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I.1

Current issues and new approaches in primate ecology and conservation

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Introduction

Primate ecology originated more than 50 years ago from the studies of Carpenter (1934, 1940) on howler monkeys and gibbons, but it has only really developed in the last 20 years following the 1960s boom in primate field studies (DeVore, 1965; Altmann, 1967; Jay, 1968). Attention was focussed on the ecological aspects of primate behaviour by the work of Crook & Gartlan (1966) and Eisenberg, Muckenhirn & Rudran (1972), when it became apparent that social behaviour was influenced by habitat, producing differences even between populations of the same species. This has led to a dichotomy in primate field studies, and in related captive and laboratory studies.

While many continue to quantify the details and dynamics of social behaviour (see *Proceedings* Volume 3; *Primate Ontogeny, Cognition and Social Behaviour* (CUP, 1986)), others have concentrated on the equally detailed study of vegetation, feeding and ranging behaviour and inter-specific relations in the community. Such studies are essential for contributing to the explanation of patterns of social behaviour observed, and for the conservation of primate populations, whether it be the protection of natural ecosystems or the management of disturbed habitats.

While concern about the over-exploitation of wildlife was first transformed into action over 80 years ago (Fitter & Scott, 1978), conservation has only developed in the last 10 years, certainly as a science (e.g Soulé & Wilcox, 1980; Sutton, Whitmore & Chadwick, 1983), as human destruction of natural ecosystems has escalated to the extent that it threatens the long-term survival of humans as well as of other animals. Because of their close relationship to humans, and their relatively large size (especially in forest ecosystems), primates have a

special role to play in the development of strategies of environmental protection and management.

Let us consider briefly recent developments and future potentials of primate ecology and conservation, and their inter-relationships.

Primate ecology

Ecological study involves quantitative descriptions of:

1. The habit in terms of (a) plant form and species composition, distribution and abundance, with the collection of samples for identification and chemical analysis, and (b) faunal composition, especially birds and mammals but also key invertebrates (i.e. potential competitors for resources)
2. The size and composition of social groups in each primate species studied, and how this varies with habitat, activity and time
3. Activity patterns and budgets, with special reference to (a) movements vertically and horizontally through the habitat, and (b) food selection at different times of the day, month and year and in successive years
4. All aspects of foraging and ingestive behaviour, in relation to more detailed captive studies of food preparation and ingestion
5. The nature and frequency of intra- and inter-specific interactions, to develop an understanding of relationships within the community.

Such information leads to the formulation of ecological strategies for each species studied, identifying the relation between foraging strategy and social system, and estimating the intake of energy relative to its output (a topic that has been little investigated in the field, mainly because of the difficulties involved in its measurement). It is also increasingly important to document spatial and temporal variation in all these aspects of ecology, so as to explain more fully patterns of habitat use within and between species.

Captive studies are essential for pursuing the investigation of energetics and useful for explaining foraging strategies, mainly food selection, in terms of the content of nutrients, digestion-inhibitors and toxins in each food. Laboratory analysis reveals the constituents of each food and the digestive capabilities of each primate for different foods.

What progress have we made with such ecological studies, and in what di. .ions are advances most needed? Crook & Gartlan (1966)

equated small social groups with forest habitats and large social groups with more open savannah habitats; there were small groups again in the most open (arid) habitats. Eisenberg *et al.* (1972) linked dietary preferences with different habitats and social structure. Such generalities provoked more precise investigation on a large scale.

Kay (1973) was among the first of many to illustrate a closer correlation between body size and diet, with the smallest primates being insectivorous, the largest folivorous, and primates of intermediate size frugivorous; smaller frugivores had insects as the main supplement, large frugivores ate leaves as well as fruit. An even closer correlation was found between the biomass (kg/km^2) of a specific primate population and diet (proportions of animal matter, fruit and foliage) by Hladik & Chivers (1978). Home-range size and metabolic needs have been included in correlative studies (Harvey & Clutton-Brock, 1981; Mace *et al.*, 1983). One of the most thorough analyses has been that of Clutton-Brock & Harvey (1977); they established seven ecological categories of primate (three nocturnal, four diurnal) from a detailed analysis of measures of body size, arboreality, frugivory/folivory, home-range size and group size.

