
REVIEW

Elisabeth H.M. Sterck · David P. Watts
Carel P. van Schaik

The evolution of female social relationships in nonhuman primates

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Abstract Considerable interspecific variation in female social relationships occurs in gregarious primates, particularly with regard to agonism and cooperation between females and to the quality of female relationships with males. This variation exists alongside variation in female philopatry and dispersal. Socioecological theories have tried to explain variation in female-female social relationships from an evolutionary perspective focused on ecological factors, notably predation and food distribution. According to the current “ecological model”, predation risk forces females of most diurnal primate species to live in groups; the strength of the contest component of competition for resources within and between groups then largely determines social relationships between females. Social relationships among gregarious females are here characterized as Dispersal-Egalitarian, Resident-Nepotistic, Resident-Nepotistic-Tolerant, or Resident-Egalitarian. This ecological model has successfully explained differences in the occurrence of formal submission signals, decided dominance relationships, coalitions and female philopatry. Group size and female rank generally affect female reproduction success as the model predicts, and studies of closely related species in different ecological circumstances underscore the importance of the model. Some cases, however, can only be explained when we extend the model to incorporate the effects of infanticide risk and habitat saturation. We review evidence in support of the ecological

model and test the power of alternative models that invoke between-group competition, forced female philopatry, demographic female recruitment, male interventions into female aggression, and male harassment. Not one of these models can replace the ecological model, which already encompasses the between-group competition. Currently the best model, which explains several phenomena that the ecological model does not, is a “socioecological model” based on the combined importance of ecological factors, habitat saturation and infanticide avoidance. We note some points of similarity and divergence with other mammalian taxa; these remain to be explored in detail.

Key words Primate social organization · Competition · Infanticide · Habitat saturation

Introduction

Non-nomadic animals tend to form social relationships regardless of their degree of spatial association, these relationships are most readily inferred when the animals are gregarious. Most diurnal nonhuman primates show female gregariousness [81% (42/52) of taxa, where taxa are genera, species or species groups within genera that are homogeneous for the relevant social traits: C.P. van Schaik, unpublished work]. Hence, they are a suitable group in which to study the evolution of female social relationships and in which to look for explanatory principles that may apply to mammals more generally.

Female social relationships vary systematically across primate taxa, although quantification of this variation is still poor. They have affiliative, sexual and aggressive components. Agonistic relationships are an especially important organizing feature in primate groups. These vary along three dimensions, the first of which is that from egalitarian to despotic (Vehrencamp 1983). Egalitarian females have no detectable or poorly defined

Elisabeth H.M. Sterck (✉)
Ethology and Socioecology, Utrecht University,
P.O. Box 80086, 3508 TB Utrecht, The Netherlands
Fax: +31.30.252.1105;
e-mail: sterck@neuretp.biol.ruu.nl

David P. Watts
Department of Anthropology, Yale University,
New Haven, CT 06250, USA

Carel P. van Schaik
Department of Biological Anthropology and Anatomy,
Duke University, Box 90383, Durham, NC 27708, USA

dyadic dominance relations; dominance hierarchies, if they can be distinguished at all, are fuzzy and non-linear. Despotic females have clearly established and often formalized (de Waal 1989) dominance relations and usually have linear dominance hierarchies. The second dimension is that from individualistic to nepotistic. In nepotistic hierarchies, female relatives tend to rank close together as a result of coalitionary support (especially from relatives, but sometimes also from non-relatives), whereas in individualistic hierarchies the ranks of female relatives tend to be independent of each other. The third dimension is that of tolerance (de Waal 1989). As tolerance increases the severity of aggression decreases (even if aggression is still common), threats toward dominants increase, and various cohesion-enhancing behaviors (e.g., reconciliation) increase (Thierry 1985; de Waal and Luttrell 1989). These three dimensions are interrelated: tolerant and nepotistic dominance systems are only possible in systems that are basically despotic.

A demographic factor also varies systematically in relation to these social dimensions. Females are philopatric and related females reside together in most species, but female dispersal is common in others (Moore 1984; Pusey and Packer 1987a; Strier 1994). Female philopatry is often, but not invariably, related to despotic systems and their variants (Wrangham 1980).

This variation reflects variation in female social strategies, i.e. the various ways in which females use social behaviour to achieve their reproductive goals. Patterns in social relationships and demographic processes constitute the social system. Since Crook and Gartlan (1966), researchers have appealed to ecological factors, in particular the abundance and distribution of predators and food, to explain the variation in social systems. The role of social factors, especially male harassment of females, has also received considerable attention recently (e.g., Wrangham 1979; Smuts and Smuts 1993; Brereton 1995; Treves and Chapman 1996). However, alternative approaches are possible. They assume that variation in the social strategies of female primates is adaptively neutral (Rowell 1979; Di Fiore and Rendall 1994) or reflects the influence of different social inventions (Thierry 1990).

The only current model that specifically examines the role of ecological factors in the evolution of female social relationships was developed by Wrangham (1980) and modified and expanded by van Schaik (1989). It assumes that coping with predation requires gregariousness in diurnal female primates, and that gregariousness leads to feeding competition among females, within and between groups (Fig. 1). The type of feeding

competition is determined by the distribution of food sources relative to group size and in turn determines female social relationships. The ecological model implicitly excludes the possibility that female interactions with males affect social relationships among females. These interactions, however, have recently received more attention as a factor regulating group structure (Brereton 1995; Treves and Chapman 1996; Sterck 1997).

The aim of this paper is to refer to ecological, demographic and social factors to explain variation in female primate social strategies. We present the ecological model (van Schaik 1989) and evaluate its power. The model gains broad support. In addition, we examine several alternative hypotheses. Among these alternatives, two factors seem to explain additional features of the primate social systems, namely the risk of infanticide and habitat saturation. We end with an attempt at synthesis using the risk of predation, risk of infanticide and food distribution as the main causal factors of social systems.

The ecological model

Group living and predation risk

The hypothesis that gregariousness in highly mobile animals such as diurnal primates serves to reduce the risk of predation has recently been extensively reviewed (Dunbar 1988; Janson 1992; Cowlshaw 1994; Isbell 1994), so we will only summarize it briefly. The proposed advantages of gregariousness are (1) improved predator detection, (2) reduced per capita risk of capture (assuming that predators take only single prey) because of the dilution and selfish herd effects and because prey clumping may reduce the per capita rate at which predators encounter prey, and (3) occasional communal defense or defense by the largest members of the group.

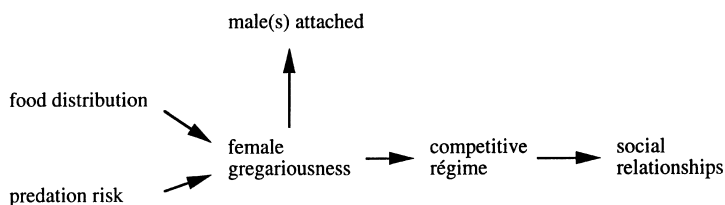


Fig. 1 Flow diagram of the ecological model of van Schaik (1989). Female gregariousness is determined by the opposing factors of predation risk and food distribution. The distribution of males depends on the gregariousness of females. The degree of female gregariousness in combination with the food distribution determines the type of food competition females experience. This in turn determines female social relationships

Group living and competition for food

Within-group competition for food or safe positions is a virtually inevitable and universal cost of group living (Janson 1988). Increased competition is expressed as decreased encounter rates with food. If the animal is to maintain constant net food intake, both foraging effort and gross intake should increase (Fig. 2). As groups become larger and competition intensifies, this compensatory response becomes insufficient: net food intake starts to decline, affecting reproductive performance or survival (through starvation). If an animal responds by being more peripheral or travelling in smaller parties (e.g., van Noordwijk and van Schaik 1987; Ron et al. 1996), it may maintain constant net food intake but face increased predation risk.

