all of New Guinea. Likewise New Guinea completely lacks many large-bodied vertebrates that are important frugivores outside the Australasian area (e.g., primates, civets, ungulates, tapirs, ursids, etc.). New Guinea has high species diversity in fruiting plants, yet relatively low frugivore diversity. Since keystone frugivores will perform an ecosystem service that is either unique or limited to relatively few species, and their removal will extend inordinately to many taxa (Menge, Berlow, Blanchette, Navarrete, & Yamada, 1994; Mills et al., 1993), (Power et al., 1996), these data on the species richness of endzoochorous plants versus frugivorous vertebrates alone increase the likelihood of finding important keystone frugivore species in New Guinea.

Degree of frugivory

Not all frugivores are equal in their impact on plants, they vary in the quantity of fruit they consume and their quality as seed dispersers (Howe, 1993; Jordano & Schupp, 2000; Loiselle & Blake, 1999; Wenny, 2000; Wutherich, Azocar, Garcia-Nunez, & Silva, 2001). We used extensive personal observations and a literature search to estimate the proportion (%) of each species' diet comprised of fruit and its quality as a seed disperser. Although these estimates were crude and subjective, they are the best approximations that can be made without decades of field work to quantify such parameters.

Size of fruits and potential diet

Our sample of 400 fleshy-fruited species is among the most complete for any single rainforest site (e.g. Gautier-Hion et al., 1985; Janson, 1983; Meehan, McConkey, & Drake, 2002). The fruit flora of New Guinea has relatively large fruits when compared to floras elsewhere (Mack, 1993). This potentially strengthens the importance of body size and handling capabilities of frugivores. In a flora lacking large-fruited species, more frugivores would potentially be able to disperse a larger proportion of seeds based on morphometrics. At CMBRS fruits of many plant species are simply too large to be swallowed or carried by the majority of frugivores-- seventy plant species can only be moved by seven frugivore species.

Choosing Keystone Frugivores

The Relative Importance Index combines several important variables in the determination of keystone status in one number. Power et al. (1993) derived an index for determining candidates for keystone predators that also incorporated abundance (biomass), but their index incorporated a measure of community change as a consequence of trait change as well. We do this by predicting the change in plant diversity as a consequence of removing different frugivores.

The species in the right tail of the index distribution are the strongest candidates for keystone frugivore status because they have relatively high population biomass, consume primarily fruit in their diets, and are high-quality seed dispersers. At what point in the tail you make a cut-off to nominate a species for keystone status is, however, still somewhat subjective. To be conservative, we selected the three species that were outliers to the distribution of index values of all species: cassowaries, hornbills and fruit pigeons. Considering the index and ability to move large fruits, we also consider the fruit bat a strong candidate for keystone status (Figure 5).

Potential impacts of keystone frugivore removal--

The critical criterion for designation as a keystone species is some disproportionate consequence of the removal of the species (Mills et al., 1993; Paine, 1969; Power et al., 1996; Simberloff, 1998). With exceptions (e.g. Fauth, 1999; Morgan Ernest & Brown, 2001; Paine, 1969), this has been a stumbling point in much of the discussion of keystone species because the manipulations necessary to test the criterion are difficult.

At CMBRS we have made detailed studies of seed dispersal by one of the candidate keystone species, the dwarf cassowary. Mack (1995) found that seed dispersal is essential in order that seeds be moved uphill; in the absence of dispersal by frugivores, seed shadows are strongly biased downhill. Even if fruiting trees could replace themselves from undispersed seeds, their populations would eventually collapse downhill, eliminating the need to demonstrate other potential benefits of dispersal (e.g., Janzen 1970, Howe and Smallwood 1982, (Augspurger, 1984; Bond, 1994; Schupp, 1993; Wenny, 2001). In any hilly to mountainous location dispersal by frugivores is essential for the maintenance of zoochorous plant populations. This seemingly obvious and critical dependence of large-seeded plants on frugivores has been almost completely overlooked by most studies of seed dispersal (e.g. studies within Estrada & Fleming, 1986; Fleming & Estrada, 1993).

Conservation implications

Identifying keystone species can have direct applications for conservation and management. Because it is not possible to monitor and manage all components of an ecosystem, we must focus our limited resources on taxa or attributes that will be the most informative and yield the greatest conservation dividend. Considerable discussion has occurred regarding whether and to what degree the keystone species concept is useful for conservation (Mills et al., 1993; Power et al., 1996; Kotliar, 2000; Simberloff, 1998).

