



British Ecological Society

The Distribution of Feeding Habits Among Animals in a Tropical Rain Forest

Author(s): J. L. Harrison

Source: *Journal of Animal Ecology*, Vol. 31, No. 1 (Feb., 1962), pp. 53-63

Published by: [British Ecological Society](#)

Stable URL: <http://www.jstor.org/stable/2332>

Accessed: 22/03/2011 19:17

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=briteco>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



British Ecological Society is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Animal Ecology*.

<http://www.jstor.org>

THE DISTRIBUTION OF FEEDING HABITS AMONG ANIMALS IN A TROPICAL RAIN FOREST

BY J. L. HARRISON

*Queensland Institute of Medical Research**

Tropical Rain forest is an enormously complicated habitat, of which the animals have been so far but little studied. Our knowledge of these animals, however, is now emerging from the taxonomic stage, and the botanical studies, upon which the zoological are inevitably based, are now sufficiently advanced to support this. In particular the invaluable work of Richards (1952) has done much to draw together scattered knowledge and make it available to the non-botanist.

The great difficulty in the study of Rain forest is one of integration. It is literally true to say that one cannot see the wood for the trees. There is no one position in which one can stand and get a good view of a complete sample of forest, and it is correspondingly difficult to visualize the relationships between, say, animals living on the forest floor and those out of sight in the canopy, perhaps a hundred feet above. In such circumstances, ideas and patterns into which one can fit (or fail to fit) one's observations assume a special value. The present paper uses the results of some observations, made over the last decade, on the food of mammals in Malaysian and Australian Rain forests to draw up a simple scheme of the classification of feeding habits within forest of this kind.

THE STRUCTURE OF TROPICAL RAIN FOREST

This subject is discussed at some length in most ecological text-books, but, since the terminology varies slightly, it needs to be summarized for the present purpose.

Physically, Rain forest is composed of woody plants. The trees of the main storey rise on 30 m or more of slim, bare trunk to small, compact crowns, which are usually more or less in contact. Below and between these are the smaller trees, of the under-storey, either young specimens of the giants, or smaller species, which fill up small gaps and generally reinforce the overhead cover, so that there is no clear view of the sky. Beneath the trees are layers of shrubs, and of sparse herbage which are developed in inverse proportion to the completeness of the overhead cover, so that Rain forest with a completely unbroken canopy is relatively bare underfoot. The whole of this structure is bound together with lianes (woody climbing plants) and plentifully sprinkled with epiphytes.

Taxonomically there is a bewildering array of species. Exceptionally stretches may be dominated by one species of tree, but normally the variety is such that two trees of the same species are rarely in view at the same time. Thus Wyatt-Smith (1949) records 227 species among the 559 trees per hectare in Lowland Rain forest near Kuala Lumpur, of which the most abundant species comprised less than 7%. When a major tree falls the resulting space is filled by the sudden rapid growth of the smaller trees, one of which will usually win the race to fill the gap. A tree is thus rarely replaced by another specimen of its own species, and the diversity is maintained.

To this diversity is added a comparative lack of seasonal variation, so that flowering and fruiting of the various species are spread throughout most of the year. Thus, even

* Now at Nanyang University, Singapore, 22.

though the trees of one species may fruit together, the individuals are so scattered that there is little variation in the availability of flower or fruit. They are never specially abundant, but on the other hand they are usually present.

Much thought has gone into elaboration of the classification of the horizontal layers into which the forest may be divided. Richards (1952) uses a system of five layers, A to E, which we may describe, for Malaysian conditions (using data from Wyatt-Smith 1952), as: A—the emergent layer, the tops of the tallest trees projecting above the general level of the forest, 30-45 m high or more in Malaya; B—the main storey, 20-30 m high, which usually forms a continuous canopy; C—the under-storey; D—the shrub layer; and E—the herb layer.

Different forests differ in the degree to which any one of these layers may provide an effective ground cover. Thus the main storey, B, may be so dense as virtually to exclude light from the under storey, C; or it may be discontinuous, so that the effectively complete cover is provided by the under-storey.

