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Social Evolution in Primates: The Role of Ecological Factors and Male Behaviour

CAREL P. VAN SCHAIK
Department of Biological Anthropology and Anatomy, Duke University,
Box 93083, Durham, NC 27708, USA

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Summary. In order to explain the variation in primate social systems, socio-ecology has focussed on the role of ecological factors to explain female associations and relationships and on the spatio-temporal distribution of mating opportunities to explain male associations and relationships. While this approach has been quite successful, it ignores male–female associations and relationships and ignores the possibility that male behaviour modifies other aspects of the social system. In this paper, the ecological approach is complemented by consideration of a social factor found to limit fitness, namely infanticide by males. Infanticide risk is proposed to have selected for male–female associations and relationships, and to have modified female–female relationships in some cases. It is also hypothesized to have selected for the unusual male bonding by species such as chimpanzees. Finally, its possible impact on between-group relations is examined. The findings suggest that infanticide is of equal importance to ecological factors, with which it may interact in sometimes complex ways, in shaping primate social systems.

INTRODUCTION

SOCIAL SYSTEMS AMONG PRIMATES vary widely from species to species (Smuts *et al.* 1987). This variation concerns both patterns of membership and spatial distribution (i.e. the associations of individuals), and the nature of the social relationships among the members of social units. Ever since the extent of this variation became apparent, attempts to explain it considered social behaviour an adaptation produced by natural selection (Crook & Gartlan 1966). Since the selective pressures were thought to be mainly ecological, this endeavour has become known as socio-ecology. The aim of this paper is to provide an overview of recent developments in primate socio-ecology.

We should be careful in defining the object of inquiry. Social systems arise through behavioural interactions between individuals. Hence, they are not adaptations; only the social strategies of individuals are. Unfortunately social strategies cannot be directly observed, but must be deduced. Deducing the social strategies requires an iterative approach, because the primary rules used by the relevant players will be modified to deal with the social and demographic context they themselves have produced. Thus, the ideal socio-ecological model merely specifies the behavioural rules used by individuals, and the social system emerges from their interactions. despite some promising starts (e.g. te Boekhorst & Hogeweg 1994), this is still a distant ideal.

Socio-ecology has dealt with this complexity by developing a priori arguments. If social strategies are adaptations, then those factors that exert the strongest limitation on lifetime reproductive success should provide the strongest selection pressures toward the evolution of social strategies, i.e. the spatial associations and social relationships that individuals engage in. Primate populations are often limited by food and predation, as shown by deliberate and accidental experiments (Mori 1979; Richard 1985). Thus, socio-ecology has focused on the role of the abundance and distribution of food and predators in shaping social strategies (Crook & Gartlan 1966; Wrangham 1980; Dunbar 1988).

It is also clear that the two sexes tend to be limited by different factors (Trivers 1972). Again, an a priori argument suggests that female social strategies mainly serve to reduce the impact of predation and feeding competition. In contrast, variation in male fitness is often largely due to differences in the number of infants sired, and we should therefore expect the associations and relationships formed by adult males to increase access to mates.

This deductive approach has engendered the fundamental paradigm of socio-ecology (Emlen & Oring 1977): the spatial distribution and social relationships among females are thought to reflect ecological conditions, in particular distribution of risks and food, whereas the distribution of males, and the social relationships among them, are determined by the spatio-temporal distribution of mating opportunities (Figure 1). This approach has been verified experimentally in small mammals (Ims 1988; Ostfeld 1990), and has also been widely applied in primates. The first section of this paper

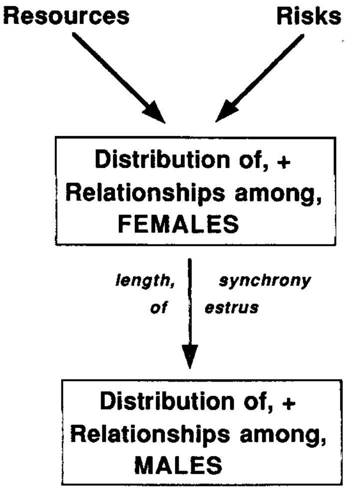

Figure 1. Ecology of social systems. The classic socio-ecological paradigm, which links female associations and relationships to ecological factors and male associations and relationships to the spatio-temporal distribution of mating opportunities.

will briefly review primate work that examines the impact of ecological factors on female distribution (spatial associations) and social relationships and on the male response to this.

However, while this approach is elegant, it inevitably oversimplifies. First, it is incomplete, in that it ignores the common existence of significant associations or social relationships between the sexes, which, as we shall see, are quite important in the order primates. Second, it may also be wrong. In particular, it is conceivable that male–female interactions might alter spatial associations and relationships among females (Wrangham 1979), those among males, and even the relations between groups. Both additions and modifications arise from the increased appreciation of the action of a different factor that limits fitness; this factor is a social one, namely infanticide by males (Watts 1990; van Schaik & Dunbar 1990; Hiraiwa-Hasegawa & Hasegawa 1994). Hence, the remainder of this paper will focus on male–female associations and relationships, and on their impact on other features of social systems.