Determining the utility of keystones as foci of conservation effort will require more field studies and these first require the identification of keystone candidates. Once studied, candidates for keystone status might not meet all criteria, yet studies of these species would likely still result in improved conservation planning (e.g., Galetti & Aleixo, 1998). In our example, failure to properly conserve the top frugivore species at CMWMA could result in a reduction in fleshy-fruited plant diversity of almost 20%, most of which are canopy tree species. Hammann and Curio (1999) predicted a loss of up to 60% of late successional trees if "large frugivores" were extirpated from a site in the Philippines, but their group of large frugivores included 19 species and did not identify keystones among them. The extinction of large frugivores could result in significant changes over time in the flora at a Ugandan site (Chapman & Chapman, 1995). Unfortunately the same large frugivores that are likely candidates for keystone status are also heavily hunted for human consumption (e.g. Bennett & Robinson, 2000).

CONCLUSIONS

If we accept that the keystone frugivore concept is useful for study or conservation, we are left with the seemingly intractable problem of how to identify them. The amount and frequency of fruit eating, the extent of dispersal versus predation, the abundance of the frugivore and the number and strength of its interactions with plants all determine what might be considered a keystone. Yet all of these are difficult to measure individually, much less across the full spectrum of community interactions. The method employed here can be improved and does not provide definitive answers. However, it is impossible to assess the utility of the keystone frugivore concept unless we first identify candidates and then study them.

ACKNOWLEDGEMENTS

We thank the Wildlife Conservation Society, the Ortenberg Foundation, the National Science Foundation, the Disney Corporation and the Eppley Foundation--principal sponsors of our studies of cassowaries at CMWMA. Many people have assisted over the years at CMBRS; we particularly acknowledge assistance from J. Ross Sinclair, Heinrich Jessen, and the Pawaiian people who hosted us. We thank the government of PNG for allowing us to study in PNG and the Forest Research Institute in Lae, Paul Katik and Wayne Takeuchi for help with plant identifications.

REFERENCES

Augspurger, C. K. (1984). Seedling survival of tropical tree species: interactions of dispersal distance, light gaps, and pathogens. *Ecology, 65*, 1705-1712.

Baptista, L. F. (1990). Observations of the feeding habits of some New Guinea birds in Madang Province. *Muruk, 4*, 71-74.

Beehler, B. M. (198x). Patterns of frugivory and the evolution of Birds of Paradise. *Proceedings of the XIX International Ornithological Congress*, 816-826.

Beehler, B. M. (1983). Frugivory and polygamy in Birds of Paradise. *Auk, 100*, 1-12.

Beehler, B. M., & Dumbacher, J. P. (1996). More examples of fruiting trees visited predominantly by birds of paradise. *Emu, 96*, 81-88.

Bell, H. L. (1983). A bird community of lowland rainforest in New Guinea. 6 foraging ecology and community structure of the avifauna. *Emu, 84*, 142-158.

Bennett, E. L., & Robinson, J. G. (2000). *Hunting of Wildlife in Tropical Forests: Implications for biodiversity and forest peoples* (Vol. 76): The World Bank.

Bonaccorso, F. J. (1998). *Bats of Papua New Guinea*. Washington, DC: Conservation International.

Bonaccorso, F. J., & Gush, T. J. (1987). Feeding behaviour and foraging strategies of captive phyllostomid fruit bats: an experimental study. *Journal of Animal Ecology, 56*, 907-920.

Bond, W. J. (1994). Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philosophical Transactions of the Royal society of London B, 344*, 83-90.

Chapman, C. A., & Chapman, L. J. (1995). Survival without Dispersers - Seedling Recruitment under Parents. *Conservation Biology, 9*(3), 675-678.

Coates, B. J. (1985). *Birds of Papua New Guinea: Non-passerines* (Vol. 2). Alderley: Dove Publications.

Coates, B. J. (1990). *Birds of Papua New Guinea: Passerines* (Vol. 2). Alderley: Dove Publications.

Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In P. J. d. Boer & G. R. Gradwell (Eds.), *Dynamics of Numbers in Populations* (Proceedings of the Advanced Study Institute ed., pp. 298-312). Osterbeek Wageningen, The Netherlands.

Estrada, A., & Fleming, T. H. (Eds.). (1986). *Frugivores and Seed Dispersal*. Dordrecht, The Netherlands: Dr W. Junk Publishers.