As Fig. 2 indicates, the level of within-group competition is not necessarily linearly related to the size and spatial cohesion of groups. Where grouping is flexible and responds to food supply, animals may be able to keep competition below the level of reduced net food intake, or even below the level of increased expenditure. In such species, party size is positively related to food availability (spider monkey, *Ateles paniscus*: Symington 1988; Chapman et al. 1995; chimpanzee, *Pan troglodytes*: Isabirye-Basuta 1988; Chapman et al. 1995; orangutan, *Pongo pygmaeus*: Sugardjito et al. 1987). Permanently gregarious species, however, should experience variation in expenditure and even net food intake as food supplies vary over time, even though they may respond to increased competition by adjusting the number of individuals using a patch (e.g., mantled howler, *Alouatta palliata*: Leighton and Leighton 1982; Chapman 1990; vervet, *Cercopithecus aethiops*: Whitten 1988; long-tailed macaque, *Macaca fascicularis*: van Schaik and van Noordwijk 1988; baboons, *Papio anubis*: Barton and Whiten 1993; Thomas langur, *Presbytis thomasi*: Sterck 1995). Considerable evidence documents

the effect of within-group competition on foraging effort and some evidence on net food intake in permanently gregarious species (review: Janson 1988, 1992).

Competition has two distinct components whose relative strength depends on resource distribution patterns (e.g., van Schaik and van Noordwijk 1988; Janson and van Schaik 1988). In scramble competition, individuals lose access to resources because others have already found and used them. Scramble competition for food predominates when limiting resource patches are either of low value, highly dispersed, or very large relative to the size of the group (or population density in the between-group case). Contest competition occurs when patches are clumped and of intermediate size and some individuals can systematically exclude others from limiting resource patches and obtain more of the resources. Within-group scramble (WGS) is the effect of group size with that of dominance removed, and within-group contest (WGC) is the dominance effect (although its strength may well vary with group size).

Where animals live in permanent groups, competition can also take place between groups, for access to food or other resources (water, refuges, good quality ranges). Between-group competition can be scramble (BGS) or contest (BGC). BGC is influenced by food patch distribution and population density, whereas BGS merely reflects population density (van Schaik 1989). The com-

Fig. 2 The relationship between the intensity of feeding competition that females experience and its effect on female food intake, energy expenditure and reproductive performance. Feeding competition is related to group size, but its effects are not linear. Below a certain (relatively small) group size, the intensity of competition can increase without an increase in energy expenditure and intake, or a decrease in reproductive output (*category A*). When group sizes are intermediate, females must spend more energy to obtain sufficient food, but can compensate by increasing food intake (*category B*). In large groups, females have to spend even more energy obtaining food, but cannot compensate by a further increase in food intake. Their reproductive output is therefore reduced (*category C*)

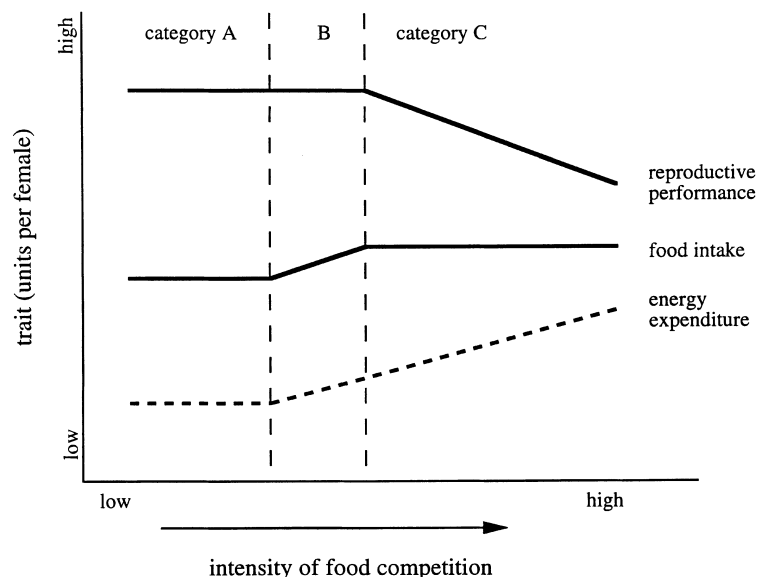


Table 1 Competitive regime and categories of female social relationships in diurnal gregarious primates. Alternative terms to the ones introduced by Wrangham (1980) are proposed, because especially the term “female bonded” leads to confusion: it can refer

to female philopatry combined with individualistic egalitarian female dominance hierarchies, or combined with decided female dominance hierarchies (despotic or tolerant) with coalitions between female kin

Social category	Competitive regime		Social response	
	Within-group contest	Between-group contest	Female philopatry	Female ranking
DE Dispersal-Egalitarian	Low	Low	No	Egalitarian
RE Resident-Egalitarian	Low	High	Yes	Egalitarian
RN Resident-Nepotistic	High	Low	Yes	Nepotistic and despotic
RNT Resident-Nepotistic-Tolerant	High (Potentially)	High	Yes	Nepotistic but tolerant

petition experienced by a group-living animal is generally a mix of these four components of competition.

Social consequences of competition

Where scramble predominates, no overt agonistic interactions over access to the limiting resources are expected, and all individuals within a group or population obtain roughly equal shares. However, contest involves agonistic interactions. Hence, variation in the strength of WGC and BGC should underlie variation in female social relationships, which fall into four general classes (Table 1). The use of categorical variables is justified because, although the underlying ecological variation is continuous, the social responses are more or less discrete. Our category labels are descriptive, to distinguish them from two earlier, influential models (Wrangham 1980; Van Schaik 1989). Wrangham (1980) distinguished “female bonded” and “non-female bonded” species among gregarious primates. Female philopatry and differentiated grooming and agonistic support among females characterized female bonded species. Van Schaik (1989) uncoupled philopatry and “bonding” (defined by him as formation of agonistic alliances), but retained the terms “female bonded” and “non-female bonded.”

When WGC is strong, females should have formal dominance and decided agonistic dominance relationships: one member of a dyad consistently wins contests, while the other loses consistently and may use formal signals of submission to indicate her subordinate status (de Waal 1989). Females should form long-term agonistic alliances with relatives, and also mutualistic coalitions with non-relatives. These coalitions produce stable, linear and nepotistic hierarchies (Chapais 1992; Pereira 1995), in which rank differences are strongly enforced (i.e., dominance relationships are despotic, *sensu* Vehrencamp 1983). We call cases in this class Resident-Nepotistic.

Females should also be philopatric: a female who attempted to transfer would lose access to allies and would probably face strong resistance to immigration from resident females in any group she tried to enter

(van Schaik 1989). We assume that these social costs are the most important costs of dispersal in gregarious primates. Ecological costs include increased predation risk and inefficient foraging in transitional or marginal habitat; unfamiliarity with resource distribution in new areas; competition to establish home ranges or territories (Waser and Jones 1983; Alberts and Altman 1995; Isbell and van Vuren 1996). Although ecological costs have been invoked to explain why females are usually the philopatric sex in mammals (Isbell and van Vuren 1996), they apply most strongly to solitary emigrants. Direct transfer between groups would remove most or all of them (Isbell et al. 1993; Watts 1996).

The ease with which females disperse has consequences. Where WGC is low and dispersal costs for females are low, females may migrate at least partly to reduce feeding competition (Wrangham 1980; Dunbar 1988; Sterck 1997) and females may distribute themselves in an approximately ideal free fashion. Groups should then tend to be near optimal size (Fig. 3), and overall competition in the group is limited. In situations with strong WGC, females can only disperse in the presence of kin, i.e., form new groups by fissioning. Then, groups are often considerably larger than optimum before they can split, and new groups are often near the minimum viable size and thus smaller than optimum. Groups near the upper equilibrium size are likely to suffer increased WGC. Thus, a positive feedback loop arises (Fig. 4): WGC constrains female dispersal, which in turn exacerbates WGC. [Henzi et al. (1997) describe a similar, but opposite, feedback loop in mountain baboons in a situation in which food is scarce and sparsely distributed but the threat of predation has also been removed].