CLASSIC SOCIO-ECOLOGY

The ecological model for female associations and relationships

Permanent gregariousness is quite common among female primates. While none of the nocturnal taxa shows female association, 79% of diurnal taxa does (42 of the 53 diurnal taxa, where a taxon is a genus or a species or group of species within a genus that is homogeneous for the relevant social variables). Female within-group coalitionary relationships (alliances) are also fairly common (26% of 34 gregarious taxa for which this information is available). It is more difficult to assess the presence of between-group alliances among females, because they may occur with low frequency and are often conditional. An estimated 23% of 31 gregarious taxa for which this is known has more than occasional between-group conflicts by females.

Briefly, the ecological model for females is as follows. Females form spatial associations because it reduces predation risk (Janson 1992). The feeding competition that inevitably arises acts as a countervailing force, leading to groups of some intermediate size (van Schaik 1983; Dunbar 1988). The social relationships among these gregarious females will depend on the competitive regime (van Schaik 1989). Where access to limiting resources is not defensible or not worth defending, competition will be by scramble, and variation in power cannot be translated into variation in access, so social behaviour is of no use to improve access to limiting resources. Thus, females should not show frequent aggression over food, should lack formal submission signals, and they should not form alliances. Female fitness will depend on group size, and the easiest way to manipulate group size is by moving to other groups or starting new ones. Females are therefore expected to migrate freely between groups, whenever ecological, social or reproductive considerations (e.g. inbreeding) make such moves advantageous. This prediction assumes that diurnal primates, being mainly gregarious, face relatively few ecological constraints on dispersal (cf. Watts 1990), although there may be serious social constraints at high densities. This type is referred to as non-female-bonded, following Wrangham's (1980) terminology.

In contrast, where the limiting resources that females compete for are monopolizable, competition is by contest. Then, power differences give rise to differences in access (e.g. net food intake or safety), and aggression is selected for. Provided certain assumptions are met (Figure 2), we therefore expect that females form decided dominance relationships, with formal submission signals that go in one direction within a dyad (bared teeth among many cercopithecines, pant grunts among chimps, spat calls in lemurs, etc.: de Waal 1986; Pereira & Kappeler, in press). They should form alliances, either because coalitionary aggression is needed to achieve access to the limiting resources (cf. Wrangham 1980) or because they can benefit through kin selection by improving the agonistic power of their relatives. Alliances with relatives are also more stable. Hence, association with relatives is expected, which can be achieved by female philopatry. When emigration occurs, it is in the form of subgroups budding off and striking

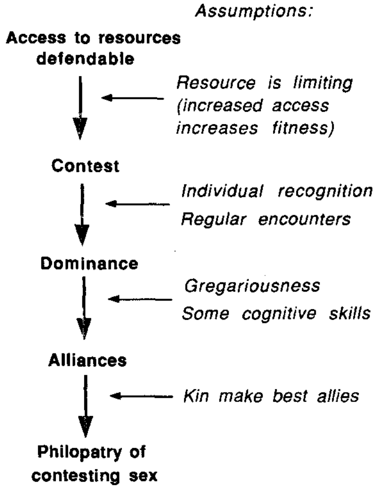

Figure 2. Diagram of the social consequences of contest competition in animals, to illustrate the derivation of the links between decided dominance relationships, alliances and philopatry of the contesting sex.

out on their own. This suite of characters is called female-bonded (Wrangham 1980; van Schaik 1989).

This basic dichotomy is complicated by the possibility that contest competition is also possible between groups rather than just between individuals (see van Schaik 1989). Strong between-group contest would change the predictions made above as follows. First, because relatives make the best allies in such between-group contests as well (especially since there is a possible collective action problem), females of non-female-bonded groups are expected to be philopatric when between-group contest is high. Second, because subordinates derive a source of power from their ability to withhold support to the large alliance, we should see a more tolerant form of dominance relations in the female-bonded groups. This leads to four types of female social structure (Table 1).

Before this model can be put to the test, it should be established that it accurately describes the situation in non-human primates. First, we should assess its internal consistency. Obviously, it was consistent with the evidence available when it was formulated, but the new descriptive material accumulated since then indicates that the association between decided dominance relationships on the one hand and female alliances on the other hand remains extremely strong. Likewise, there are no examples of taxa where decided dominance and alliances are accompanied by routine dispersal of the females (review: Sterck *et al.*, in manuscript). Second, detailed long-term field studies allow evaluation of the effect of dominance

Table 1. The predicted effects of the nature of competition for limiting resources on female social relationships and dispersal (based on van Schaik 1989).

Competition		Social response		
WG[b] contest	BG[c] contest	Female philopatry	Female relationships (dominance) type	Designation[a]
Low	Low	No[d]	(none) egalitarian	Non-female-bonded
Low	High	Yes	(none) egalitarian	Female-resident
High	Low	Yes	(yes) despotic	Female-bonded
High[e]	High	Yes	(yes) tolerant	Tolerant female-bonded

[a] The definitions of these designations deviate from those originally used by Wrangham (1980).
[b] WG = within-group
[c] BG = between-group
[d] Dispersal is not compulsory, but likely to be the norm.
[e] WG contest is at least potentially high. In practice, tolerant dominance relations may lead to a relaxation of within-group contest for access to limiting resources or their reproductive consequences.

rank on energy budgets and reproduction. Crude ranks can often be recognized among females in non-female-bonded groups on the basis of displacements with no or mutual aggression. However, these ranks do not affect aspects of energy budgets or reproduction in two well-studied non-female-bonded species, gorillas (*Gorilla g. beringei*) and thomas langurs (*Presbytis thomasi*), whereas predictable dominance effects are commonly found among many female-bonded species (Silk 1993; review in Sterck *et al.*, in manuscript).