Fauth, J. E. (1999). Identifying potential keystone species from field data - an example from temporary ponds. *Ecology Letters, 2*(1), 36-43.

Fleming, T. H., & Estrada, A. (Eds.). (1993). *Frugivory and seed dispersal: ecological and evolutionary aspects* (Vol. Advances in vegetation science 15). Catemaco, Veracruz, Mexico: Kluwer Academic Press.

Frith, H. J., Crome, F. H. J., & Wolfe, T. O. (1976). Food of the fruit-pigeons in New Guinea. *Emu, 76*, 49-58.

Galetti, M., & Aleixo, A. (1998). Effects of palm heart harvesting on avian frugivores in the Atlantic rain forest of Brazil. *Journal of Applied Ecology, 35*(2), 286-293.

Gautier-Hion, A., Duplantier, J.-M., Quris, R., Feer, F., Sourd, C., Decpoux, J.-P., Duost, G., Emmons, L., Erard, C., Hecketsweiler, P., Moungazi, A., Roussilhon, C., & Thiollay, J.-M. (1985). Fruit characteristics as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia, 65*, 324-337.

Hamann, A., & Curio, E. (1999). Interactions among frugivores and fleshy fruit trees in a Philippine submontane rainforest. *Conservation Biology, 13*(4), 766-773.

Heads, M. (2001). Birds of paradise, biogeography and ecology in New Guinea: a review. *Journal of Biogeography, 28*, 893-927.

Hicks, R. K. (1988). Feeding observations at a fruiting Pipturus. *Muruk, 3*, 15.

Hicks, R. K., & Hicks, J. H. (1988a). Feeding observations of Short-tailed Paradigalla. *Muruk, 3*, 14.

Hicks, R. K., & Hicks, J. H. (1988b). Observations of birds feeding in a fruiting Planchonella. *Muruk, 3*, 10-11.

Hopkins, H. C. F. (1988). Some feeding records for Birds of Paradise. *Muruk, 3*, 12-13.

Hopkins, H. C. F. (1992). Some records of birds feeding on flowers and fruits in montane forest, near Myola, Oro Province, and Tari Gap, Southern Highlands Province, P.N.G. *Muruk, 5*, 86-89.