Even these refined techniques, however, do not produce conclusive results. The ecological categories tend to be too broad, some are more cohesive than others and some variables vary more than others between ecological categories; the data come from many sources and are not always truly comparable. Altmann pointed out as early as 1974 that a variety of confounding variables impeded this approach of correlation, and Richard (1985) stressed the value of examining the distribution of single variables to understand the functional significance of different forms of social organisation.

The sequence of events started by Crook & Gartlan (1966) was initiated by Hall's (1963) conclusion that group size represents adaptations to different environments; this followed on from the observation that smaller groups occurred in more impoverished environments. It is perhaps a pity that the former was pursued at the expense of the latter, since the inconclusive results would seem to stem from a failure to appreciate that it is habitat quality which is the key to primate socio-ecology, and that it can be as variable within habitat types as between them.

Abundant data are now available on the habitats and diets of different primates (e.g. Clutton-Brock, 1977; Davies, Caldecott & Chivers, 1984; and from community studies, see below). Dietary information is mainly in terms of the time spent eating diff nt foods,

which is the most accessible information to the field worker, and the most relevant to the ecological aspects of activity budgets. For understanding nutrition and energetics, however, the most relevant information is the weight of each food consumed, and progress is slowly being made to produce such data (e.g. Hladik & Hladik, 1972; Goodall, 1977; Hladik, 1977*a*, 1977*b*, 1978; Iwamoto, 1978; Chivers & Raemaekers: Chapter II.3). Such studies mark the start of the analysis of foods for nutrients – sugars, protein, fats, vitamins, minerals and trace elements – which led on to the analysis of foods for secondary compounds – digestion inhibitors and toxins – (McKey *et al.*, 1978, 1981; Oates, Waterman & Choo, 1980; Milton, 1980; Vellayan, 1981; Waterman & Choo, 1981; Wrangham & Waterman, 1982; Ganzhorn: Chapter II.1; Harrison: Chapter II.2).

Feeding behaviour can now be explained as a compromise between obtaining essential nutrients and avoiding harmful substances (although Waterman (1983) cautions us from over-emphasising the role of secondary compounds in food selection). Primates generally select a diet rich in protein and carbohydrate and low in fibre (and tannins or alkaloids). Thus, we are beginning to understand why many primates have such a varied diet, why they select the plant species and parts that they do, and why they eat what they do when preferred fruits are scarce. This requires knowledge of what is available in each habitat, when and in what amounts (see below). Consideration is now being given to passage rates through the gastrointestinal tract for different diets in different species (e.g. Milton, 1984), because of its significance for digestion, but little attention has been given to the role of taste in food selection (Hladik & Chivers, 1978), perhaps because of the experimental difficulties involved. The study of energy intake in relation to expenditure is also being developed (e.g. Waser & Homewood, 1979; Mace *et al.*, 1983).

This has shifted the research emphasis into the laboratory, but field workers are still pre-eminent in its development since it has proved difficult to involve laboratory workers, with the notable exception of Peter Waterman (but see Nordin, 1981; Kemnitz & Neu: Chapter II.6); nutritionists seem generally to be totally involved with human problems. The impetus for field work is still sustained by the questions posed by plant and food chemistry. For example, seed-eating by colobine monkeys in West Africa was thought to be a consequence of poor soils producing plants so well defended chemically that even the colobine monkeys with their sacculated stomachs could not find sufficient digestible leafy foods (McKey *et al.*, 1981); parallel situations

have been found in South-east Asian colobines in North-east Borneo (Davies *et al.*, 1984) and in gibbons on the Mentawai Islands (Whitten, 1980). Now, however, Harrison (Chapter II.2) has found the same West African colobine monkey eating even more seeds in forest growing on rich soils. The answers will come from more extensive, problem-orientated field work.

While these dietary studies have been used to explain the evolution of primate social systems (e.g. Wrangham, 1980), they become more meaningful in a broader sense when considered in relation to the evolution of flowering plants (Ripley, 1984) and the co-evolution of plants and animals (Freeland & Janzen, 1974; Gilbert & Raven, 1975). The relationship between primates and their habitats needs further elucidation by primate ecologists, along with a clearer understanding of the inter-relationships between primate species in the same habitat, and between primates and other animals, particularly those occupying similar ecological niches.

