

Feeding and ranging in the forest

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Five New World Primates: A Study in Comparative Ecology.

By John Terborgh.

Princeton University Press: 1984. Pp. 260. Hbk \$40, £40; pbk \$13.50, £10.40.

ADDITIONS to the literature on New World monkey behavioural ecology are rare enough, so a monograph dealing with five species at once is particularly newsworthy. In 1976 John Terborgh, originally an ornithologist but now a convert to primatology, opened up a field site in pristine Amazonian rain forest on the Rio Manu in Peru, and in *Five New World Primates* he has summarized a fascinating array of behavioural and ecological observations. As the first contribution to a new series, *Monographs in Behavior and Ecology*, the book sets a standard that augurs well for the future. It is essential reading for anyone interested in primate behaviour and ecology, or in the subject of behavioural ecology in a wider sense.

Terborgh's account deals in detail with five out of the unusually high total of 11 primate species found at the Manu site, and includes useful information on the other six. Although the fieldwork spanned little more than a year, a demanding rota of observations shared with four assistants permitted a remarkable weekly average of 50 hours' systematic data collection for the five main species: two capuchins (*Cebus apella* and *C. albifrons*), two tamarins (*Saguinus imperator* and *S. fuscicollis*) and a squirrel monkey (*Saimiri sciureus*). The author modestly describes much of the work as "first-order descriptive natural history", yet even at that level the information provided is of great value. However, the text goes far beyond description

Plants in paperback



Great Plantain (*Plantago major*), depicted by Sybil J. Roles. The drawing is reproduced from the new paperback edition of *Flora of the British Isles, Illustrations*, the companion volumes to Clapham, Tutin and Warburg's classic work. The illustrations are published in four volumes by Cambridge University Press, price £8.95, \$17.95 each volume.

because of the emphasis on standardized collection of quantitative data on feeding and ranging behaviour. Further, there are special advantages in conducting a study of several species simultaneously — comparisons between sympatric species are particularly productive because many environmental variables are held constant, and it is also possible to obtain quite precise information on divergent specializations that reduce competition between species.

Terborgh's data on feeding and ranging behaviour permit construction of detailed profiles of the five species studied, the profiles in turn providing a basis for comparison both between these species and with other primates. Overall, the picture built up by Terborgh reveals a stark contrast with the better-known Old World monkey species. For example, the Manu primates feed far more extensively on animal prey (notably arthropods), whereas leaf-eating is insignificant. There are also quite substantial differences in feeding behaviour between the five species, these dietary differences being matched by general differences in habitat use. There is, therefore, good evidence for some avoidance of competition between species.

However there is also some overlap between the five species in their feeding activities and thus some observable competitive interaction (especially between the tamarin species). It is therefore all the more striking that there are two special cases of mixed troop formation (polyspecific association), which further enhance the importance of Terborgh's work. First, there is a definite tendency for *Saimiri* to form mixed troops with either of the *Cebus* species. This has been reported previously, but Terborgh's quantitative data show quite clearly that it is *Saimiri* rather than *Cebus* that seek the association. For instance, whereas *Saimiri* travel relatively rapidly when alone and slow down when in association with *Cebus* (often after switching direction to make contact), the converse is true of the capuchins. Terborgh rejects a suggestion that *Cebus* benefits from the association by preying on insects flushed by *Saimiri* and concludes instead that *Saimiri* may benefit through greater protection from predators and through the more detailed local knowledge of fruit sources presumably possessed by the less widely ranging *Cebus*.

The second case of troop association is even more noteworthy in that an *S. imperator* group typically shares a territory with a group of *S. fuscicollis*, while both groups vigorously repel conspecific intruders. Unlike *Saimiri* and *Cebus*, however, the two tamarin species do not actually move as mixed troops, though their ranging patterns are closely coordinated. In this case, Terborgh invokes Cody's "local depletion hypothesis" (originally proposed for mixed flocks of birds), according to which the two tamarin species increase foraging efficiency by avoiding previously depleted areas. It is, however, odd that the tamarins

diverge in their patterns of feeding on arthropod prey, whereas they are extremely similar in their feeding on fruit. Further, Cody's hypothesis does not seem to resolve the basic paradox that arises with any mixed troop: why does a group of species A associate with a group of species B rather than forming a larger single-species group?

Inevitably, such an ambitious study has its shortcomings. Because of the overriding need to standardize observation methods, focal animal sampling (requiring recognition of individuals) was ruled out and replaced by the less rigorous technique of opportunistic scan sampling. This latter method predisposes towards recording the most obvious activities of the most obvious individuals. The reasons for adopting scan sampling are understandable, but the potential effects of observational bias on inferred activity budgets really required some detailed discussion. Also, although Terborgh and his team took pains to assess fruit distribution and productivity at the Manu site, there was no comparable assessment of arthropod availability. This is undoubtedly linked to Terborgh's general tendency to dismiss competition for arthropods as a determining influence in relationships between the five species, in favour of arguments based on fruit availability and on risks of predation. For this and other reasons, Terborgh's overall attempts to interpret the behaviour of the Manu primates in relation to ecological factors are not entirely convincing.

Finally, although Terborgh draws upon the ornithological literature in interpreting the behavioural ecology of the Manu primates, there is surprisingly little reference to directly comparable research on Old World sympatric primate species — for example that of the Gautiers on monkeys in Gabon (including the best examples known of polyspecific association among primates) and of Chivers *et al.* on monkeys and lesser apes in Malaysia, of Charles-Dominique on nocturnal prosimians in West Madagascar, and of Charles-Dominique *et al.* on nocturnal prosimians in West Madagascar. All of these studies establish general principles of direct relevance to Terborgh's work at Manu, but it is left to the reader to make the comparisons and the connections.

However such points pale into insignificance given the dedication required to carry out such a field study at all. The introductory account of the practical problems involved is enough to arouse the reader's unstinted admiration. In this book Terborgh has greatly extended our understanding of the behavioural ecology of Amazonian primates. As noted in the epilogue, one of the benefits of such understanding may be the development of effective conservation measures for primates in this fast-disappearing rain forest habitat. □

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