Hopkins, M., & Hiaso, J. (1994). *Varirata National Park trail guide* (Christensen Research Institute ed. Vol. 11). Madang: Christensen Research Institute.
Howe, H. F. (1977). Bird activity and seed dispersal of a tropical wet forest tree. *Ecology, 58*, 539-550.
Howe, H. F. (1993). Aspects of variation in a neotropical seed dispersal system. *Vegetatio, 107/108*, 149-162.
Hyndman, D. C., & Menzies, J. I. (1990). Rain forests of the Ok Tedi headwaters, New Guinea: an ecological analysis. *Journal of Biogeography, 17*, 241-273.
Janson, C. H. (1983). Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science, 219*, 187-189.
Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *American Naturalist, 104*, 501-528.
Jordano, P., & Schupp, E. W. (2000). Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahleb*. *Ecological Monographs, 70*, 591-615.
Kannan, R., & James, D. A. (1999). Fruiting phenology and the conservation of the Great Pied Hornbill (Buceros bicornis) in the Western Ghats of southern India. *Biotropica, 31*(1), 167-177.
Kotliar, N. B. (2000). Application of the new keystone-species concept to prairie dogs: How well does it work? *Conservation Biology, 14*(6), 1715-1721.
Lamothe, L. (1979). Diet of some birds in Araucaria and Pinus forests in New Guinea. *Emu, 79*, 36-37.
Loiselle, B. A., & Blake, J. G. (1999). Dispersal of melastome seeds by fruit-eating birds of tropical forest understory. *ECOLOGY, 80*(1), 330-336.
Mack, A. L. (1993). The sizes of vertebrate-dispersed fruits: a neotropical-paleotropical comparison. *American Naturalist, 142*, 840-856.
Mack, A. L., & Wright, D. D. (1996). Notes on the occurrence and feeding of birds at Crater Mountain Biological Research Station, Papua New Guinea. *Emu, 96*, 89-101.
Meehan, H. J., McConkey, K. R., & Drake, D. R. (2002). Potential disruptions to seed dispersal mutualisms in Tonga, Western Polynesia. *Journal of Biogeography, 29*(5-6), 695-712.
Menge, B. A., Berlow, E. L., Blanchette, C. A., Navarrete, S. A., & Yamada, S. B. (1994). The Keystone Species Concept - Variation in Interaction Strength in a Rocky Intertidal Habitat. *Ecological Monographs, 64*(3), 249-286.
Mills, L. S., Soule, M. E., & Doak, D. F. (1993). The keystone-species concept in ecology and conservation. *Bioscience, 43*, 219-224.
Mittermeier, R. A., Myers, N., Thomsen, J. B., Fonseca, G. A. B. D., & Olivieri, S. (1998). Biodiversity Hotspots and mjor tropical wilderness areas: approaches to setting conservation priorities. *Conservation Biology, 12*, 516-520.
Morgan Ernest, S. K., & Brown, J. H. (2001). Delayed compensation for missing keystone species by colonization. *Science, 292*, 101-104.
Olson, D. M., & Dinerstein, E. (1998). The global 200: a representation approach to conserving earth's most biologically valuable ecoregions. *Conservation Biology, 12*, 502-515.
Paine, R. T. (1969). A note on trophic complexity and community stability. *American Naturalist, 103*, 91-93.
Paine, R. T. (1995). A Conversation on Refining the Concept of Keystone Species. *Conservation Biology, 9*(4), 962-964.
Peckover, W. S. (1985). Seed dispersal of Amorphophallus paeoniifolius by birds of paradise in Papua New Guinea. *Aroideana, 8*, 70-71.
Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., Daily, G., Castilla, J. C., Lubchenco, J., & Paine, R. T. (1996). Challenges in the quest for keystones. *Bioscience, 46*(8), 609-620.
Pratt, T. K. (1984). Examples of tropical frugivores defending fruit-bearing plants. *Condor, 86*, 123-129.
Pratt, T. K., & Stiles, E. W. (1985). The influence of fruit size and structure on composition of frugivore assemblages in New Guinea. *Biotropica, 17*, 314-321.
Ridley, H. N. (1930). *The dispersal of plants throughout the world*. Ashford, Kent: L. Reeve and Co.
Schupp, E. W. (1993). Quantity, quality and the effectivenenss of seed dispersal by animals. *Vegetatio, 107/108*, 15-29.
Shanahan, M., So, S., Compton, S. G., & Corlett, R. (2001). Fig-eating by vertebrate frugivores: a global review. *Biological Reviews, 76*(4), 529-572.

Simberloff, D. (1998). Flagships, umbrellas, and keystones: Is single-species management passe in the landscape era? *Biological Conservation, 83*(3), 247-257.
Takeuchi, W. (1999). New plants from Crater Mt., Papua New Guinea, and an annotated checklist of the species. *SIDA, 18*, 941-986.
Terborgh, J. W., & Diamond, J. M. (1970). Niche overlap in feeding assemblages of New Guinea birds. *Wilson Bulletin, 89*, 29-52.
Van Schaik, C. P., Terborgh, J. W., & Wright, S. J. (1993). The Phenology of Tropical Forests - Adaptive Significance and Consequences for Primary Consumers. *Annual Review of Ecology and Systematics, 24*, 353-377.
Wahlberg, N. (1992). Observations of birds feeding in a fruiting fig Ficus sp. in Varirata National Park. *Muruk, 5*, 109-110.
Wenny, D. G. (2000). Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *ECOLOGICAL MONOGRAPHS, 70*(2), 331-351.
Wenny, D. G. (2001). Advantages of seed dispersal: A re-evaluation of directed dispersal. *EVOLUTIONARY ECOLOGY, 3*(1), 51-74.
Westoby, M. (1988). Comparing Australian ecosystems to those elsewhere. *Bioscience, 38*, 549-556.
Wheelwright, N. T. (1985). Fruit size, gape width, and the diets of fruit-eating birds. *Ecology, 66*, 808-818.
Woolley, P. A., & Allison, A. (1982). Observations on the feeding and reproductive status of captive feather-tailed possums, Distoechurus pennatus (Marsupialia: Burramyidae). *Australian Mammalogy, 5*, 285-287.
Wright, D. D. (1998). ***Fruit choice by the Dwarf Cassowary, Casuarius bennetti, over a three year period in Papua New Guinea.*** Unpublished Dissertation, University of Miami, Coral Gables, FL.
Wright, D. D., Jessen, J. H., Burke, P. B., & Garza, H. G. S. (1997). Tree and liana enumeration and diversity on a one-hectare plot in Papua New Guinea. *Biotropica, 29*, 250-260.
Wutherich, D., Azocar, A., Garcia-Nunez, C., & Silva, J. F. (2001). Seed dispersal in Palicourea rigida, a common treelet species from neotropical savannas. *Journal of Tropical Ecology, 17*, 449-458.
Zacharias, M. A., & Roff, J. C. (2001). Use of focal species in marine conservation and management: a review and critique. *Aquatic Conservation-Marine and Freshwater Ecosystems, 11*(1), 59-76.