When WGC is weak, females would gain little from establishing strong, decided dominance relationships or from using nepotistic or mutualistic coalitions to compete for food and rank. Consequently, they should not form formal dominance relations or establish stable, linear dominance hierarchies. Also, coalitions, particularly with nonrelatives, should be uncommon or absent, and females should not rely on long-term alliances. Females can disperse (transfer), because they do not lose coalitions partners and usually face little or no resistance

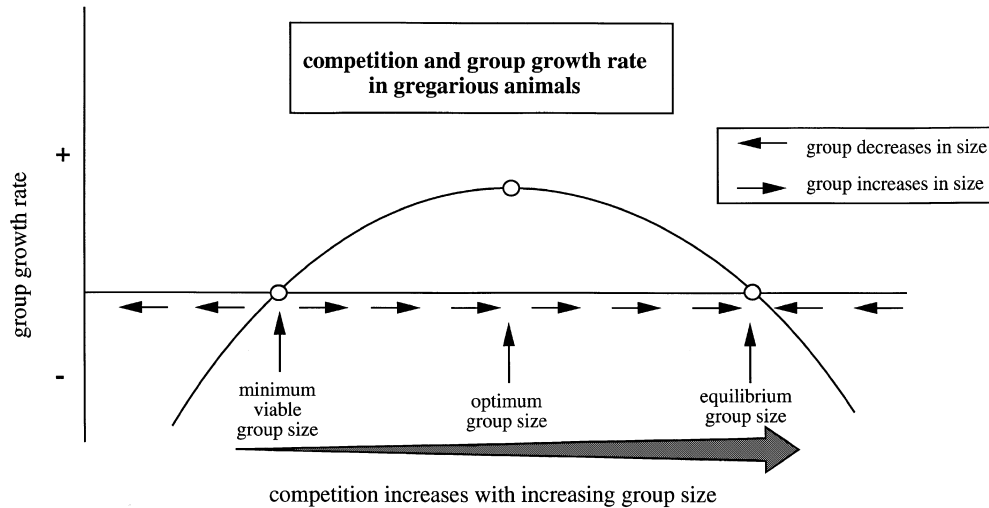


Fig. 3 The dynamic relationship between group size and group growth rate in gregarious primates. Within-group competition increases with group size. Groups below the minimum viable group size will decrease in size and eventually cease to exist. Groups above the *minimum size* and below the *equilibrium size* will grow. Groups at the *optimum size* have maximum growth rate. Groups at equilibrium size do not grow or decrease in size. Groups larger than the equilibrium size will become smaller

to immigration. Given other social or demographic pressures (e.g. inbreeding avoidance, infanticide risk), they generally do so. We name this class Dispersal-Egalitarian.

Although the strength of WGC varies continuously, the social responses may not (Fig. 5). An intermediate system of female social relationships may arise where food distribution is such that contest occurs, but the benefits are too small to lead to predictable kin support and consistent philopatry (which have costs). Females are thus still likely to disperse despite their forming decided dominance relations. However, this social response is expected only under a narrow range of conditions that are unstable over time, so we should see it only rarely in nature.

Strong BGC can in principle co-occur with either weak or strong WGC (van Schaik 1989). If only BGC is strong, and WGC is weak, females need not form decided agonistic dominance relationships, and within-group coalitions are unimportant. However, while success in BGC is important to all females, an individual can withhold her participation in such contests but gain from the participation of others. Females can solve this “collective action problem” (Hawkes 1992) by residing with female relatives, and so should be philopatric. We call this class Resident-Egalitarian. This category is not likely to have intermediates with the Dispersing-Egalitarian category, because female residence must be the norm to achieve success in between-group contests.

Finally, where WGC and BGC are both strong, they should interact. We expect formal dominance relationships, stable, linear dominance hierarchies established and maintained by coalitional support, and female

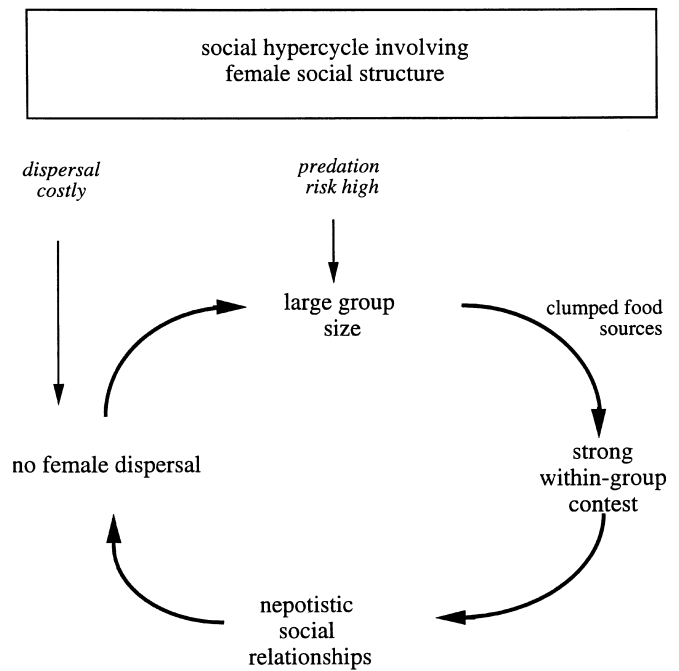
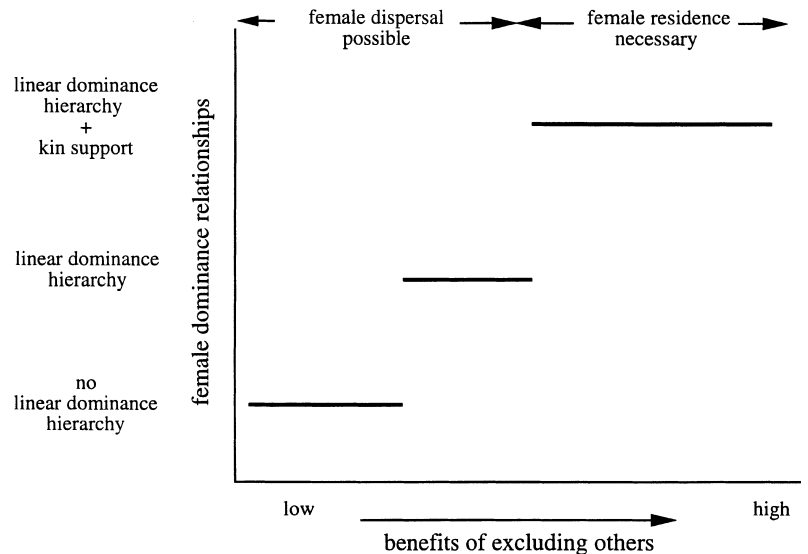


Fig. 4 The social hypercycle involving female social structure. Large group size leads to strong *within-group contest competition* (WGC). This in turn affects female dominance relationships: females form coalitions with kin against other females (*nepotistic social relationships*). This prevents female dispersal, which means that groups grow above the optimum size before they eventually split. Once females are in this cycle they cannot easily convert to the opposite strategy of low WGC, egalitarian relationships, female dispersal and small (optimum) group sizes

philopatry. But high-ranking females risk losing the support of low-ranking females in BGC if they enforce dominance too strongly, because low-ranking females gain less from cooperation in BGC. Dominance relationships should then become more tolerant, in that dominants allow subordinates regular access to food or important social partners rather than monopolizing these (van Schaik 1989). We label this class Resident-Nepotistic-Tolerant, but the degree of tolerance can vary.

Fig. 5 The relationship between the reproductive benefits of excluding other females from access to resources (X -axis), dominance relationships (Y -axis), and female dispersal patterns



Evaluating the ecological model

In the ecological model, the abundance and distribution of food and predation risk are the independent factors that determine the potential competitive regime. The actual regime, measured by estimating the four competition components from female behavior, energetics or demography (Janson and van Schaik 1988), is similar to the potential one if the animals behave optimally. As we shall see, social factors and extrinsic effects (e.g., habitat disturbance) may lead to suboptimal behavior.