These three storeys, however, are a refinement of classification into which, at present, the zoologist has insufficient data to fit his animals. It may be summarized by saying that in Tropical Rain forest the ‘canopy’, consisting of layers A to C, forms a complete unbroken vegetable layer, which effectively excludes bright light (other than sun-flecks) from the forest floor, and which provides a continuous zone within which animals may move.

ZONATION OF ANIMAL LIFE

There is no doubt that, as our knowledge increases, it will be possible to correlate different animal communities with the different layers enumerated above. Colquhoun & Morley (1943) found it necessary to distinguish five layers in an English oak-wood to accommodate a bird fauna of less than thirty species, so the subdivisions necessary to define niches for the three hundred or more birds of Malayan forest can well be imagined. With such a bewildering array of possibilities, it is clearly desirable to provide some simple, basic scheme of classification.

Mammals provide a good subject for a classification of this sort, and, as a result of many years collecting in Malaysia, a clear impression had been gained as to where any one species was to be found. Some years ago, an attempt was made to follow such examples as those of Allee (1926), and divided up the species of mammals, other than bats, recorded from forests of the Malay Peninsula into three zones, using this impression as criterion. The result, in numbers of species was (Harrison 1957):

Canopy mammals	23 species
Under-canopy mammals	23 species
Ground mammals	51 species*

Having obtained this classification an attempt was made to work backwards and define the layers represented by them. The classification was then found to be unsatisfactory in two particulars. The group of ‘under-canopy animals’, although representing a recognizable community, did not correspond to any layer that could be called an ‘under-canopy’; rather they were animals with a vertical distribution, to be found both in the canopy and on the ground. Secondly the group ‘ground mammals’ appeared to contain two different elements: small mammals, such as rats, with considerable climbing abilities, which were

* A misprint in Harrison (1957) shows nineteen ‘ground rats’ instead of the correct figure of nine.

not always easy to differentiate clearly from the 'under-canopy' group; and large animals, such as elephants and deer, with no climbing ability, but which were able to crop leaves from the bushes and smaller trees.

Table 1. *Malayan mammals: numbers of different species known to occur in the Lowland forest of the Malay Peninsula classified by level and by feeding habits*

F = Fruit; L = leaves; V = vegetable matter; I = insects, etc.; C = carnivorous

Group	Genus or sub-family	No. of species	Feeding habits
1. Canopy mammals (23)			
Primates	<i>Hylobates</i> (gibbons)	2	2 F
	<i>Presbytis</i> (leaf monkeys)	3	3 L
	<i>Nycticebus</i> (slow loris)	1	1 FI
Rodents	<i>Ratufa</i> (giant squirrels)	2	2 F
	Flying squirrels	10	4 F, 6 IF
	Arboreal rats (<i>Hapalomys</i> , etc.)	3	3 F
Other mammals	<i>Cynocephalus</i> (flying lemur)	1	1 L
	<i>Ptilocercus</i> (pen-tail tree-shrew)	1	1 I
2. Middle-zone mammals (21)			
Primates	<i>Macaca</i> (monkeys)	2	2 IF
Carnivores	<i>Martes</i> (marten)	1	1 C
	<i>Prionodon</i> (linsang)	1	1 C
	Paradoxurinae (civets)	5	5 IF
	<i>Neofelis</i> (clouded leopard)	1	1 C
Rodents	<i>Callosciurus</i> (tree squirrels)	7	7 IF
	<i>Rattus</i> (tree rats)	2	1 F, 1 IF
Insectivores	<i>Tupaia</i> (tree-shrews)	2	2 IF
3. Large ground mammals (17)			
Elephant	<i>Elephas</i>	1	1 L
Perissodactyls	<i>Didermocerus</i> (rhinocerus)	1	1 L
	<i>Tapirus</i> (tapir)	1	1 L
	<i>Sus</i> (pigs)	2	2 V
Artiodactyls	Cervidae (deer)	2	2 L
	<i>Tragulus</i> (mouse deer)	2	2 F
	<i>Bos</i> (Gaur)	1	1 L
Carnivores	<i>Panthera</i> (tiger and leopard)	2	2 C
	<i>Helarctos</i> (bear)	1	1 IVC
	<i>Cuon</i> (wild dog)	1	1 C
Rodents	Hystriidae (porcupines)	3	3 V
4. Small ground mammals (28)			
Carnivores	Viverrinae (civets)	4	4 IF
	<i>Felis</i> (small cats)	4	4 C
	<i>Mustela</i> (stoat)	1	1 C
Rodents	<i>Lariscus</i> and <i>Rhinosciurus</i> (ground squirrels)	2	1 F, 1 I
	<i>Rattus</i> (ground rats)	6	1 V, 5 IF
	<i>Rhizomys</i> (bamboo rats)	2	2 V
Insectivores	Erinaceidae (moonrat and short-tailed shrew)	2	2 I
	Soricidae (shrews)	6	6 I
Others	<i>Manis</i> (scaly anteater)	1	1 I