Long-term community studies (e.g. Madagascar: Charles-Dominique *et al.*, 1980; Uganda: Struhsaker, 1978; Malaysia: Chivers, 1980; Peru: Terborgh, 1983; Panama: Leigh, Rand & Windsor, 1982) have shown how primates of different sizes, social structure and diet are integrated into a community within the same habitat, by minimising competition through the development of different strategies. In Malaysia, for example, lorises forage individually for insects and fruit by night, monogamous family groups of gibbons defend territories in which they exploit small fruit sources, multi-male groups of macaques forage widely for large fruit sources, and one-male groups of langurs exploit foliage intensively, consuming the seeds of fruit eaten, rather than dispersing them directly as do the more frugivorous primates. Such studies allow comparison of different species of the same genus in the same habitat (see also Hladik, 1977*a*; Fleagle & Mittermeier, 1980; Nash: Chapter III.4) and in different habitats (e.g. Lindburg, 1980; Caldecott & Fa, unpublished; Davies & Oates, unpublished), as well as of the same species in different habitats (e.g. Hrdy, 1977).

These studies of foraging strategies and niche separation are best studied in long-term research programmes in well-established field stations. There is a good geographical spread of such stations of differing longevity, intensity of study and continuity, except in the highly threatened forests of South America (Table 1). While the research returns from such long-established sites, with their ever-extending data-bases, are exponential, the inevitable focus on particular species, while productive in some respects, will be limiting in

others. Hence the continuing need for studies in other sites, mainly to accumulate information on, and improve our understanding of, ecological variation in all the features mentioned above within and between species. As with the colobine monkeys, it is only by increasing the number of studies on feeding behaviour in relation to habitat, that the data from long-term stations can be fully explained and the ecology of the taxon properly understood.

Thus, there is a need to consolidate on, and improve the financial viability of, the network of long-term research stations for ecological research, and to develop problem-orientated research programmes at such stations and wherever else may be necessary, with the appropriate laboratory follow-up. In ecological terms the emphasis should be on plants (their diversity, production cycles of leaves, flowers and fruit, pollination and seed dispersal), and the diets and foraging strategies of primates (and other competing animals) – that is, the use of such resources by each species within the community framework.

Table 1. *New and old sites of long-term studies of primate socio-ecology*

Africa	Asia	America
Tiwai Island (Sierra Leone)	Polonnaruwa (Sri Lanka)	Hacienda la Pacifica and Santa Rosa National Park, Guanacaste (Costa Rica)
Tai Forest (Ivory Coast)	Aligarh	Barro Colorado Island (Panama)
Korup Forest Reserve (Cameroun)	Jodhpur	Raleighvallen-Voltzberg Reserve (Surinam)
Makokou	Anamalai Wildlife Sanctuary (India)	Fuframa, near Manaus
Lope-Okanda Reserve (Gabon)	Khao Yai National Park (Thailand)	Fazenda Montes Claros, Minas Gerais (Brazil)
Parc des Volcans (Rwanda)	Krau Game Reserve (West Malaysia)	
Kibale Forest (Uganda)	Sepilok Reserve, Sabah	
Amboseli National Park (Kenya)	Samunsam Reserve, Sarawak (East Malaysia)	
Gombe Stream Reserve	Gunung Leuser Reserve (Sumatra)	
Mahale Mountains	Tanjong Puting Reserve and Kutai Forest Reserve, Kalimantan (Indonesia)	
Mikumi National Park (Tanzania)		
Berenty Reserve (Madagascar)		

Primate conservation

Conservation, in the broadest sense, involves:

1. The protection of the full diversity of natural ecosystems;
2. The management of disturbed habitats for sustained yields of plant and animal products, which requires that the resident species flourish; and
3. The rescue of primates (and other animals) made homeless by habitat clearance for agriculture, for translocation and/or (as a last resort) for captive breeding for research on nutrition and reproduction (in particular), essential health research and/or reintroduction to semi-natural habitats for education (including tourism) and research.