Actual tests of the model consider the relation between ecological conditions and female social relationships. Because of the limited phenotypic plasticity of a species' social behaviour, experimental manipulations of ecological variables need not always produce the predicted social changes. The best tests are probably comparisons that examine ecological differences between closely related but socially distinct species. One such test (Mitchell *et al.* 1991) concerns two squirrel monkeys, the Peruvian *Saimiri sciureus*, and the Costa Rican *S. oerstedi*. These two species are quite similar, in that groups are about the same size, face serious predation risk by raptors, and have similar diets and activity budgets. Yet, *S. sciureus* is clearly female-bonded (showing frequent resource-based aggression, dominance, alliances, and female philopatry), whereas *S. oerstedi* is non-female-bonded (showing 70 times lower aggression rates, no dominance, no alliances, and female breeding dispersal). An extreme ecological difference was found in the fruit trees, in which females have most of their conflicts: the Peruvian *S. sciureus* lives in a tropical rain forest where trees have the normal range of crown and crop sizes. The Costa Rican *S. oerstedi* live in forests with densely packed tiny trees with minute fruit crops that are exploited in a dispersed fashion.

Because of the low resolution of such semi-qualitative comparisons, many more such tests are needed for a proper evaluation of the model. The provisional results of other such comparisons, with baboons (*Papio spp.*), also support the model (R. Barton, personal communication; G. Cowlishaw, personal communication).

No non-ecological alternatives for the variation in female social relationships have been published. Those that can be developed (Sterck *et al.*, in manuscript) do not lead to the rejection of the ecological model. In conclusion, the ecological model provides for now the most satisfactory explanation for variation in female social relationships.

Male associations and relationships

The classic socio-ecological approach for males states that their distribution reflects the spatio-temporal distribution of mating opportunities (Emlen & Oring 1977). Thus, the associations and relationships formed by males should improve their ability to gain access to mates. Associations are less common among males than among females: 60% vs. 79% of diurnal taxa (using same conventions as above). Within-group alliances are also less common among males: they occur in 12% of the 25 diurnal taxa with male association whose social behaviour is well known, as opposed to 26% among females (only taxa with male association are included because spatial association is a precondition for alliance formation). Thus, primate males are both less likely to associate among themselves and to form alliances when associated.

The sex difference in association is straightforward. Males can derive the benefit of reduced predation risk by associating with females. On the other hand, they will derive strong mating benefits from excluding other males from access to females. Indeed, as in other mammals, the number of males in a group of primates is generally considered a function of the extent to which one male can monopolize sexual access to females (Clutton-Brock 1989; Altmann 1990).

Several factors may explain the reduced incidence of within-group alliances among males. First, males will benefit from excluding other males from mating, even if they cannot exclude these other males from being in the group. Second, male alliances tend to be less stable due to the faster rise and fall of a male's fighting power, and thus of his value as an ally. Third, there is a fundamental difference in the nature of the resources the two sexes compete for. Females compete for access to food, males for fertilizations. If two females compete for food, both will gain since both will obtain access to more food than they would obtain alone. In contrast, while collaborating males may each gain more matings, this does not mean that each gains more fertilizations: the total amount of fertilizations in a group is a constant quantity. Preliminary quantification of this argument showed that only a few pairs of mid-rankers showed the expected gains that would make it profitable for them to form an alliance (C. van Schaik & C. Nunn, in preparation), very similar to the pattern observed in baboons (e.g. Noë 1990).

Male alliances that function in between-group conflicts are probably more common than those within groups, although they remain opportunistic. This is not unexpected because the total amount of fertlizations is no longer a fixed quantity in between-group competition, as males can increase their tenure or even increase the number of females attracted by collaborating. Not easily reconciled with the classic approach is the occurrence of male bonding and philopatry where solitary females occupy indefensible ranges, such as in chimpanzees (*Pan troglodytes*), spider monkeys (*Ateles spp.*) and woolly spider monkeys (*Brachyeles arachnoides*) (Nishida & Hiraiwa-Hasegawa 1987; Wrangham 1987; Strier 1992). So far, no satisfactory explanation has been offered for this unusual situation, and I will return to it later.

MALE–FEMALE ASSOCIATIONS

As this brief survey shows, the classic socio-ecological framework explains many of the features of primate societies. However, it ignores male–female associations, and I will discuss these now.

Permanent male–female association is not self-evident. Given internal fertilization and lactation, i.e. obligatory female association with the zygote and the infant, desertion after fertilization is a viable male option. Hence, desertion is quite common, especially where mating is seasonal or at least predictable and punctuated by long periods of no mating. It is therefore not surprising that permanent male–female association is rather uncommon among mammals (see e.g. Wilson 1975). Curiously, primates are the order in which permanent male–female association is by far the most common; indeed, among diurnal species it is almost 100% (see Smuts *et al.* 1987). Mate guarding does not explain this pattern since even the most seasonal breeders have year-round male–female association.