The mammal communities may, therefore, be re-defined as follows: (1) THE CANOPY MAMMALS confined to the continuous leafy layer which provides a complete and continuous cover (corresponding to Richards's layers A, B, and C); these animals normally have no contact with the ground. (2) MIDDLE-ZONE MAMMALS of scansorial habit which range

vertically up and down the tree-trunks between the canopy and the ground. (3) LARGE GROUND MAMMALS, living on the ground surface, too heavy for scrambling among bushes, and with no climbing ability. (4) SMALL GROUND MAMMALS which live on and in the ground surface, ranging on to bushes, fallen trees, and the lower parts of tree-trunks (Richards's layers D and E). It is comparatively easy to allot mammals to one or another of the groups defined in this way, and this has been done in Table 1 for all the species recorded from Lowland Forest in Malaya (Harrison 1957). Occasional allocations are arbitrary. Thus, the Malay bear (*Helictus*) has been allotted to group (3) on size, although its climbing ability could put it into group (2). *Neofelis* has been allotted to group (2), and *Panthera pardus* to group (3), although there is not a great deal of difference in their climbing abilities. This, however, is saying no more than that not all animals will fit into an arbitrary scheme of classification.

Feeding habits within zones

Normal food is much more difficult to determine than normal dwelling place, especially for the smaller species. Luckily the results of a number of stomach examinations are now available (Harrison 1954, and in press, a), and it is possible to decide with reasonable confidence what the various species normally eat. The results of these decisions have been summarized in Table 1, classified as: L for leaf, F for fruit and nectar, V for vegetable, I for insect-eating, and C for carnivorous. 'Vegetable' is an all-embracing term for vegetable matter of all kinds, mostly tubers, stem and bud material, but including fruit, leaves and, presumably, fungi; the class is included for such animals as ground rats which appear to eat a very wide range of foods. All invertebrates eaten, and some small vertebrates, such as small geckos, have been included in I for insects, but the flesh of the larger vertebrates comes under C for carnivorous. Species taking a mixed diet are shown with two or more food groups — thus, most rats are IV eating both insects and vegetable matter.

Table 2. *Malayan mammals: summary of the numbers of species by zone and feeding habits and (in parentheses) their percentages of the whole fauna*

Zone	No. of species	No. of species with diet of:			
		Plant (F, L and V)	Mixed (IV, IF, etc)	Insect (I)	Flesh (C)
Canopy	23 (26)	15 (17)	7 (8)	1 (1)	0
Middle zone	21 (24)	1 (1)	17 (19)	0	3 (3)
Large Ground Mammals	17 (19)	13 (15)	1 (1)	0	3 (3)
Small Ground Mammals	28 (31)	4 (4)	9 (10)	10 (11)	5 (6)
Total	89 (100)	33 (37)	34 (38)	11 (12)	11 (12)

When the numbers taking plant foods of all kind, mixed, insect, or flesh food, are added together by zones we get the distribution shown in Table 2. It is at once clear that the mammals of each community exhibit a characteristic pattern of feeding. The canopy mammals are predominantly plant feeders, the middle-zone mammals are overwhelmingly mixed feeders, the small ground mammals are about equally mixed feeders or insectivorous, while the large ground mammals are overwhelming plant feeders — indeed the sole exception (the Malay Bear) has already been noted as possibly more correctly to be placed in the middle zone. Carnivores are generally distributed, although, having a wide range of movement, none can be considered as confined to the canopy.