Most studies that address the model only assess whether the expected social and fitness consequences occur in particular cases, given a particular food distribution and competitive regime. To test the model properly requires systematic measures of the independent variables, generalizable across studies. In the absence of such data, we can test the model indirectly by trying to document that the predicted social categories exist and are linked to the proposed ecological conditions; by experimentally manipulating the proposed independent variables and evaluating “natural experiments”; and, most importantly, by comparing the ecology of closely related species with different social systems.

Tests of internal consistency

Do the predicted social categories exist?

Data on 27 well-studied taxa are largely consistent with several predictions that follow from the model about the clustering of female social traits. The first prediction concerns associations among social features. Frequent coalitions, often but not always exclusively between relatives, should co-occur with decided agonistic relationships (i.e., with agonistic dominance relationships), whereas they should be rare in species with undecided

agonistic relationships between females. As expected, decided dominance relationships and frequent coalitions are either both present (7 species) or absent (26 species) (Table 2).

Decided dominance relationships are often characterized by formal submission signals that are unidirectional within dyads: bared teeth in various cercopithecines (de Waal 1989; Preuschoft 1995), spat calls in ring-tailed lemurs (*Lemur catta*: Pereira and Kappeler 1997), and pant grunts in chimpanzees (de Waal 1989). In at least some cases (chimpanzee: de Waal 1989; mountain gorilla, *Gorilla gorilla beringei*: Watts 1994), formal dominance relationships exist between females and males, but not between females; their absence between females is thus not due to the lack of appropriate signals.

A second prediction of the ecological model is that no species should show female dispersal in combination with decided dominance relationships and frequent nepotistic or mutualistic coalitions. Indeed, none of the 25 species for which data are available from the wild show this pattern (Table 2). Also, as predicted, several species (patas monkey, *Erythrocebus patas*; several guenons, *Cercopithecus* spp.) show female philopatry, but no formal dominance, little coalitionary aggression, and weak agonistic dominance hierarchies. This underscores the need to distinguish between the Resident-Nepotistic and Resident-Egalitarian patterns (pace Wrangham 1980).

Finally, the model predicts that most species show either the Resident-Nepotistic or Dispersing-Egalitarian pattern, because the effects of WGC should generally outweigh those of BGC (van Schaik 1989). As expected, only 3 taxa listed in Table 2 are Resident-Egalitarian, versus 7 Resident-Nepotistic and 12 Dispersing-Egalitarian taxa. Also as predicted, Resident-Nepotistic species differ in the degree to which females show agonistic tolerance (de Waal 1989; Thierry 1990), affiliate disproportionately with female kin, and reconcile with unrelated females (Aureli et al. 1997). Most of those listed in Table 2 are Resident-Nepotistic, but some cer-

Table 2 Association between female within-group coalitions, female dominance relationships and female philopatry among non-human primates with multi-female groups

Species	Coalitions frequent	Nepotistic	Formal submission	Linear	Philopatry the norm	Social category	Diet ^a	Refs ^d
<i>Eulemur fulvus</i>	–	–	–	–	–	DE	fru/fol	1
<i>Lemur catta</i>	–	–	+	–	–	DE	fru/fol	2
<i>Propithecus verreauxi</i>	–	– ?	–	–	– ?	DE ?	fol	3
<i>Cebus</i> spp. ^b	+	+	+	+	+	RN	fru/ins	4
<i>C. olivaceus</i> (Hato Piñero)	?	?	–	–	+	RE ?	fru/ins	5
<i>Alouatta seniculus</i>	–	–	–	–	–	DE	fru/fol	6
<i>A. palliata</i>	–	–	–	+	–	DE ?	fru/fol	7
<i>Ateles</i> spp.	–	–	–	–	–	DE	fru/fol	8
<i>Brachyteles</i>	–	–	–	–	–	DE	fru	9
<i>Saimiri sciureus</i>	+	+	+	+	+	RN	fru	10
<i>S. oerstedii</i>	–	–	–	–	–	DE	fru	11
<i>Cercopithecus aethiops</i>	+	+	+	+	+	RN	fru/fol	12
<i>Cercopithecus</i> spp. (most)	–	–	–	–	+	RE	fru/fol	13
<i>Erythrocebus patas</i>	–	–	–	–	+	RE	fru/ins	14
<i>Cercocebus</i> spp.	–	–	–	–	+	RE	fru	15
<i>Macaca</i> spp. (most)	+	+	+	+	+	RN	fru	16
<i>M. nigra</i> (Sulawesi spp.)	+	+	–	+	+	RNT	fru	17
<i>Theropithecus gelada</i>	+	+	+	+	+	RN	fol	18
<i>Papio</i> spp. (most)	+	+	+	+	+	RN	fru/fol	19
<i>P. ursinus</i> (mountains) ^c	–	–	–	–	–	DE	fru	20
<i>P. hamadryas</i> ^c	–	–	–	–	–	DE	fru	21
<i>Colobus badius</i>	–	–	–	–	–	DE	fol/fru	22
<i>C. guereza</i>	–	–	–	–	+	RE ?	fru/fol	23
<i>Presbytis entellus</i> (Jodhpur/Abu/Ramnagar)	–	–	–	+	+	RE ?	fol/fru	24
<i>P. thomasi</i>	–	–	–	–	–	DE	fol/fru	25
<i>Gorilla gorilla beringei</i>	–	–	–	–	–	DE	fol	26
<i>Pan troglodytes</i>	–	–	–	–	–	DE	fru	27
<i>P. paniscus</i>	–	–	–	–	–	DE	fru	28

^a diet: fru = frugivore; fol = folivore; ins = insectivore, after Plavcan and van Schaik 1992 and Smuts et al. 1987

^b *Cebus apella*; *C. Capuchinus*; and *C. olivaceus* (Hato Masaguaral)

^c *Papio ursinus* (mountains) and *P. hamadryas* are conservatively counted as one taxon

^d References: 1. Kappeler 1993; Overdorff 1993; 2. Sussman 1991; Pereira 1993; A. Jolly, (pers. comm.); 3. Richard 1985; 4. Janson 1985, 1988; O'Brien 1991, 1993; Robinson 1988a, b; Perry 1996 a, b; 5. L.E. Miller (pers. comm.); 6. Crockett 1984; 7. Glander 1992; Jones 1980; 8. Symington 1990; 9. Strier 1989; Strier et al. 1993; 10. Mitchell et al. 1991; Boinski and Mitchell 1994; 11. Mitchell et al. 1991; Boinski and Mitchell 1994; 12. Cheney and Seyfarth 1990; 13. Cords 1987; Struhsaker and Leland 1987; 14. Chism and Rowell 1986; Loy et al. 1993; 15. M.F. Kinnaird (pers. comm.); Gust and Gordon 1994; Gust 1995; 16. van Schaik et al. 1983; Walters and Seyfarth 1987; Preuschoft 1995; 17. M.F. Kinnaird (pers. comm.); Thierry et al. 1994; Petit and Thierry 1995; Preuschoft 1995; 18. Dunbar 1984; 19. Waltos and Seyfarth 1987; 20. Byrne et al. 1987, 1990; Whiten et al. 1987; 21. Stammbach 1987; Zinner 1993; 22. Struhsaker and Leland 1987; Marsh 1979; 23. Oates 1977; Dunbar 1987; 24. Hrdy 1977; Borries 1989; Borries et al. 1991; Koenig et al. 1997; 25. Sterck 1995; Steenbeek 1996; Sterck and Steenbeek 1997. 26. Harcourt 1979; Watts 1994, 1997; 27. Goodall 1986; 28. Kuroda 1980; G. Hohmann (pers. comm.).

copithecines show the Resident-Nepotistic-Tolerant pattern (e.g., Sulawesi macaque, *Macaca tonkeana*: Thierry 1985; stump-tailed macaque, *M. arctoides*: de Waal and Luttrell 1989).