Wildlife Conservation Society, Papua New Guinea Program, Box 277, Goroka, EHP, PAPUA NEW GUINEA

Appendix 1. List of frugivore species at the Crater Mountain study site, Papua New Guinea. The proportion of fruit potentially dispersed refers to those fruits of the 400 species measured in the study area that are both small enough and light enough to be handled by that species. The Relative Importance Index is a unit-less index based on the frugivore's abundance, degree of frugivory and size relative to other frugivores; larger values indicate greater importance as seed dispersers (see methods). The most important 15 frugivores in terms of number of plant species potentially dispersed are bold-faced as are the 15 most important in terms of the index. Note: the same species is not necessarily bold-faced for both categories.

Family	**Genus**	**Species**	**Proportion of fruit species potentially dispersed**	**Relative Importance Index**
Mammals				
Pteropodidae	*Dobsonia*	*magna*	**0.9650**	**0.0174**
Muridae	*Uromys*	*caudimaculatus*	**0.9525**	0.0127
Phalangeridae	*Phalanger*	*gymnotis*	**0.9525**	0.0133
Phalangeridae	*Spilocuscus*	*maculatus*	**0.9525**	0.0147
Macropodidae	*Dorcopsulus*	*macleayi*	**0.8925**	0.0133
Pteropodidae	*Nyctimene*	*cyclotis*	0.5950	0.0128
Pteropodidae	*Paranyctimene*	*raptor*	0.5325	0.0126
Acrobatidae	*Distoechurus*	*pennatus*	0.5200	0.0072
Peroryctidae	*Echymipera*	*kalubu*	0.5200	0.0121
Birds				
Casuariidae	*Casuarius*	*bennetti*	**0.9875**	**0.0281**
Bucerotidae	*Rhyticeros*	*plicatus*	**0.8925**	**0.0205**
Columbidae	*Ducula*	*zoeae*	**0.8175**	**0.0194**
Columbidae	*Ducula*	*chalconota*	**0.8175**	**0.0171**
Columbidae	*Ducula*	*rufigaster*	**0.8175**	**0.0154**
Columbidae	*Ducula*	*pinon*	**0.8175**	**0.0148**
Columbidae	*Otidiphaps*	*nobilis*	**0.8175**	0.0132
Corvidae	*Corvus*	*tristis*	**0.8175**	0.0129
Megapodiidae	*Talegalla*	*jobiensis*	**0.8175**	0.0124
Psittacidae	*Eclectus*	*roratus*	**0.8175**	0.0121
Columbidae	*Ptilinopus*	*magnificus*	0.7550	0.0124
Columbidae	*Columba*	*vitiensis*	0.6950	0.0125
Columbidae	*Gymnophaps*	*albertisii*	0.6950	**0.0176**