AUSTRALIAN RAIN FOREST MAMMALS

Tropical Rain forest, botanically very closely related to that of Malaysia, occurs as a narrow fringe on the north-eastern coast of Queensland. The mammal fauna is poorer than that of Malaya (Harrison 1960, and in press, b) and, with the exception of rats and pigs, it is composed of animals which are taxonomically very different. Tate (1952) records twenty-eight species other than bats from the Rain forest of the Cape York Peninsula, and these, with the exception of the platypus (*Ornithorhynchus*), which is almost wholly aquatic, but with the addition of feral pigs, which Tate does not list, are shown by zones and diets in Table 3. The information on feeding habits is from that given by Troughton (1946) and Harrison (in press, b) but is not so complete as that for the Malayan species.

Table 3. *Australian mammals: numbers of different species recorded from Rain forest of the Cape York Peninsula classified as in Table 1*

F = Fruit; L = leaves; V = vegetable matter; I = insects, etc.; C = carnivorous

Group	Genus or family	No of species	Feeding habits
1. Canopy mammals (8)			
Marsupials	<i>Phalanger</i> (cuscuses)	2	2 FI
	<i>Petaurus</i> (gliders)	2	2 FI
	<i>Pseudocheirus</i> (ring-tails)	3	3 L
	<i>Schoinobates</i> (greater glider)	1	1 L
2. Middle-zone mammals (9)			
Marsupials	<i>Antechinus</i> (marsupial mouse)	1	1 I
	<i>Dasyurops</i> (native cat)	1	1 C
	<i>Trichosurus</i> (brush-tail possum)	1	1 VI
	<i>Dactylopsila</i> (striped possum)	1	1 I
	<i>Eudromicia</i> (pigmy possum)	1	1 VI
	<i>Dendrolagus</i> (tree-kangaroos)	2	2 L
Rodents	<i>Melomys</i> (naked-tailed rat)	1	1 VI
	<i>Uromys</i> (giant naked-tailed rat)	1	1 VI
3. Large ground mammals (3)			
Marsupials	<i>Thylogale</i> (pademelon or scrub-wallaby)	1	1 L
	<i>Protemnodon</i> (wallaby)	1	1 L
Artiodactyls	<i>Sus</i> (feral pig)	1	1 V
4. Small ground mammals (8)			
Monotremes	<i>Tachyglossus</i> (echidna)	1	1 I
Marsupials	<i>Sminthopsis</i> (marsupial mouse)	1	1 I
	<i>Perameles</i> (bandicoot)	1	1 I
	<i>Echimypera</i> (bandicoot)	1	1 I
	<i>Hypsiprymmodon</i> (rat-kangaroo)	1	1 IF
Rodents	<i>Hydromys</i> (water rat)	1	1 C
	<i>Rattus</i> (rats)	2	2 IV

The results are summarized in Table 4, and the similarity to Table 2 is at once apparent. Again plant feeders predominate in the canopy, and among the large ground mammals; mixed feeders predominate in the middle zone; while mixed and insect feeders are about equal among the small ground mammals. The two species of tree-kangaroo (*Dendrolagus*), shown as plant feeders in the middle zone, could, perhaps, be looked upon as displaced members of the large ground-mammal community.

MALAYAN BIRDS

A comparable study of the birds of the Malayan Rain forest was attempted by allotting the forest species, classed as resident in the Malayan check-list (Gibson-Hill 1949) to groups by zone and food. Insufficient personal knowledge of the group made it necessary to extract the required information from books (largely from Smythies 1953 and Madoc 1956) and several difficulties were encountered. The range of food taken did not always seem to be known with sufficient accuracy, but the chief difficulty was in allotting to zone.