Why is this? Other factors than ecological ones may also limit fitness, and may thus exert selective pressure towards the evolutions of social strategies. The major social problem for primate females is infanticide by males that have not mated with the female before (Hiraiwa-Hasegawa &

Hasegawa 1994). Infanticide is estimated to be responsible for 35% of infant mortality in hanuman langurs (*Presbytis entellus*; Sommer 1994), 37% in mountain gorillas (Watts 1990) and as much as 64% in red howler monkeys (*Alouatta seniculus*; Crockett & Sekulic 1984). While these numbers are likely to be lower for most other populations, they demonstrate that infanticide can exert a strong selective pressure on primate social strategies.

Although broad comparative data are still lacking, infanticide may well be more prevalent in primates than in most other mammals (but see Pusey & Packer 1994 on lions, *Panthera leo*). Several factors may conspire to make it particularly acute in primates. First, primates have very slow life histories (Harvey *et al.* 1987), making the period of vulnerability to male infanticide long. Second, primate infants are generally conspicuous (not hidden in nests or dens) and defenseless (unable to run away or fight back very effectively). Third, perhaps primate females show greater site tenacity than many other mammalian taxa, which increases the probability that an infanticidal male can mate with the female once she returns to oestrus, thus rendering infanticide a beneficial male strategy.

Various social strategies could evolve that would reduce a female's risk of infanticide. First, mating behaviour can be modified (along with physiological changes). For instance, females could actively pursue promiscuity when sexually receptive and show situation-dependent receptivity, as during pregnancy or post partum (Hardy & Whitten 1987). Second, females could migrate away from groups in which infanticide is likely (see below). Third, females could ally with effective protectors. Evidence suggests that males, specifically the possible sires of the females' infants, play a special role in preventing infanticide by unfamiliar males: males that were reproductively active are often associated with infants (van Schaik & Dunbar 1990), infanticide is most likely when male representation in the group changes (Hiraiwa-Hasegawa & Hasegawa 1994; Sommer 1994), and when males are removed (by accident or experimentally) infanticide is highly likely (e.g. Sugiyama 1966).

Association with the male may therefore be the optimal strategy for a female, despite the costs of feeding competition that this will usually entail. This hypothesis leads to one very strong prediction. If permanent association between males and females in primates serves to reduce the risk of infanticide, it should only be found where females are spatially associated with their infants, usually because they carry them. Conversely, where the infant is not with its mother, but parked or left in a nest, permanent male–female association is not expected. A comparative test of this hypothesis finds strong support for this prediction in primates (C. van Schaik & P. Kappeler, in preparation). There are also no plausible alternatives for the observed taxonomic distribution of male–female association. For instance, activity period or litter size, provide a poorer fit than the mode of infant care.

The permanent association of males and females allows for the evolution of a rich variety of male–female social relationships. However, there is little quantitative description of these relationships, and also no theorizing about them (Smuts 1987).

SOCIAL CONSEQUENCES OF INFANTICIDE AVOIDANCE

The patterns in male–female associations and relationships indicate that infanticide risk is likely to be a potent selective force in primate social evolution. The obvious next step is to explore how infanticide risk may have affected the associations and relationships among females, among males, and perhaps even among groups.

Infanticide and social relationships among females

Since females were found to be less effective in reducing the risk of infanticide than males, it is unlikely that infanticide risk could have selected for female association directly. The ecological model claims that female association (gregariousness) serves to reduce predation risk. These female groups are then joined by one or more males. The competitive regime determines the nature of the social relationships among the females (see Figure 3.a).

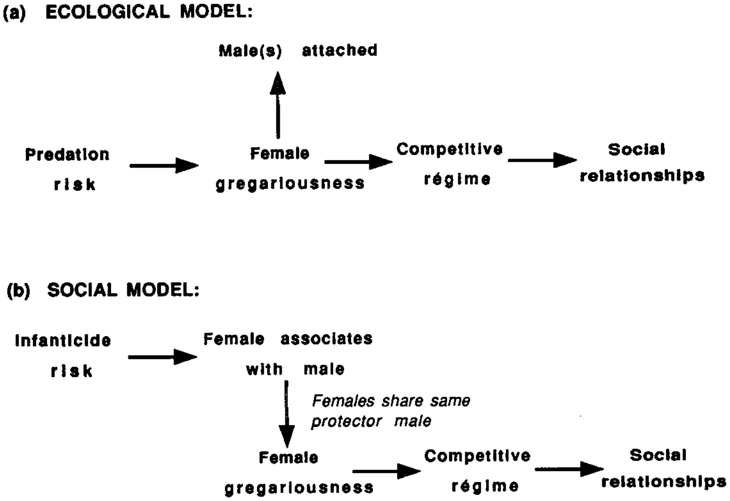

Figure 3. Female social relationships. Two alternative ways, ecological (a) or social (b), of deriving the non-female-bonded model of female social relationships in primates.

However, infanticide risk could indirectly lead to female association. Assume that females respond to the risk of infanticide by associating with a male. In fact, this is the hypothesized route to bonded monogamy in primates (van Schaik & Dunbar 1990). However, if the costs of female association are low, if females can transfer easily, if there is variation in the quality of males as protectors, and if females can share the anti-infanticide service of a male up to a point, then they could form groups around effective protectors (Wrangham 1979; Watts 1990). These groups are likely to be fairly small, because their size is set by the ratio of breeding females to able-bodied adult males. They are likely to be non-female-bonded because of the need for female migration and the low costs of association (Figure 3.b).