Columbidae	*Ptilinopus*	*ornatus*	0.6950	0.0141
Columbidae	*Ptilinopus*	*perlatus*	0.6950	0.0139
Columbidae	*Ptilinopus*	*rivoli*	0.6950	**0.0155**
Columbidae	*Ptilinopus*	*superbus*	0.6950	**0.0154**
Columbidae	*Reinwardtoena*	*reinwardtsi*	0.6950	0.0130
Megapodiidae	*Aepypodius*	*arfakianus*	0.6950	0.0113
Megapodiidae	*Megapodius*	*freycinet*	0.6950	0.0108
Paradisaeidae	*Manucodia*	*chalybata*	0.6950	0.0136
Paradisaeidae	*Paradisaea*	*raggiana*	0.6950	**0.0157**
Paradisaeidae	*Parotia*	*carolae*	0.6950	0.0110
Paradisaeidae	*Parotia*	*lawesii*	0.6950	0.0103
Psittacidae	*Alisterus*	*chloropterus*	0.6950	0.0098
Psittacidae	*Geoffroyus*	*simplex*	0.6950	0.0117
Psittacidae	*Psittrichas*	*fulgidus*	0.6950	**0.0150**
Sturnidae	*Mino*	*dumontii*	0.6950	0.0120
Campephagidae	*Coracina*	*boyeri*	0.5200	0.0094
Campephagidae	*Coracina*	*caeruleogrisea*	0.5200	0.0101
Columbidae	*Henicophaps*	*albifrons*	0.5200	0.0090
Columbidae	*Macropygia*	*nigrirostris*	0.5200	0.0132
Columbidae	*Macropygia*	*amboinensis*	0.5200	0.0135
Columbidae	*Ptilinopus*	*coronulatus*	0.5200	0.0116
Columbidae	*Ptilinopus*	*pulchellus*	0.5200	**0.0165**
Cuculidae	*Eudynamis*	*scolopacea*	0.5200	0.0072
Meliphagidae	*Melipotes*	*fumigatus*	0.5200	0.0097
Meliphagidae	*Philemon*	*buceroides*	0.5200	0.0092
Oriolidae	*Oriolus*	*szalayi*	0.5200	0.0114
Pachycephalidae	*Pitohui*	*dichrous*	0.5200	0.0081
Pachycephalidae	*Pitohui*	*cristatus*	0.5200	0.0086
Pachycephalidae	*Pitohui*	*ferrugineus*	0.5200	0.0094
Pachycephalidae	*Pitohui*	*kirhocephalus*	0.5200	0.0101
Paradisaeidae	*Cicinnurus*	*regius*	0.5200	0.0097
Paradisaeidae	*Cicinnurus*	*magnificus*	0.5200	**0.0153**

Psittacidae	*Pseudeos*	*fuscata*	0.5200	0.0100
Psittacidae	*Trichoglossus*	*haematodus*	0.5200	0.0095
Ptilonorhynchidae	*Ailuroedus*	*melanotis*	0.5200	0.0086
Ptilonorhynchidae	*Ailuroedus*	*buccoides*	0.5200	0.0115
Columbidae	*Ptilinopus*	*naina*	0.5150	0.0111
Cuculidae	*Microdynamis*	*parva*	0.4950	0.0116
Meliphagidae	*Meliphaga*	*aruensis*	0.4175	0.0108
Meliphagidae	*Meliphaga*	*mimikae*	0.4150	0.0138
Meliphagidae	*Pycnopygius*	*ixoides*	0.4150	0.0072
Meliphagidae	*Meliphaga*	*albonotata*	0.4125	0.0070
Meliphagidae	*Meliphaga*	*analoga*	0.4100	0.0062
Psittacidae	*Loriculus*	*aurantiifrons*	0.2600	0.0070
Campephagidae	*Lalage*	*leucomela*	0.2550	0.0091
Columbidae	*Gallicolumba*	*jobiensis*	0.2550	0.0062
Columbidae	*Gallicolumba*	*rufigula*	0.2550	0.0078
Cuculidae	*Cuculus*	*saturatus*	0.2550	0.0051
Dicaeidae	*Melanocharis*	*longicauda*	0.2550	0.0085
Dicaeidae	*Melanocharis*	*nigra*	0.2550	**0.0169**
Meliphagidae	*Lichenostomus*	*obscurus*	0.2550	0.0082
Meliphagidae	*Pycnopygius*	*cinereus*	0.2550	0.0056
Meliphagidae	*Xanthotis*	*flaviventer*	0.2550	0.0102
Meliphagidae	*Xanthotis*	*polygramma*	0.2550	0.0104
Psittacidae	*Charmosyna*	*wilhelminae*	0.2550	0.0041
Psittacidae	*Charmosyna*	*multistriata*	0.2550	0.0044
Psittacidae	*Charmosyna*	*pulchella*	0.2550	0.0096
Psittacidae	*Charmosyna*	*placentis*	0.2550	0.0097
Psittacidae	*Cyclopsitta*	*diophthalma*	0.2550	0.0079
Psittacidae	*Cyclopsitta*	*gulielmiterti*	0.2550	0.0126
Psittacidae	*Lorius*	*lory*	0.2550	0.0098
Psittacidae	*Psittaculirostris*	*desmarestii*	0.2550	0.0098
Psittacidae	*Trichoglossus*	*goldei*	0.2550	0.0049
Zosteropidae	*Zosterops*	*novaeguineae*	0.2125	0.0066

Zosteropidae	*Zosterops*	*atrifrons*	0.1550	0.0103
Dicaeidae	*Dicaeum*	*pectorale*	0.0750	0.0104