Table 4. *Australian mammals: numbers and percentages (in parentheses) of species by zone and feeding habits*

Zone	No. of species	No of species with diet of:			
		Plant	Mixed	Insect	Flesh
Canopy	8 (29)	4 (14)	4 (14)	0	0
Middle zone	9 (32)	2 (7)	4 (14)	2 (7)	1 (4)
Large Ground Mammals	3 (11)	3 (11)	0	0	0
Small Ground Mammals	8 (29)	0	3 (11)	4 (14)	1 (4)
Total	28 (100)	9 (32)	11 (39)	6 (21)	2 (7)

As noted by Colquhoun & Morley (1943) in their study, a bird species may have a very wide range of possible zones, although it may be characteristic of one of them, and published statements often indicate the range rather than the characteristic zone. A further source of possible confusion is from the varying accessibility of the canopy. In good forest, the canopy is high overhead, but at edges of watercourses, for instance, or in clearings caused by falling trees or shifting cultivation, the canopy, in effect, slopes down to ground level, often bringing the canopy species with it. The observation of a rare bird along a watercourse may, therefore, indicate its liking for watercourses, but the possibility must be borne in mind that it may, in fact, be a bird of the canopy which is usually confined to an inaccessible part of the forest.

Table 5. *Malayan birds: numbers and percentages (in parentheses) of species by zone and feeding habits*

Zone	No. of species	No. of species with a diet of:			
		Plant	Mixed	Insect	Flesh
Upper Air	17 (6)	0	0	12 (4)	5 (2)
Canopy	79 (26)	38 (13)	26 (8)	15 (5)	0
Middle zone	163 (53)	0	30 (10)	121 (40)	12 (4)
Ground	47 (15)	4 (1)	17 (6)	26 (8)	0
Total	306 (100)	42 (14)	73 (24)	174 (57)	17 (6)

Making due allowances, however, the scheme of classification shown in Table 5 was produced. It was not found practicable to distinguish any division corresponding to the large and the small ground mammals, but it was found necessary to add a zone, the 'upper air', above the canopy. Birds are, of course, well adapted to a 'middle-zone' existence, and, as might be expected, most of the species were allotted here.

The pattern of feeding clearly resembles that of the mammals. Thus plant feeders again

predominate in the canopy, although there are a number of insectivorous species. The ground species show a very close analogy with the small ground mammals in being predominantly either mixed or insect feeders. Carnivorous species are, again, generally distributed, none being confined to either canopy or ground.

In the middle zone, however, there has been a marked shift from the mixed feeding habit to the wholly insectivorous one, and it seems more satisfactory to regard the middle-zone animals as belonging to different communities, a flying community of birds and a scansorial community of mammals. Some of the birds (*e.g.* tree-creepers and wood-peckers) could perhaps be regarded as belonging rather to the scansorial community, but personal knowledge of the group is not sufficient to permit this refinement.

The upper air community could, perhaps, be regarded as a specialized part of the middle-zone flying community.

AUSTRALIAN BIRDS

A similar classification was made of the birds of the Tropical Rain forest in Australia. The difficulty here was to decide which species to count as from Rain forest, and a fairly generous criterion gave a list of 117 species (Table 6). Keast (1959) counts only eighty-one species as 'specific to or reaching their greatest abundance in' Rain forest (presumably including Temperate Rain forest), but the object here was to count all species which occurred at all. The calculation, which was based largely on Leach (1958) and the North

Table 6. *Australian birds: numbers and percentages (in parentheses) of species by zone and feeding habits*

Zone	No. of species	No. of species with a diet of:			
		Plant	Mixed	Insect	Flesh
Upper Air	14 (12)	0	0	6 (5)	8 (7)
Canopy	24 (21)	10 (9)	13 (11)	1 (1)	0
Middle zone	67 (57)	4 (3)	8 (7)	49 (42)	6 (5)
Large ground species	1 (1)	1 (1)	0	0	0
Small ground species	11 (9)	1 (1)	5 (4)	5 (4)	0
Total	117 (100)	16 (14)	26 (22)	61 (52)	14 (12)

Queensland Naturalists' Club list (1949), was carried out a year after the Malayan calculation, and was unlikely to have been influenced for the decisions made for that. The only major difference from the Malayan classification was the inclusion of the 'large ground animal' community to accommodate the cassowary, a giant, flightless, fruit-eating species standing about as high as a deer.

The similarity between the Malayan and Australian distribution is, again, striking. Most of the differences can be attributed to a less exact knowledge of the habits of Australian Rain-forest birds, but the proportion of birds recorded from the upper-air community is significantly in excess of the proportion recorded from Malaya. The actual numbers, however, are comparable, and it seems likely that this upper-air community should be regarded as a sample of the upper-air fauna of Australia generally, and not especially of Rain forest. It would not, therefore, reflect the impoverishment which is a feature of the fauna of Australian Rain forest.