Not all cases fit easily into the model, however, as we discuss below.

Competitive regime, behavior and reproductive success

Significant rank effects on some aspect of female energy budgets or offspring production should accompany decided dominance relationships and frequent coalitions between females. Conversely, species with undecided or weak dominance relations should not show significant rank effects on energy intake and reproductive success, although WGS may affect these variables. Most studies of species with strong female

hierarchies show the expected positive relationships between female rank and food intake (e.g. vervet: Whitten 1983; Japanese macaque, *Macaca fuscata*: Mori 1979; Saito 1997; baboons: Barton and Whiten 1993) or reproductive success (reviewed in Harcourt 1987, 1989; Silk 1993), and many show positive group size effects on energy expenditure (e.g., long-tailed macaque: van Schaik et al. 1983; brown capuchin, *Cebus apella*: Janson 1988; reviewed in Janson and Goldsmith 1995) and negative effects on reproductive rate (reviewed in van Schaik 1983).

The few studies that give a detailed picture of both WGC and WGS effects on behaviour and reproduction also support the ecological model (Table 3). Long-tailed macaques (Resident-Nepotistic) show strong WGC and WGS effects (van Schaik and van Noordwijk 1988). Conversely, Thomas langurs and mountain gorillas (Dispersing-Egalitarian) show weak effects of WGC and

Table 3 Effect of group size and rank on measures of female performance and reproduction (*DJL* = day journey length, % = % time)

	Long-tailed macaques	Thomas langurs	Mountain gorillas
Formal dominance	Yes	No	No
Female philopatry	Yes	No	No
Between-group fights	No	No	No
Social category	RN	DE	DE
Group size ^a			
DJL ^c	+2.3%	+7.2%	+7.4%
%(R + G) ^d	-0.8	-1.5	-
%(Feed)	+0.5	+2.3	+0.8
%(Travel)	+0.8	+14.3	-
Birth rate	-2.2	-3.6	-2.9
Yearlings	-2.3	-6.1	-4.4
rank ^b			
%(R + G) ^d	1.10	0.99	-
%(Feed)	0.98	1.07	-
%(Travel)	0.90	0.75	-
Birth rate	1.21	1.02	1.09
Yearlings	1.22	0.98	1.14

^a Effect per added female unless as note^c; the effect of the number of adult females in a group on the parameter of interest was calculated as the regression of the parameter on groups size. The effect per added female was expressed as the slope of the regression divided by the intercept of the regression

^b Average value of the parameter of interest for females with a rank above the average in a group, divided by the average value for females with a rank below the average in a group

^c Effect per added independent individual (i.e. excluding infants); calculated as in note^a, except expressed per independent individual, and not per adult female (slope of regression/intercept regression)

^d %(R + G): percentage of time spent resting or grooming

WGS on reproduction, although group size (WGS) but not rank (WGC) influences their behavior (Table 3; Watts 1996).

The vervets of Amboseli showed no effect of rank, but positive effects of group size (Cheney et al. 1988), consistent with an RE or RNT social structure, but clear rank effects on grooming and aggression (Cheney 1992), consistent with an RN structure. In contrast, Whitten (1983) found a positive effect of rank on reproduction in a vervet group at Samburu/Isiolo that fed heavily on clumped food sources, but not in a second group that had a more evenly distributed food supply. Monopolization of feeding sites generally becomes more advantageous, hence WGC increases, as they become more clumped (Harcourt 1987; van Schaik 1989). The correlates of reproductive success in the Amboseli population might be a product of the unusual circumstances of this dwindling population (see below).

Testing the link with ecology

Ecological conditions: diet and food distribution

The ecological model specifies food distribution as the causal factor. However, almost no studies have successfully quantified patch size distributions. In a com-

parison of sympatric, but distantly related, species, Sterck (1995) showed that a DE species (Thomas langur) used patches that were more abundant than, but equally as large as, those of an RN species (long-tailed macaque). In a study of one group of a RN species (Japanese macaques), Saito (1997) compared feeding efficiency and associated agonistic behavior in patches that varied in size, dispersion, and quality. He found that WGC effects were strongest (and the advantages of high rank most apparent) when the monkeys fed in rich but small patches that were far apart.

Thus far, BGC has not been quantified in relation to WGC or WGS in RNT or RE species. However, to be consistent with the ecological model, field studies of these species should at least demonstrate regular between-group antagonism in which females typically participate. Studies of several RE species show this: patas monkeys (Chism and Rowell 1986), several other guenon species (Cords 1987; Hill 1994), and agile mangabeys (*Cercopithecus galeritus*: Kinnaird 1992). The only detailed field study of a RNT species is on the Celebes macaque on the oceanic island of Sulawesi (*Macaca nigra*: Kinnaird and O'Brien 1994). This frugivorous species forms large groups, which spread widely during foraging and often break into subgroups that coordinate their movements in large home ranges. The groups show significant BGC during lean seasons. Thus, these weak tests of the social impact of BGC are consistent with expectations.

Comparative tests

Two comparative tests of closely related species that differ in social organization and ecology also address the model. The Peruvian common squirrel monkey (*Saimiri sciureus*) is RN, while the Costa Rican red-backed squirrel monkey (*S. oerstedii*) is DE (Mitchell et al. 1991; Boinski and Mitchell 1994). The two species have similar group sizes and diets, and face similar predation risk. However, Peruvian squirrel monkeys use relatively large fruit trees, while the Costa Rican ones mainly use extensive stands of small trees with tiny fruit crops and would not profit from contesting access to such highly dispersed food. As a result, contests over food were over 70 times more common in Peru.

The second comparison concerns savannah baboons (Barton et al. 1996). A population in an East African savannah habitat, where some food occurs in concentrated patches, showed decided dominance relationships, coalitions, female philopatry, and a clear effect of dominance rank on net food intake (Barton and Whiten 1993). In the other population, in montane grassland without predators and with highly dispersed food, the study group spread out so widely that females rarely interacted. They did not have clear dominance hierarchies or form coalitions. Female transfer occurs in this population (Byrne et al. 1990), and group fission also keeps average group size small (Henzi et al. 1997). Per

capita feeding supplants were 61 times more common in the savannah population (Barton et al. 1996).

Experimental studies

Evolutionary models like the “ecological model” assume that long-term exposure to a limited range of ecological conditions has led to social strategies that produce the best average fitness return in these conditions. Ontogenetically, these strategies arise through the interaction of genetic predispositions and learning. Many strategic responses are conditional, and thus subject to experimental manipulation that can give insights into the effects of ecological variables on social relationships.

However, two serious shortcomings limit our ability to interpret the results of such manipulations. First, animals may be unable to modify some aspects of social behavior in response to short-term social or ecological experience (Nagel 1973; Berger 1988), either because learning takes time or can only take place during sensitive periods in juvenility, or because the predicted social response is not within their norm of reaction. Second, animals may not be able to interpret the altered conditions correctly, for instance because in nature ecological conditions fluctuate. Thus, in a species normally subject to significant WGC, periods when WGC is low and WGS is relatively more important should not cause loss of dominance-oriented behavior. Indeed, this is abundantly shown in captivity where species tend to retain their species-typical social structure.

Experimental manipulations of ecological conditions must therefore be interpreted with caution. Gore (1993) and Zinner (1993), for example, offered highly clumped food to female hamadryas baboons (*Papio hamadryas*), a species in which females normally do not have strong dominance relationships. The females formed a linear agonistic dominance hierarchy, but aggressive bidirectionality within dyads was still relatively high and they did not develop formal dominance.

Conclusion

The ecological model links female social relationships to spatial patterning of individuals in relation to food distribution, and thus to competitive regimes. It has so far withstood evaluation and testing rather well, although the paucity of relevant data for especially the effects of BGC makes it impossible to evaluate it fully.

