Predation and Primate Evolution

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ABSTRACT. This paper presents the results of a general review of predation on nonhuman primates as a selective force in primate evolution. Testable hypotheses derived from the literature on predation on primates, concerning sexual dimorphism, male defense, group size, solitaries, transfer, subgrouping, and sex ratio, were applied to the available data on populations with varying predation rates in search of significant correlations. All seven hypotheses were supported, indicating that predation is and has been an important determinant of primate evolutionary history. Suggestions for accumulating a larger and more accurate body of information on predation rates on primates are offered.

Key Words: Predation; Selection; Primate evolution; Demography; Fieldwork.

INTRODUCTION

Primatologists seem to be far from reaching a consensus on the importance of predation in primate evolution. The early fieldworkers assumed predation was responsible for many features of the behavior and anatomy of the species they studied, even though they almost never observed actual attacks (e.g., Carpenter, 1934; Chance, 1955; DeVore & Hall, 1965; Nishida, 1968). DeVore and Hall (1965) described predation as "the most important single factor in the interpretation of baboon ecology and social behavior," and Hamburg (1971) said it was "of central adaptive significance" for terrestrial species.

Not long after these statements, other observers began to protest that their study populations seemed to have little or no predation. The role of predation was then questioned by many writers (e.g., Bouvier, 1979; Dittus, 1979; Dunbar & Dunbar, 1974; Eisenberg et al., 1972; Rodman, 1973; Wrangham, 1979, 1980). Over the last ten years, descriptive analyses of primate societies have frequently contained statements to the effect that predation as a selective factor was a trivial influence for the population in question, the species, or even the whole Order Primates.

Others continue to emphasize the selective influence of predation, though many of these are referring to other Orders or even Classes of vertebrate (e.g., Alexander et al., 1979; Beneshof & Thornhill, 1979; Clutton-Brock & Harvey, 1977; Curtin & Dolhinow, 1978; Jones, 1981; Krebs & Davies, 1981; van Schaik, 1983). In my own study of chacma baboons (Anderson, 1981a, b), many of the differences observed between the behavior of baboons at Suikerbosrand and that of baboons at other sites in South and East Africa seemed to be best explained by the absence of predators at Suikerbosrand. Of the possible agents of directional selection that might be affecting Suikerbosrand baboons atypically, the cold, dry, high-altitude winters and the absence of any baboon predators could explain all the differences.

The present paper attempts to determine the importance of predation as a selective force by evaluating its influence in all the primate species for which relevant information exists.
Enough data on predation have been accumulated in the last 25 years of primate field studies to make such a review finally worthwhile. Although the gaps in the data are still woefully large, they can only be closed after many more years of study; while if large numbers of researchers continue to dismiss the topic as unimportant, the data to answer some of these questions may never be complete.

**EFFECTS OF PREDATION: THE HYPOTHESES**

Many features of primate society have been explained as responses to predation by those who believe predation to be a significant selective factor, and several of these explanations can be turned into predictions and tested for correlation in populations living under high and low levels of predation.

The first set of hypotheses concerns group-living. Almost all primates are gregarious rather than solitary. This is usually explained as a means to decrease the risk that any one individual will be selected by a predator (ALEXANDER et al., 1979; CLUTTON-BROCK & HARVEY, 1977; CROOK et al., 1976; JONES, 1981; RUBENSTEIN, 1978; SMITH, 1977; VAN SCHAIK et al., 1983b; first proposed by HAMILTON, 1971); or because of the greater vigilance possible with more individuals (CLUTTON-BROCK, 1974; EISENBERG et al., 1972; HORN, 1968; VAN SCHAIK, 1983; WRAINTHAM, 1980). If a species is gregarious, group sizes should be larger where predation risk is higher and smaller where the risk is lower (ALTMANN, 1974; BUSSE, 1977; CROOK, 1972; Goss-Custard et al., 1972; HAMILTON et al., 1978; HLADIK, 1979; SUZUKI, 1979; VAN SCHAIK, 1983; WASSER & HOMEWOOD, 1979; WILSON, 1975; YOSHBA, 1968). Species which live in small groups may form polyspecific associations to obtain the protective benefits of a larger group (GARTLAN & STRUHSAKER, 1972; GAUTIER-HION et al., 1983). Dispersal and subgrouping should be rare where predation is frequent (ANDERSON, 1981a; NISHIDA, 1972), with few or no solitaries (ALTMANN & ALTMANN, 1970; DEVORE, 1963; SIMONDS, 1973; STRUHSAKER, 1975; WRAINTHAM, 1974). Since males of most species are larger and more powerful than females, only they should transfer between groups where predation risk is high, because a female temporarily on her own in the process of transferring would be more vulnerable to predation (BUSSE, 1980; HARCOURT, 1978; Packer, 1979). BUSSE's data (1980) show higher predation mortality among females both because they are smaller and less well-equipped to fight and also because they are slower and clumsier when carrying an infant.

The second group of hypotheses concerns adult male anatomy and behavior. Where the risk of predation is highest, groups should contain the highest percentages of adult males (CARPENTER, 1934; CROOK, 1970; CURTIN, 1977; EISENBERG et al., 1972; Goss-Custard et al., 1972; HALL, 1965; LEUTENEGGER & KELLEY, 1977; SUZUKI, 1979; WILSON, 1975; YOSHBA, 1968). Presumably this prediction should hold whether or not males defend other group members, since the higher the percentage of group members that a predator would be reluctant to attack, the greater the likelihood should be that it would choose another species or group.

Where predation risk is high, males of a species should be larger and better-equipped to fight than in populations where predation is lower (DENHAM, 1971; HARCOURT & STEWART, 1977; HARVEY & CAVANAGH, 1978; JORDE & SPUBLER, 1974; LEUTENEGGER & KELLEY, 1977; LOVEJOY, 1981; MACKINNON, 1974). Unfortunately, there are virtually no species within which there are enough different populations documented under different predation conditions for which weights of males in each population are known to test this hypothesis.