BATS

Bats have, so far, been left out of this discussion, because our knowledge of them is so much less complete than for other mammals or birds. Some seventy-two species are recorded from the Malay Peninsula, all of which can be considered forest species. Of these eleven are fruit-bats (*Megachiroptera*), feeding mostly on fruit or nectar and spending much of their time hanging or scrambling in the canopy. The remaining sixty-one are *Microchiroptera* ('insectivorous bats') either truly insectivorous, or carnivorous (on small birds, etc.), living in tree-holes, caves, or other small cavities, and hunting mostly in the air beneath the canopy, or sometimes above it. With our present knowledge, no more than an informed guess is possible for the allocation of these species to zones, but it would probably be fair to allot them as follows:

Upper air	5 all insectivorous	(7%)
Canopy	11 all plant feeders	(15%)
Middle zone, flying	51 insectivorous	(71%)
	5 carnivorous	(7%)

The Australian Rain-forest species are even less well known than the Malayan. Tate (1952) records twenty-six species from the Cape York Peninsula, noting three of them as from open forest, and five as probably from Rain forest. Counting the remaining eighteen as Rain-forest species also, and guessing at the habits of most (a reasonable procedure, as they are closely related to the Malayan species) we get:

Canopy	3 plant and 1 mixed feeder (13% and 4%)
Middle zone, flying	18 insectivorous and 1 carnivorous (79% and 4%)

DISCUSSION

A synthesis of these classifications is presented in Fig. 1. Owing to the great excess of numbers of species of birds over mammals, the percentage distributions of birds, bats and other mammals have been taken as equivalent and it is the mean percentage of the three which is represented by each block of the diagram, but in fact the total numbers of species of all groups is found to give a similar pattern of distribution. It is to be noted that the Malayan and the Australian agree very closely, although the species and even families of animals concerned are not the same.

The birds and mammals of both Malaysian and Australian Tropical Rain forests may, therefore, be assembled into the following six communities:

(1) UPPER AIR COMMUNITY: Birds and bats which hunt above the canopy; mostly insectivorous, but with a large proportion of carnivores.

(2) CANOPY COMMUNITY: Birds, fruit-bats, and other mammals confined to this zone; predominantly feeding on leaves, fruit, or nectar, but with a few insectivorous and mixed feeders.

(3) MIDDLE-ZONE FLYING ANIMALS: Birds and insectivorous bats; predominantly insectivorous, with a few carnivores.

(4) MIDDLE-ZONE SCANSORIAL ANIMALS: Mammals which range up and down the trunks, entering both the canopy and ground zones; predominantly mixed feeders, with a few carnivores.

(5) LARGE GROUND ANIMALS: Large mammals and rarely birds living on the ground, without climbing ability, but of great range, either by reaching up into the canopy, or by

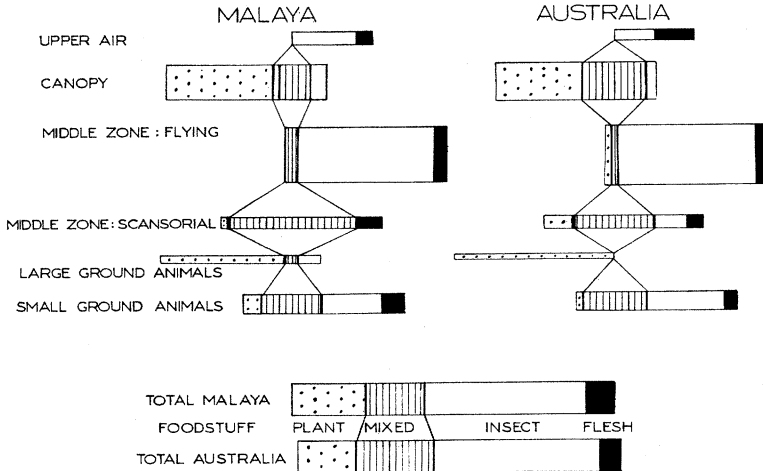


FIG. 1. Patterns of the distribution of feeding habits in Malaya and Australia compared. Areas are proportional to mean percentages of the total numbers of species; Malaya: 306 birds, 72 bats, and 89 other mammals (total 467); Australia: 117 birds, 23 bats, and 28 other mammals (total 168). The vertical scale represents proportion of the total in that zone, the horizontal scale proportions of those in the zone with each diet.