Nonetheless, not all cases easily fit the model, and we need to deal with several discrepancies. We note five here; the list is probably not exhaustive. First, females in some species occasionally evict other females from groups and transfer, if it occurs at all, is difficult (e.g., red howlers, *Alouatta seniculus*: Crockett and Pope 1993; mantled howlers, Glander 1992; ring-tailed lemurs: Vick and Pereira 1989). The model does not account for female eviction and forced dispersal. Second, WGC pro-

duces despotic female hierarchies and affects female reproductive success in female mantled howlers (Jones 1980; Glander 1992) and some hanuman langurs (*Presbytis entellus*: Borries 1993), but females do not form nepotistic dominance hierarchies. Third, ring-tailed lemurs show formal dominance but have unstable, non-linear hierarchies, perhaps because of sensory constraints on their ability to give consistent coalitionary support (Pereira 1993, 1995). Fourth, female mountain gorillas and Thomas langurs commonly transfer, but do not follow an ideal-free distribution with regard to feeding competition. Fifth, mountain gorilla females associate permanently with males despite low predation risk. We shall try to introduce additional factors in order to incorporate these discrepancies into the model.

Additional factors

Introduction

Assuming that the ecological model is correctly formulated in general, the observed discrepancies may arise for two classes of reasons. First, they may reflect non-adaptive situations (disequilibria), in which recent human-induced ecological changes have produced behavioral changes as allowed by the norm of reaction but not those expected under the model, because insufficient time has been available for required genetic changes. We do not need to modify the ecological model if such disequilibrium causes the discrepancies.

Second, additional selective forces not recognized in the model may impinge on female social relationships, so we need to expand the model. The most likely missing factor is sexual coercion (Smuts 1985; Smuts and Smuts 1993). Infanticide, an extreme form of coercion, is a potentially omnipresent selective force on female social strategies because of its major impact on female reproductive success. High dispersal costs also can affect social relationships adaptively or non-adaptively.

Habitat saturation: disequilibrium?

Recent environmental change may influence some aspects of female social relationships, but not others, and thereby obscure the original patterns of social behavior and even lead to non-adaptive behavior (cf. van Schaik and Kappeler 1996; Sterck, in press). Habitat fragmentation and elimination of predators by humans can lead to habitat saturation by nonhuman primate populations. These processes create high dispersal costs and the formation of unusually large groups, which increases the strength of WGC, and can turn animals that would normally be Dispersing-Egalitarian into more despotic ones (Sterck, in press; cf. Fig. 4). For example, females in hanuman langur populations in areas highly disturbed by humans form linear dominance hierarchies, and rank

strongly influences their reproductive success (Borries et al. 1991). However, they neither exhibit formal signals of submission nor use coalitions to make the hierarchies nepotistic (Borries 1993). They thus seem to be female resident despotic (FRD), a category that does not fit into the model. In principle, females could transfer to minimize WGC effects, but they resist immigration (Hrdy 1977; Borries 1993) and female dispersal seems to be too costly. Although targeting aggression between females and eviction might be expected in this population (below), none has been observed, perhaps because this "natural experiment" has so far had only a limited effect on the female behavioural repertoire.

Forest fragmentation and elimination of predators may have similarly affected Costa Rican mantled howler monkeys (*Alouatta palliata*). Females form linear dominance hierarchies (Jones 1980), and infant survival is highly correlated with female rank (Glander 1992), as expected if the level of WGC for food is high. Yet they neither have formal signals of submission nor use coalitions to make the hierarchies nepotistic (Jones 1980; Glander 1992). Females evict other females from groups and strongly resist immigrants, who have difficulty entering groups and succeed only with male help (Glander 1992). These howlers may also reflect the impact of a recent natural experiment.

Extreme natural deviations from average circumstances can also disrupt the fit between behaviour and environment, provided they are rare. For example, habitat deterioration in Amboseli led to population declines in baboons (Altmann et al. 1985) and vervets (Cheney and Seyfarth 1990). It greatly increased the vulnerability of vervets to predation, and the extreme concentration of water sources may have forced them into a situation with unusually high BGC relative to other known vervet populations (see below).

Habitat saturation as a possible selective force

Habitat saturation and high dispersal costs can also arise naturally, for instance in fragmented natural habitats (e.g., forest islands, or small gallery forests in savanna landscapes) or on islands without predators where densities are high. The ecological model recognizes this situation and predicts social consequences of strong BGC. However, another expected consequence, not incorporated into the original model, is targeted aggression in which single females or multiple females acting simultaneously attempt to evict other females. Eviction is common in among red howlers (*Alouatta seniculus*) in fragmented gallery forest in Venezuela (Crockett and Pope 1993). Targeting also occurs in captive groups of mangabeys and in various guenon species (e.g., Rowell 1987; Kaplan 1987; Gust and Gordon 1994), as well as in captive, free-ranging ring-tailed lemurs, in which it regulates the number of females per group (Vick and Pereira 1989; Pereira 1993, 1995). The same, or closely related, species also tend to

show strong between-group antagonism in the wild. This suggests that targeting and eviction are not artifacts of captivity, but rather responses to large group size and high within-group competition in situations where transfer of establishment of new groups is difficult for females (cf. Pereira 1993, 1995).

High population density can exacerbate both WGC and BGC and make evictions more common. For example, females engage in targeting and in BGC in the high density population of wild ring-tailed lemurs at Berenty, but not at less crowded Beza Mahafaly (M. Pereira, personal communication). Targeting thus seems to be within the species' behavioural norm of reaction. However, given that human disturbance can underlie density effects, we need to look further for targeting in wild situations with natural densities to determine how important a selective force habitat saturation has been on female social strategies. In general, however, habitat saturation may affect female social relationships, and is therefore an additional factor to the distribution of resources and risks considered so far.

Infanticide avoidance as a selective force

The ecological hypothesis omits the possible effects of male coercion (Smuts and Smuts 1993) on females, even though infanticide can be a major source of infant mortality (Hrdy et al. 1995). Abundant evidence from wild populations supports the hypothesis that infanticide by males is an evolved reproductive tactic (ibid; Hrdy and Hausfater 1984; Struhsaker and Leland 1987; Newton 1987; but see Bartlett et al. 1993). Because it reduces female reproductive success, females are expected to evolve strategies that reduce infanticide risk.

In theory, females could use an array of counter-strategies, including cooperative defense with other females (Hrdy 1979; van Schaik 1996; Treves and Chapman 1996). However, where a female carries her offspring or is at least directly associated with them (all anthropoids, many prosimians) her best option is to get male protection for them (van Schaik and Kappeler 1993; C.P. van Schaik and P.M. Kappeler, unpublished work). This can come from the male who sired the infant, or, in multi-male groups, from the most likely father (van Schaik and Kappeler 1993; Hrdy and Whitten 1987). Infanticide risk reduction can help to explain permanent male-female association and to account for variation in female dispersal patterns (van Schaik 1996), and it may explain why females form multi-female DE groups.

Because males protect females against infanticide, which is often associated with male immigration (e.g., Sugiyama 1965; Hrdy 1974) or hostile encounters with extra-group males (Fossey 1984; Watts 1989; Sterck 1997), females may choose mates based on their protective ability. For this to happen, costs of female gregariousness must be low, females must be able to transfer easily and to share male anti-infanticidal services at least somewhat, and males must vary consider-

ably in their protective ability. The first two conditions describe DE species, in which multi-female groups must be the result of female clustering around effective protectors (Marsh 1979; Wrangham 1979). These groups are probably small when they have single males, because their size is set by the ratio of breeding females to able-bodied adult males in the population, and because large female groups may be more attractive targets for male attacks and take-over attempts (Dunbar 1984; C.M. Crockett and C.H. Janson, unpublished work, cited in Janson and Goldsmith 1995). Multi-male and age-graded male groups can attract more females (e.g., gorillas; Robbins 1995). Male protective ability changes with age, and females should sometimes leave old males for younger ones who are more effective. This scenario thus offers an alternative path leading to DE groups. The external force that brings females together in groups is protection offered by a male, rather than the risk of predation as in the ecological model.