Female emigration decisions were studied in two non-female-bonded species, the mountain gorilla (Watts 1990) and thomas langur (Sterck & Steenbeek, in manuscript). In both species, females tend to transfer into smaller groups, consistent with the observed significant scramble component in their within-group competition. This pattern supports the original ecological model. However, female migration decisions are also clearly linked to infanticide risk: in gorillas females tend to transfer after their infants are killed, and in the langurs they tend to transfer during the brief periods when they are least vulnerable to infanticide. Furthermore, female transfer decisions seem to be guided primarily by the identity of the target male rather than the group of females.

The most plausible interpretation is that predation risk and infanticide risk operate simultaneously and both provide significant pressure toward the observed system in these two species. The relative importance of each factor is bound to vary with the ecological conditions. For instance, the langurs show various patterns compatible with the predation reduction function of grouping (small groups avoid the ground layer; males form all-male bands). And the social model can not explain large non-female-bonded groups in high-predation environments such as those of *Saimiri*. But it is possible that infanticide risk could be a significant contributing factor to non-female-bonded groups, and maybe even the predominant one in some species facing negligible predation risk.

Infanticide and male associations and relationships

Male bonding

At first sight, it is extremely unlikely that infanticide could have affected male social relationships. Males reduce the risk of losing their offspring to infanticidal rivals by forming associations and relationships with females. However, what are a male's options if females are solitary and if the costs of permanent male–female association are too high, as is observed among large arboreal frugivores such as spider monkeys, orangutans (*Pongo pygmaeus*) and chimpanzees?

In general, where a male cannot defend access to females directly, he could defend access to the range containing the female or females (cf. Clutton-Brock 1989). This may be effective in defence of mating access especially when female oestrus is brief and advertised. However, for infanticide prevention to be effective all male trespassing has to be minimized. I hypothesize that male alliances may provide this protection. The best studied example of male bonding is the chimpanzee, in which males form parties that patrol the boundaries of a communal range and respond in highly antagonistic fashion toward male strangers, sometimes with lethal consequences (Manson & Wrangham 1991). This should serve to make males very reluctant to enter unfamiliar territory, which thus provides a measure of safety to females. Females, moreover, tend to stay away from the boundary area when they have infants (Goodall 1986).

It is difficult to test this hypothesis, but no other plausible scenarios have been presented so far. It seems worthy of further investigation, especially since male bonding probably represents the ancestral hominid system (Foley & Lee 1989).

The number of males in a group

In female groups with permanent male representation, the number of males is an important determinant of social behaviour (e.g. Hamilton & Bulger 1992). The classic socio-ecological approach proposes that the number of males in a group is determined by the potential for monopolization of potentially fertile matings. However, in small groups, it may be in the females' interest to allow multiple males to be attached to the group despite the increase in feeding competition caused by this, because their presence may reduce the risk of predation or of infanticide. Females may exert some direct influence over male immigration (Smuts 1987). Furthermore, the monopolization potential is determined in part by female behaviour, such as the degree to which females invite promiscuity, and by the temporal clumping of female attractivity, which depends on the length and accuracy of ovulation signalling and the degree of synchrony among females. Natural selection can affect all these traits, and thus the monopolization potential. Females may therefore have some control over the number of males in their group.

Males may help to reduce the risk of predation to females and their offspring because of their higher vigilance levels and consequently greater ability to detect predators, and their tendency to face down predators (van

Schaik & van Noordwijk 1989). Thus, one could predict that where predation risk is particularly severe but feeding competition does not allow for large female groups, groups should be more likely to contain multiple adult males. This prediction was tested by van Schaik & Hörstermann (1994) in a controlled comparison of arboreal folivores in three different continents: American howler monkeys, African colobus (*Colobus spp.*) and Asian langurs. Large monkey-eating eagles are absent in the range of the Asian langurs and one population of African colobus, and, as predicted, in these populations average-sized female groups are most likely to contain a single adult male at a given group size (Figure 4). Alternative hypotheses did not produce this pattern. These findings are therefore consistent with the hypothesis that predation risk can affect male representation in primate groups.

The number of males in a group may also affect the risk that a female is subject to infanticide. Infanticide is expected to be less likely if a group contains multiple reproductively active males because male immigration is less likely to be in the form of violent take-overs of top dominance, and potentially infanticidal newcomers face several possible sires of the infants (of course this assumes promiscuous matings in multi-male groups, but this is a common phenomenon in the larger ones: Hrdy & Whitten 1987). Comparisons have shown that infanticide risk is lower in multi-male groups than in single-male groups in hanuman langurs (Newton 1986) and mountain gorillas (Robbins 1995). This argument would predict that it would generally be to the females' advantage to live in groups with multiple adult males unless the feeding competition that this produces is too severe or unless females have alternative means of reducing infanticide risk.