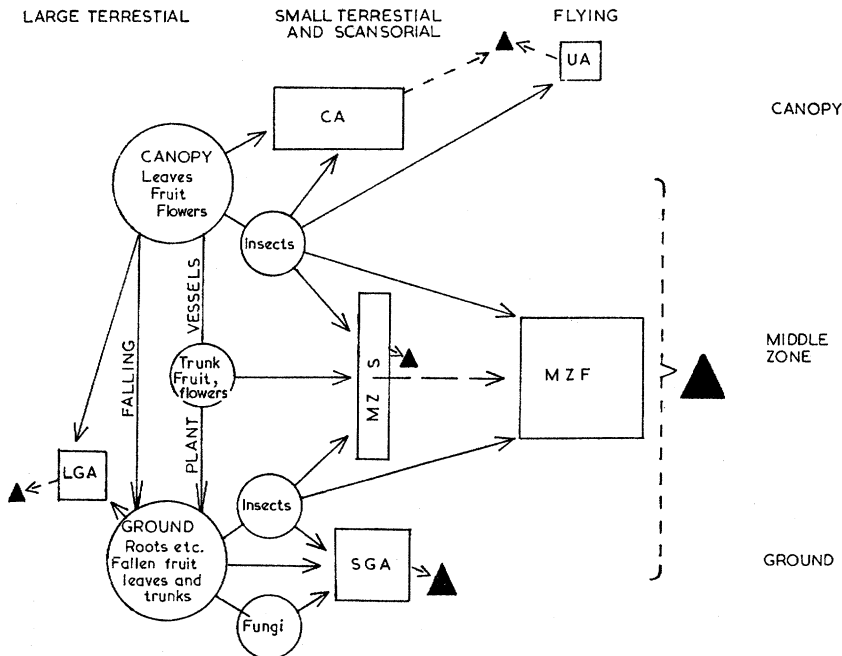


FIG. 2. Diagram of the food chains in Rain forest, using the proportions found in Malaya. Sources of foods are represented by circles, the principal groups of mammals and birds by rectangles, and the attendant predators by black triangles. Areas of the rectangles and triangles are proportional to numbers of species. CA = Canopy Animals, LGA = Large Ground Animals, MZF = Middle-Zone Flying animals, MZS = Middle-Zone Scansorial animals, SGA = Small Ground Animals, UA = animals of the Upper Air.

covering a large area of forest; plant feeders, feeding largely by browsing on leaves, but exceptionally feeding on fallen fruit (*e.g.* mouse-deer and cassowary), or rooting for tubers, etc. (pigs), with attendant large carnivores.

(6) SMALL GROUND ANIMALS: Birds and small mammals, capable of some climbing, which search the ground litter and the lower parts of tree-trunks; predominantly either insectivorous or mixed feeders, but with a fair proportion of vegetable feeders, and some carnivorous.

The relation between these groups is expressed as a diagram of food-chains in Fig. 2. The canopy is clearly the primary producing layer, and the herbivorous animals are either confined to it, or, as ground animals, are big enough to reach the lower parts of it from the ground. Animals confined to the canopy are therefore usually leaf, nectar, or fruit eating. Large ground mammals may be big enough to browse on the leaves of the lower parts of the canopy, or they may use their speed and range of movement to seek places where, as noted above, the canopy in effect comes down to ground level.

Food material manufactured in the canopy can be distributed by the falling of fruit, leaves and branches, or through the vessels of the plant to form trunks, buttresses, roots and storage organs. A few ground-dwelling animals may be expected to rely upon fallen fruit, but dead leaves and fallen trunks cannot be utilized directly by vertebrates. Fungi and insects, however, can make use of this material, and can make it available to vertebrates in the form of their own bodies, so that the majority of the ground-dwelling vertebrates may be expected to search for insects and fungi among the ground litter.