Is this scenario plausible? It is supported by data on female emigration in two well-studied DE species, mountain gorillas (Stewart and Harcourt 1987; Watts 1989, 1990) and Thomas langurs (Sterck 1997; R. Steenbeek personal communication). Natal and secondary transfer is the norm in both species, and infanticide risk clearly influences transfer decisions. Most transfers are by nulliparae and by parous females without dependent infants. Some are by parous females whose infants have just been killed by extra-group males, or, in gorillas, by females whose groups have just lost their single males and whose infants, if they have any, are killed by extra-group males. In both these situations, gorilla females subsequently tend to mate with the infanticidal males (Watts 1989), and this is also likely in Thomas langurs (Sterck 1997).

In both species, females also tend to transfer into smaller groups (which may also be newer groups); this implies that feeding competition can also influence transfer decisions (Watts 1990; Sterck 1997). However, the importance of group size in mountain gorillas is clearly secondary (Watts 1996). In this species, one-male groups disintegrate after male deaths: females with infants try to avoid strange males, at least initially, while females without infants quickly join them. This shows that gregariousness offers females more than anti-predator benefits; otherwise, females could simply stay together and accept solitary males (Thomas langur: Steenbeek 1996) or transfer en masse (gorilla: Watts 1996). The logic of this model requires female breeding dispersal (not merely natal dispersal), but no solid data base exists that allows us to evaluate breeding dispersal rates in DE species.

Alternative models

Besides the demonstrated or plausible adaptive or non-adaptive influences on female social relationships dis-

cussed above, several hypotheses for variation in female social relationships that are probably not correct can be or have been formulated. In this section, we discuss these ideas.

Ecological alternative: all BGC

The ecological model discussed above is built on the earlier model of Wrangham (1980). Wrangham discounted the importance of predation risk and saw BGC as the overriding influence on female social relationships, although he still invoked WGC to account for dominance hierarchies within groups (otherwise females should have egalitarian relationships). However, the simple "FB/non-FB" dichotomy ignored too much of the range of variation in female social relationships (van Schaik 1989; above). Isbell (1991) extended Wrangham's model by noting that species that rely crucially on limiting, but widely dispersed, food patches should be RE, but many other observations inconsistent with the model remain.

Several deserve mention. First, "FB" groups often fail to defend apparently economically defensible ranges (Mitani and Rodman 1979; Henzi and Lycett 1995; Perry 1996b), and may avoid each other instead (Kawanaka 1973; Ransom 1981; Cowlshaw 1995). Second, the only study that included relevant measures showed that BGC was negligible compared to WGC in a "FB" species (brown capuchins; Janson 1985). Third, some species show pronounced BGC, yet they have egalitarian social relationships (e.g., crested mangabeys; Kinnaird 1992). Fourth, in the presence of WGC, high BGC should lead to tolerant relationships among females, yet most "FB" species are not very tolerant.

Most importantly, for the model to hold, per capita birth rate in "FB" species should be directly proportional to group size up to some upper limit. However, the relationship between these two variables is negative in many populations of "FB" species for which data exist. Crude analyses using infant/female ratios from censuses to estimate birth rates suggested that group size often negatively affected birth rate (van Schaik 1983; Dunbar 1988). More recently, estimates of reproductive success have indicated similar trends (e.g., ring-tailed lemurs: Sussman 1991; A. Jolly, personal communication; long-tailed macaques: van Noordwijk and van Schaik 1994).

Note that the ecological model includes a role for BGC. Given sufficient environmental heterogeneity, the positive relationship of group size to success in BGC could counterbalance the negative effects of WGC. Two studies have documented positive relationships between group size and reproductive success. In one case (Amboseli vervets: Cheney and Seyfarth 1987), the study population may have been anomalous (above). The second case (wedge-capped capuchin, *Cebus olivaceus*: Robinson 1988a, b) is inconclusive because it did not involve analysis of WGC. Also, vigilance and group size

were positively related in both of these cases (Isbell and Young 1993; de Ruiter 1986); large groups may thus have had feeding benefits (because their members had less need than members of smaller groups to scan for predators, rather than to feed) that translated into reproductive benefits (Janson 1992).

Demographic alternative: byproduct of female philopatry

If females are philopatric for independent ecological or demographic reasons, their social relationships might arise as a byproduct of this philopatry. Philopatry makes alliances possible because it keeps related females together, whereas alliances are unlikely when females disperse and reside with non-relative (Waser 1988; Di Fiore and Rendall 1994). Thus, when female relatives reside together, they will form despotic, nepotistic dominance hierarchies.

While plausible, this idea does not explain the primate pattern (Isbell and van Vuren 1996). First, several species with female philopatry do not form decided dominance relationships and coalitions (see Table 2). Second, mountain gorilla females occasionally resides in the same group as female kin, yet they do not use alliances to establish and maintain decided dominance relationships (Watts 1994). Third, the byproduct idea does not explain why non-related females in groups usually fail to form decided dominance relations (see Table 2).

Demographic alternative: byproduct of interbirth intervals

Demographic factors play a major role in shaping the fine structure of female dominance hierarchies, as demonstrated by the simulations of Datta (1992; Datta and Beauchamp 1991), because interbirth intervals and early survival determine the availability of suitable female allies. This result could be construed as implying that demographic differences alone are responsible for the contrast between the types of hierarchy seen in nepotistic vs non-nepotistic taxa (e.g., the RN and RNT vs RE and DE categories). However, this interpretation ignores the crucial role of alliances. In Datta's model, females form alliances whenever suitable female kin are present. Thus, the model explains subtle variation in patterns of rank inheritance within the RN and RNT categories (see Datta 1992), but not why females in some species (RE and DE) consistently fail to form alliances and thus rank inheritance, even when female relatives of the right age cohort are present as potential allies.

Social alternative: male policing

The continuous or near-continuous presence of males is a fact of life for females in most diurnal primates. When

females form groups, whether this reduces predation risk or confers other benefits, this inevitably leads to conflicts. Males sometimes intervene in female disputes and prevent decisive outcomes. These interventions may minimize the impact of WGC among females, and may prevent the development of dominance relations because a female likely to lose an altercation would behave so as to increase the likelihood of male intervention, thus ending the conflict (cf. Watts 1994; Sterck and Steenbeek 1997). When females can easily transfer, those who are intrinsically poor competitors may gain by choosing males who are effective protectors against the negative effects of competition with other females. Male intervention should thus lead to egalitarian social relationships.

Intensive male policing is rare (e.g., Oswalt and Erwin 1976). It is much more likely in single-male than multi-male groups (e.g., baboons: Hamilton and Bulger 1992), probably because males in multi-male groups face a collective action problem in trying to police female conflicts. This leads to a simple but strong prediction: if male policing causes egalitarian relationship structures, they should be limited to single-male groups.

This prediction is not met. First, it is inconsistent with the interspecific pattern. Several egalitarian species live in multi-male groups (e.g., red-backed squirrel monkey: Boinski and Mitchell 1994; red colobus, *Colobus badius*: Struhsaker and Leland 1987), just as some despotic-nepotistic species form single-male groups (e.g., gelada, *Theropithecus gelada*: Dunbar 1984). Second, if egalitarianism depends on male behavior, more females in large than small groups should have decided dominance relationships, because female group size constrains male policing abilities. Mountain gorilla data do not support this prediction (Watts 1994).

Baboons provide further evidence against the male policing hypothesis. Individual males sometimes give agonistic support to their female friends against other females, as well as against males, and also sometimes support juvenile females in contests (Smuts 1985; Pereira 1989; Noe and Sluijter 1990). However, they influence neither rank acquisition by juveniles nor dominance relationships among adults.

Social alternative: male harassment

In several species, females form coalitions to defend themselves against male attacks (e.g., hanuman langurs: Hrdy 1977). Brereton (1995) argues that the ability to form these defensive coalitions has provided an important selective pressure toward the formation of resident-nepotistic female groups in primates (the "coercion defense hypothesis"). The ability to form coalitions effective in collective defense against male harassment could also make possible coalitions in female-female competition. The question thus is whether coercion defense or female resource competition has selected for the coalitions and philopatry among females.