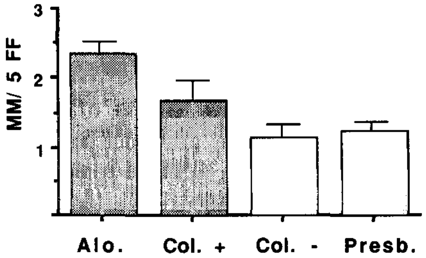

Figure 4. The mean (+ standard error) number of adult males in a group of five adult females as estimated from regression equations relating the number of males to the number of females in groups of different arboreal folivores. The comparison is between taxa inside the range of large monkey-eating eagles (Alo, Col+) and those outside the range of such eagles (Col−, Presb). Alo = *Alouatta*; Col = *Colobus*; Presb = arboreal Southeast Asian *Presbytis* (excluding *P. entellus*). The grand mean group size of these species is about 5 females. The differences among these estimated values are highly significant. From van Schaik & Hörstermann (1994).

It is difficult to make general predictions for the degree of feeding competition imposed by males, but females have another strategy to reduce infanticide risk, namely breeding dispersal or transfer. Females can reduce the risk of infanticide if they can transfer to other groups during times of reduced vulnerability before a situation develops in which take-over by another male is likely and they would become vulnerable to infanticide. A recent comparative review of Asian langurs confirms this: where females could no longer move freely between groups, they were twice as likely to lose an infant to infanticide than where they could (Sterck, in manuscript).

This leads to a modified prediction. Having multiple males in the group or being able to disperse are complementary female social options to reduce infanticide risk. While each may have a cost, the absence of both is unlikely

Table 2. The relationship between the female breeding dispersal (absent in female-boned and female-resident taxa) and the representation of adult males in primate groups for taxa in which both social features are known[a]

Female breeding philopatry	Single-male groups[b]	Multi-male groups[b]
Present[c]	Cercopithecus non-aethiops Erythrocebus Theropithecus	Lemur catta Cebus Saimiri sciureus Cercocebus (?) Cercopithecus aethiops most Papio Macaca
Absent[d,e]	Nasalis (?) Rhinopithecus (?) Colobus badius p.p. Presbytis/Trachypithecus Papio hamadryas Gorilla g. beringei	Propithecus (?) Eulemur fulvus Saimiri oerstedi Alouatta (?) Brachyteles Ateles Colobus badius Papio ursinus p.p. Pan troglodytes

[a] Social designations compiled from various sources.

[b] A taxon is considered multi-male if many groups contain multiple males or if there is a strong positive relationships between number of females and number of males (cf. van Schaik & Hörstermann 1994).

[c] Includes female-bonded, tolerant female-bonded, and female-resident (see Table 1).

[d] Includes non-female-bonded (see Table 1).

[e] It is assumed that females in non-female-bonded show breeding dispersal in addition to the much better known natal dispersal (this assumption is known to be correct for most non-female-bonded taxa with single-male groups). *Presbytis entellus* is not included because of the possible human impact on female dispersal (Sterck, in press).

if infanticide reduction is an important objective of female social strategies. Thus, the combination of female philopatry and single-male groups should be rare.

At first sight, comparative data on primate social systems do not provide strong support for this hypothesis (Table 2). The combination of female philopatry and single adult males is found in several taxa. However, in the gelada (*Theropithecus gelada*) a second male, the 'follower', may reside in the group (Dunbar 1984), which is likely to reduce infanticide risk. In the other two taxa, guenons, *Cercopithecus* non-*aethiops*, and patas, *Erythrocebus patas*, influxes of many males during the mating season are common (Cords 1988). This phenomenon, too, may be seen as an anti-infanticide strategy, in which paternity is confused to some extent, with the effect that infanticide by new resident males is less likely. Depending on one's inclination, these phenomena may be regarded as a refutation of the initial hypothesis, or as indicating that alternative tactics can be adopted to minimize the impact of infanticide risk where the use of the common strategies is precluded. Finally, it might be argued that multi-male groups are surprisingly common among primates in general, but again the proper comparisons with representatives of other mammalian orders have not been undertaken.

In conclusion, there is some evidence in support of the notion that the number of males associated with a group of females is governed in part by the need for male protection against infanticidal males or predators. However, much more work is needed before this conclusion can be accepted unequivocally.

Infanticide risk and between-group relations

Finally, could infanticide risk have affected the nature of between-group relations? At the outset, it is interesting to note that in most species and situations, between-group relations in primates are tantamount to between-group antagonism. Theorizing to date about the possible functions of between-group antagonism has exclusively focused on defence of resources and of mates, and there is evidence for both (Cheney 1987; Kinnaird 1992; van Schaik *et al.* 1992; Cowlishaw 1995), although a thorough review of the evidence in favour of these functions is long overdue.

An additional function is possible. There is a surprising number of reports that indicate that infanticide can also occur during between-group encounters: in savanna baboons (*Papio anubis*: Shopland 1982; Collins *et al.* 1984), vervets (*Cercopithecus aethiops*: Cheney *et al.* 1988), ringtailed lemurs (*Lemur catta*: Hood 1994), hanuman langurs (Sommer 1994), gorillas (Watts 1990) and thomas langurs (R. Steenbeek, personal communication).

In fact, in some cases, such as thomas langurs, males that are already attached to a group of females make violent sneak-attacks on other groups. Such attacks may be selectively advantageous, if females are more likely to transfer into the group of the infanticidal male (because he is the best protector against future attacks). All this suggests that infanticide risk may affect between-group relations in primates.

How can this suggestion be tested? Some simple predictions can be made for the behaviour of individuals or classes during group conflicts. First, when a group contains no infants its members should be more likely to actively engage other groups. Second, females with infants are expected to hang back during encounters. These predictions have not yet been tested systematically, but preliminary support for them comes from van Schaik & Dunbar's (1990) analysis of Mitani's (1987) gibbon experiments.