This requires the identification of areas for total protection and for sustained management through ecological survey and study, and the appropriate political and financial lobbying for their establishment, followed by rigorous monitoring and management. From the primate viewpoint, zoogeographical (Marsh, in press) and socio-ecological (Raemaekers & Chivers, 1980; Chivers, in press) considerations are essential, to provide a regional overview to what will inevitably be a national activity. From the human viewpoint, long-term environmental stability and economic prosperity (Myers, 1979, 1983) are essential. At first glance the needs of primates and humans might appear incompatible, but this is clearly not so; recent events in Africa (droughts and famine), Asia (devastating floods, soil erosion and fires) and South America (droughts and famine, disruption of river-based economies) show that environmental mismanagement works to the detriment of both wildlife and people.

Tropical rain-forest is the most threatened primate habitat (see also Mittermeier: Chapter VI.7), because of its economic important (in the short term according to current practices) and because its inhabitants are more specialised in their arboreal adaptations than those primates exploiting more terrestrial niches. Since such primates are wholly or mostly arboreal, and because they are among the largest of forest animals, they are excellent indicators of the health of the forests concerned, and, because of their close relationship to humans, ideal focal ('flagship') species for publicising the threats to their habitats. This is just a means to an end, however, since it is the whole ecosystem (and its diversity) which one is seeking to conserve – for humans as well as primates, and all the other animals and plants on which they depend.

The long-term value of tropical forests has been widely publicised (e.g. IUCN/WWF campaigns; Myers, 1979, 1983); they are both environmental and economic, global as well as local (Table 2). However widely the problems are appreciated, the pressures are such that the appropriate solutions are not being implemented sufficiently rapidly. It is a matter of immediate economic necessity *versus* long-term stability, the transition from the former to the latter being difficult. The crisis is growing as developing countries seek to escape from the spiral of large incomes from the sale of timber and forest products in the short term with much uncertainty about the future, into a long-term strategy of survival and prosperity from sustained yields. However much income for development can be derived from sacrificing the forest, and whatever one's beliefs about the viability of monocultures in monsoonal or ever-wet regions, the costs in terms of environmental catastrophes and poor or lost yields are likely to be prohibitive (e.g. Myers, 1979, 1983; Furtado, 1980; Sutton *et al.*, 1983).

The solutions have three aspects (Table 2):

1. The establishment of national parks and reserves to give total protection to watersheds (thereby protecting ecosystems at higher altitudes) and representative areas of lowland ecosys-

Table 2. *Conservation of tropical rain-forests (from Chivers, in press)*

Values (long-term)	Pressures	Solutions
Water and soil balance Climate rainfall pattern atmospheric gas balance	Hunting Harvesting Farming	Total protection of watersheds and significant representatives of each ecosystem, especially those with high plant/animal diversity
40–50% world's plant and animal species genetic diversity pivotal plant/animal links	Pet trade Power water oil	Wide-ranging management of buffer zones to reserves for sustained yields
Sustained yields timber, canes, fibres gums, waxes, resins, foods–plant and animal medicines	Selective logging Clear-felling for timber for fuel for agriculture	Agro-forestry and agriculture in areas cleared of forest, with improved efficiency
Education and research Recreation		

tems (which tend to be the most abundant and diverse in terms of flora and fauna)

2. The efficient management of substantial buffer zones to these sanctuaries, and of other available tracts of forests and other ecosystems, for sustained yields of the great variety of plant and animal products available
3. The more efficient use of land already deforested for agriculture, with the development of agro-forestry where possible.

These approaches are already being developed in various tropical countries, but the international community must give more support in terms of funds and expertise, to make full use of the available manpower and, at the same time, reducing the excessive demand for products such as cheap timber and beef. If forest clearance can be reduced (preferably to zero), and protected and managed areas can be increased, there is still time to restore a long-term balance. For example, while forest clearance has continued in South-east Asia, the area of protected forests has increased in the last few years (Table 3), even though figures for protected forests may include significant areas of production forest.

Primate ecology and conservation

The ecologist is a significant member of the band of environmental scientists who have an important role to play in the long-term strategy of maintaining environmental stability and promoting the economic productivity of various ecosystems.