In the middle zone fruit is available borne directly on the trunks of trees (*e.g.* many figs) or by epiphytes, from which also leaves are available. The most abundant food, however, will be insects derived either from the ground, or from the canopy, and distributed by flight. The most successful middle-zone feeders can therefore be expected to be insectivorous birds and bats, capable of catching insects on the wing. Middle-zone mammals will find food less easily, and may be expected to exploit a wide range of possible foodstuffs.

It may be helpful to draw a comparison between the Rain forest and a body of water such as a lake or sea. The canopy represents the phytoplankton, exploited directly by insects, comparable to zoo-plankton, and larger animals comparable to nekton. Food is carried down to the deeper layers and to the bottom (*i.e.* the middle zone and the ground) in the form of fallen leaves, fruit and insect bodies, comparable to the bodies of planktonic organisms, there to be exploited by middle-zone birds and bats corresponding to nektonic organisms of the deeper layers; middle-zone mammals, corresponding to periphytic organisms; and small ground mammals, corresponding to benthic organisms. The large ground mammals are perhaps to be compared to whales; but we must not push an analogy too far.

The declared object is, not to produce a complete scheme of classification, but to select a pattern from a confusing mass of observations into which further observations may be fitted, or, what is more stimulating to thought, into which further observations may fail to fit.

SUMMARY

Based on experience in Malaysia and Australia, a classification is proposed of the birds and mammals of Tropical Rain forest into six communities defined by the level at which

they occur and their range of foodstuffs. The communities are: (1) Upper Air, insectivorous and carnivorous birds and bats; (2) Canopy, birds and mammals feeding largely on leaves and fruit; (3) Middle-zone flying, mainly insectivorous birds and bats; (4) Middle-zone scansorial, mammals of mixed feeding habits ranging up and down the trunks; (5) Large Ground, large herbivorous species; and (6) Small Ground, small mammals and birds of varied diet searching the forest floor.

REFERENCES

- Allee, W. C. (1926). Distributions of animals in a Tropical Rain forest with relation to environmental factors. *Ecology* 7, 445-68.
- Colquhoun, M. K. & Morley, A. (1943). Vertical zonation in woodland bird communities. *J. Anim. Ecol.* 12, 75-81.
- Gibson-Hill, C. A. (1949). An annotated check-list of the birds of Malaya. *Bull. Raffles Mus.* 20, 1-299.
- Harrison, J. L. (1954). The natural food of some rats and other mammals. *Bull. Raffles Mus.* 25, 157-65.
- Harrison, J. L. (1957). Malaysian parasites — XXXIII. The hosts. *Stud. Inst. Med. Res. Malaya*, 28, 409-26.
- Harrison, J. L. (in press, a). The natural food of some Malayan mammals. *Bull. Raffles Mus.*
- Harrison, J. L. (in press, b). Mammals of Innisfail — I. Species and distribution. *Aust. J. Zool.*
- Keast, A. (1959). Australian birds: their zoogeography and adaptations to an arid continent. Chapter VI in *Biogeography and ecology in Australia*. (pp. 89-114). Den Haag.
- Leach, J. A. (1958). *An Australian Bird Book*. 9th ed. Revised by P. C. Morrison. Melbourne.
- Madoc, G. C. (1956). *An Introduction to Malayan Birds*. Kuala Lumpur.
- North Queensland Naturalists' Club, & Whittell, H. M., (1949). *List of Birds occurring in North Queensland*. N.Q.N.C. Publication 5.
- Richards, P. W. (1952). *The Tropical Rain-forest, an Ecological Study*. Cambridge.
- Smythies, B.E. (1953). *The Birds of Burma*. Edinburgh.
- Tate, G. H. H. (1952). Results of the Archbold expeditions. No. 66: Mammals of Cape York Peninsula, with a note on the occurrence of rain-forest in Queensland. *Bull. Amer. Mus. Nat. Hist.* 98 (7), 567-616.
- Troughton, E. (1946). *Furred Animals of Australia*, 3rd ed. Sydney.
- Wyatt-Smith, J. (1949). A note on tropical lowland evergreen Rain forest in Malaya. *Malayan Forester*, 12 (2), 1-6.
- Wyatt-Smith, J. (1952). Malayan forest types (part 1). *Malay. Nat. J.* 7, 45-55.