Predictions on the rate and nature of between-group conflicts can also be developed. The critical prediction made by the infanticide prevention hypothesis is that the adults and infants of primate groups should avoid intermingling even when no contested resources are present and when there is no mating activity. However, developing further predictions is beset by problems. First, it is often difficult to separate mate defence and infant defence functions in group-level phenomena. Second, groups are not homogeneous units, but are composed of a multiplicity of players of both sexes, who are simultaneously pursuing different, partly incompatible, objectives. Third, between-group relations are affected by the collective action problem (see Hawkes 1992). Individuals produce, at some cost to themselves, a benefit (e.g. they acquire a resource such as food, mates, or safety for infants) to which all group members will subsequently have access. If some beneficiaries do not assist in this process, and thus do not share the cost, the best course of action of the producers of the benefit may be to stop providing the benefit, unless these free-riders are close relatives. In between-group relations, this translates into avoidance of conflicts (and perhaps the adoption of 'bourgeois'-like solutions).

A compilation of primate studies indicates that groups containing multiple adult males are indeed less likely to have conflicts with their neighbours (Figure 5), indicating between-group avoidance in multi-male groups. There are also reports of vocally mediated avoidance of close contact between groups in populations where all groups contain multiple males (e.g. Waser 1976). Given this effect it is not surprising that group composition also affects range overlap (Figure 6). This effect is retained in each of the four radiations represented in the data set. Range overlap is not correlated with the defensibility of the range, as measured by Mitani & Rodman's (1979) D-index ($R = -0.085$, $n = 24$). This result indicates that

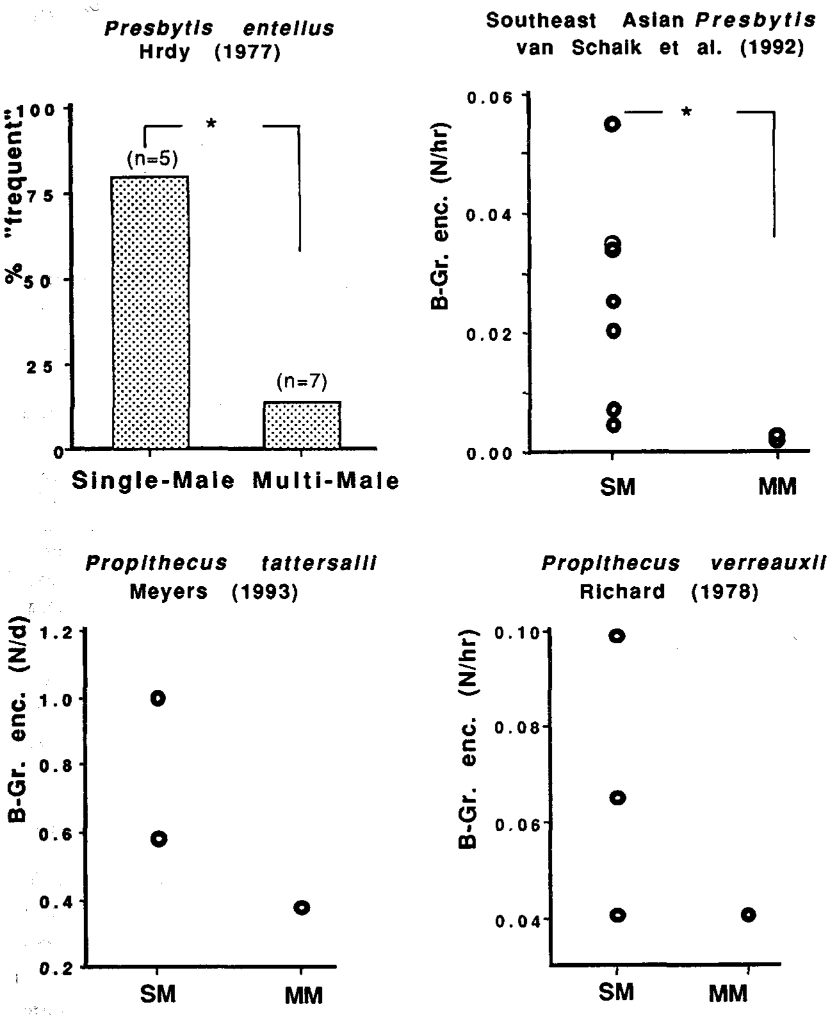

Figure 5. Between-group antagonism: single-male vs. multi-male groups. Rates of (predominantly antagonistic) encounters between groups for groups containing multiple adult males from species or populations containing groups of both kinds, in langurs and sifakas (*Propithecus spp.*). Asterisks indicate significance at the $P = 0.05$ level.

social factors, probably the collective action problem, may prevent the expression of the expected functions of between-group relations, such as resource defence. On the other hand, between-group avoidance facilitates infant defence.

In conclusion, at this time there is no solid evidence that the nature of between-group relations serves to reduce infanticide risk, but I believe the suggestion deserves serious scrutiny in the future.