The primate ecologist is already identifying the ecological and behavioural needs of a wide variety of primates (although not necessarily the most endangered ones), which are central to the establishment of protected areas with the correct (and adequate) resources, and to the management of disturbed areas. Surveys are only really meaningful in the light of systematic data collected during long-term studies. Primate ecologists have a major contribution to make in identifying critical situations and in pressing for the appropriate remedies; for example, they are contributing to the action plans being developed for Africa (Oates, unpublished), Madagascar (Pollock, unpublished), Asia (Eudey, unpublished) and the Americas (Mittermeier, unpublished) as the Primate Specialist Group's (of the Species Survival Commission of IUCN) contribution to the World Conservation Strategy.

A start has already been made, somewhat belatedly, in assessing the tolerance of various primates to disturbance (Wilson & [illegible]son, 1975;

Table 3. *Protected forests in some South-east Asian countries (from Chivers, in press)*

Country	Total land area km²	1975[a] Forested area km²	%	Protected forests km²	%	1985[b] Protected forests actual + proposed km²	%	(proposed only) %
'Assam'	121900	47900	39	235	0.2	4937	4	(0)
Bangladesh	142776					4498	3	(1)
Burma	678033					11886	2	(1)
Thailand	514910	94452	18			41484	8	(0)
West Malaysia	128013	66950	52	8150	6	39138	31	(5)
East Malaysia	201727	128700	64	1740	1	71297	35	(2)
Indonesia								
Sumatra	473970	260000	55	18280	4	76597	16	(3)
Java	126501	28000	22	2422	2	12294	10	(4)
Kalimantan	539500	419000	78	11410	2	105724	20	(11)

[a] from Chivers (1977)
[b] from Protected Areas Data Unit, Conservation Monitoring Centre, Cambridge

Marsh & Wilson, 1981; Johns, 1983 and in progress; Johns & Skorupa, in press). In South-east Asia, for example, while orang-utans and proboscis monkeys are intolerant of disturbance, gibbons and langurs (and macaques) seem to survive well, at least in the long term, after light selective logging (10 trees/ha or 4% of trees), even though up to 45% of trees may be damaged in the process.

Although Wolfheim (1983) suggests that larger primates are more vulnerable to disturbance, because they need more food and space, occur at lower densities, breed more slowly, are more vulnerable to hunters and tend to be more recently derived and specialised, Johns & Skorupa (in press) show, by an elegant analysis, that diet is a stronger indicator of survival ability than is body size. The extent and rate at which disturbed forests regenerate exploitable foods is probably crucial, and the more rapid regeneration of foliage than fruit will favour the more folivorous primates. Complementing the study of primate survival in disturbed habitats, is the study of primates (and other animals) in forest patches of different sizes (Lovejoy *et al.*, 1983), which has important implications for reserve design and topical theories about island biogeography (e.g. Soulé & Wilcox, 1980).

Thus, there is plenty of scope for ecologists in disturbed habitats, and in helping to resolve the conflict between humans and primates in more open habitats fringing cultivated areas (see Part V). Ecologists take a back seat, however, in those aspects of conservation involving captive breeding, when the integration of reproductive physiology and behaviour becomes essential. The reintroduction of surplus captive animals, and the translocation of homeless animals, bring the ecologist to the fore again. These are conservation tools that have not been adequately considered or tested for primates as they have for other mammals, although there are important exceptions (Beck *et al.*, in press; Strum, in press). Costs and practical problems tend to be prohibitive, but we need to pursue actively all possibilities. In addition to educational and conservation publicity values, reintroduction does seem to be feasible for the smaller primates that are easy to breed and maintain in captivity. For larger primates, translocation offers the best prospects if suitable, unpopulated habitat is available. It is the social complexity of primates which tends to prevent their successful movement, especially from captivity, but there are exceptions which we need to identify without delay.

Finally, it should be emphasised that all primatologists, especially ecologists, must be prepared to devote considerable time and energy to applying the academic fruits of their labours to the conservation

problems outlined above, or the subjects of their more erudite research will be lost for ever. Success ultimately lies in being able to influence commerce and politics in order to secure environmental stability and long-term productivity (see Part VII; Sutton *et al.*, 1983). We must step beyond the bounds of academic research and coordinate our efforts with sympathetic industrialists and economists in the political arena, where the crucial decisions are made.

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