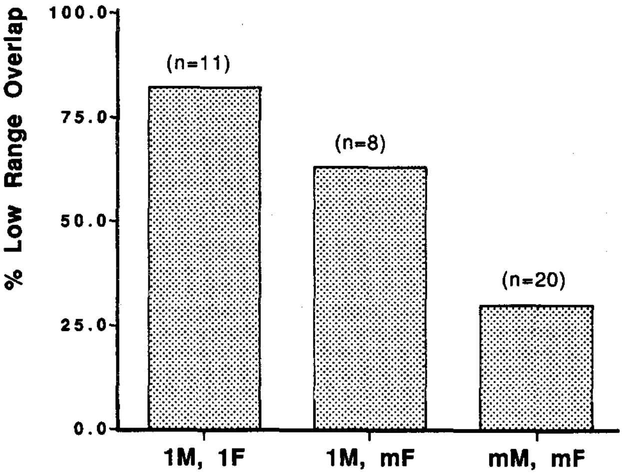

Figure 6. Group composition and range overlap. The percentage of studies with low home range overlap in relation to group composition (M = male, F = female; m = multiple). Low overlap is defined here as less than 30% qualitative overlap, corresponding to approximately the highest overlap shown by behaviourally territorial groups of gibbons (van Schaik & Dunbar 1990). The data are taken from the two most extensive published compilations (Mitani & Rodman 1979; Cheney 1987).

DISCUSSION

The assumptions of socio-ecology

Beginning with Crook & Gartlan (1966), socio-ecology has adopted an adaptationist stance, and has focused on the effect of ecological factors, in particular the abundance and distribution of food and predators, on female distribution and relationships, and on the effect of the spatio-temporal distribution of mating opportunities in determining male distribution and relationships. More recently, the role of social forces is increasingly highlighted, especially harassment of females and killing of infants by males (e.g. Wrangham 1979; Smuts & Smuts 1993). This paper has attempted to integrate the impacts of social and ecological forces on social features. While it is still early, there seems to be increasing evidence that infanticide risk is a selective force similar in strength to ecological factors, with which it may interact in complex ways.

It has often been stressed that social structure and organization are correlated with phylogeny (Struhsaker 1969; Di Fiore & Rendall 1994). The influence of phylogeny can be subsumed under the socio-ecological approach, if it is thought to reflect its correlation with features of morphology, physiology, life style and life history, all of which mediate the impact of external factors (cf. Harvey & Pagel 1991). For instance, dispersal opportunities will be severely curtailed in animals that rely on elaborate dwellings that require a major collective effort to build (e.g. Waser 1988). Likewise, variation in altriciality or litter size constrain the social options of adults. More subtly, phylogenetic position may affect cognitive capabilities, and thus the possible complexity of social relationships (Cheney & Seyfarth 1990).

The true alternative to the adaptationist approach of socio-ecology is the long-standing critical undercurrent that essentially considers social behaviour to express adaptively neutral variation whose correlation with phylogeny is entirely due to common descent (Rowell 1979; Di Fiore & Rendall 1994), or assumes that social inventions, while adaptive, are so rare that only a small and arbitrary set of taxa will have them (Thierry 1990). The adaptive approach is adopted here especially because it is more heuristic in that testable hypotheses are more easily framed and tested. To the extent that these hypotheses are supported by empirical data, this vindicates the adaptive approach. However, as shown by the discussion of female philopatry and male representation in primate groups, one of the greatest obstacles in testing these hypotheses is the occurrence of alternative strategies and tactics which may have arisen where the common strategy was less effective or too costly. This seemingly endless list of functionally equivalent alternative strategies introduces an element of faith into the adoption of the approach.

Testing socio-ecological models

Socio-ecological hypotheses are evolutionary models. Some tests of these models have employed experimental manipulations of ecological conditions (e.g. Gore 1993). For such manipulations to work, the predicted social change must be within the norm of reaction of the species. The increased appreciation of the existence of alternative strategies (Dunbar 1983) and the resulting flexibility (e.g. Hamilton *et al.* 1976) has led to the assumption of near-infinite behavioural flexibility (Dunbar 1989). However, many species maintain a similar social system in captivity, despite wide variation in conditions; and studies of hybrid baboons indicate that some social behaviour cannot easily be modified by short-term experience (e.g. Nagel 1973). An additional technical problem with experiments is that animals may not be able to interpret the modified conditions correctly when they do not last long enough or alternate with other conditions (cf. Berger 1988).

Lack of phenotypic plasticity is less likely to plague experiments that manipulate the social or demographic context because variation in these variables is more likely at ecological time scales. There is surprisingly little documentation of the social consequences of intraspecific variation in group composition, group density, etc.

Regardless, comparisons between taxa remain one of the most powerful ways to test these models, and the preliminary comparisons presented here attest to their suitability. However, the limited phenotypic plasticity referred to above means that the populations compared must live in undisturbed habitats, so as to ensure we study the impact of ecological and demographic conditions that prevailed during history rather than the impact of unintended and undocumented recent experimental alterations. This caveat is not a gratuitous one: habitat disturbance and modification and fragmentation, leading to unbalanced ecological communities and sometimes to hyper-abundance of primates where they are protected, are beginning to affect many of the field sites where the data are collected that are used in these comparisons. For instance, some of the observed behavioural differences between the chimpanzee populations of Gombe and Mahale are likely due to the small size and lack of dispersal opportunities at Gombe relative to the more natural situation at Mahale (Nishida *et al.* 1990).

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