Although this model may explain some behavioural patterns in primates, it does not account for the variation in female social relationships: it does not explain why females have coalitionary aggression among themselves in some taxa but not in others (e.g., hanuman langurs: Borries 1993), or why females should have decided dominance in the first place. Brereton also ascribes the formation of DE groups to situations where high dimorphism or male bonding overcomes collective defense by females. Females should then resort to forming a protective relationship with another male. However, several DE groups are found among species with no sexual dimorphism or male bonding (e.g. Thomas langurs: Sterck 1997). Also, in some highly dimorphic RN species, females rely on male protection instead of coercion defense (e.g., baboons: Smuts 1985). Males may generally be the most effective protectors against male harassment (e.g. Wrangham 1979).

Thus, the coercion defense hypothesis is neither needed to explain female social relationships nor sufficiently general to explain interspecific variation.

Social alternative: costly reproduction and reproductive suppression

WGC affects female reproductive success via nutritional status or predation risk. Targeting and eviction can have similar adverse nutritional effects by forcing females into marginal habitat (Crockett and Pope 1993). Females can impair each other's fertility more directly, however, by aggressively disrupting ovarian cycles, inducing abortions, or otherwise making successful conception or implantation more difficult. Social harassment, sometimes by coalitions of relatives, may sometimes contribute to rank-related variation in reproductive success in RN species (e.g., geladas: Dunbar 1984; savannah baboons: Wasser and Starling 1988; Packer et al. 1995; Altmann et al. 1995), although both the reality of the effect in geladas and the general proposal that high ranking females can benefit from harassing subordinates have been questioned (Harcourt 1987; Packer et al. 1995; but see Altmann et al. 1995). In any case, the role of nepotism in social harassment probably does not explain the origin of RN structures; the abundant evidence for nutritional effects on reproduction make the socioecological model a better explanation.

Callitrichids are exceptions, however. Their variable social and mating systems include some multi-female groups, in which females have individualistic and despotic dominance relationships. Females also disperse from natal groups, but dispersal costs are high. Given these costs, plus high costs of reproduction (in particular, relatively fast infant growth; Goldizen 1990; Mitani and Watts 1997), obligate cooperative breeding, and limited breeding opportunities, subordinate females may often do better to help raise offspring of dominant females than to disperse and try to breed, and may sometimes eventually acquire breeding positions in their

natal groups (Goldizen 1990; Garber 1994). Contest for allocaretaking leads to reproductive suppression of subordinate females (Goldizen 1990; Garber 1994; Digby 1995; Digby and Ferrari 1994). Usually suppression is complete; when subordinates breed, they risk infanticide by dominants (Digby 1994), and probably have little chance of raising offspring successfully even without infanticide. Callitrichid maternal energetics and mating systems find parallels among communally breeding carnivores (e.g., dwarf mongoose: Creel and Waser 1994; reviewed in Creel and Creel 1991). They are unusual for primates, but partial reproductive suppression, coupled with targeted aggression, may be common in RN species (above; cf. Pereira 1995) and in other cases where dispersal costs are high and female transfer difficult (e.g., red howlers).

Synthesis

The ecological model assumes that predation risk forces females to live in groups. When females live together, they compete for resources, and the nature of this competition shapes female social relationships. Within- and between-group contest lead to four classes of female social relationships: Dispersing-Egalitarian, Resident-Nepotistic, Resident-Nepotistic-Tolerant, and Resident-Egalitarian. The model explains variations in female social relationships reasonably well and correctly predicts most of the observed associations among social variables across taxa. Critical comparative tests of related species with contrasting social systems also support this model, but only a few of these tests have been conducted, and their eventual number will be limited.

In retrospect, it was probably naive (although heuristically a necessary first step) to assume that only ecology affects social relationships among females. Various additional factors may also have an effect, and they may interact in as yet unanticipated ways with ecology. Specifically, we have examined here the effects of a demographic factor (habitat saturation) and a social one (male behavior). The impact of infanticide risk is most readily incorporated into the model. Like predation, infanticide enhances the formation of female groups. Females can reduce infanticide risk by associating with males, and can share male protection with other females. Infanticide risk and predation risk can, in fact, select for similar social solutions, and these solutions can serve dual functions (Fig. 6). The next generation of models will need to incorporate the impact of all recognized relevant factors as influences on female social relationships and decision making.

One problem is that we had to assume that disequilibrium caused some discrepancies. A model that can better deal with these anomalies would be superior.

Future work is needed on primates in natural areas with a complete array of predators present and without human-induced habitat fragmentation; studies on the

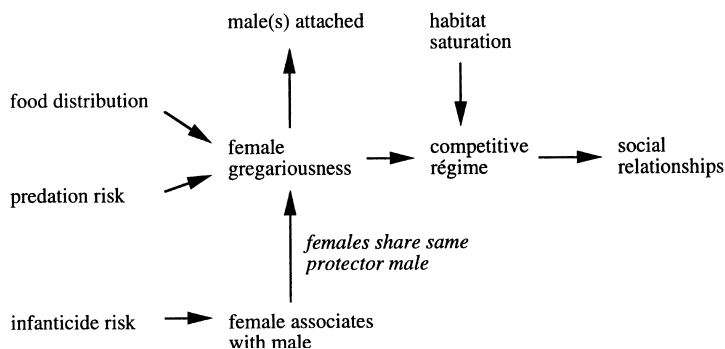


Fig. 6 Flow diagram of the proposed socioecological model. Female gregariousness is determined by opposing pressures from predation and/or infanticide risk and from food distribution. The distribution of males depends on a combination of female gregariousness and female choice of protector males. The remainder of the model follows van Schaik (1989): female gregariousness in combination with food distribution determines the type of food competition females experience; this in turn determines female social relationships

relative strength of WGC and BGC in a number of species, especially RE and RNT species; and on the question whether primates are limited at all by food, and so have a high potential for between-group contest, or just because they aggregate in groups and so create especially within-group competition that would not otherwise exist.

Comparisons with other mammalian taxa

Detailed comparison of primates with other mammals is beyond the scope of this paper, but we briefly note some taxa for which this should be useful.

Carnivores

Food patch size and dispersion strongly influence female gregariousness in carnivores (Packer and Pusey 1988; Packer and Ruttan 1988; Caro 1989, 1994; Mills 1989; Owens and Owens 1996). Most carnivores are solitary, and where multi-female groups are formed the contest for helpers often produces reproductive suppression or at least serious skews in reproductive success (Creel and Creel 1991). In European badgers (*Meles meles*), which do not breed cooperatively, the strength of the dominance effect on reproductive suppression varies inversely with food abundance (Woodroffe and MacDonald 1995).

However, where females form stable groups or fission-fusion systems in which reproduction is not suppressed, we should expect RNT-like social structures because both WGC and BGC are potentially high. Female lions (*Panther leo*), for instance, live in prides consisting mainly of philopatric female relatives. They have highly clumped food, although the presence of dangerous weapons may reduce the escalation of conflicts and may

explain why females do not form dominance hierarchies (Packer and Pusey 1982). They also face strong BGC for territories, hunt cooperatively, and show communal infant nursing and cooperative defense against infanticidal males, all of which should favor tolerance (Pusey and Packer 1987b; Packer et al. 1990; Heinsohn and Packer 1995). Thus, female lions have relationships like the primate RNT category taken to an extreme.

Coalitions between relatives occur in spotted hyaenas (*Crocuta crocuta*; Jenks et al. 1995; Holekamp and Smale 1991). Interventions by high-ranking females in their offspring's conflicts lead to dominance hierarchies that resemble those in RN primates. Clan females also cooperate in contests with other clans, but there is no indication for high tolerance. Female brown hyaenas (*Hyaena brunnea*) in the Kalahari face high BGC for feeding territories but adult clan members defend the feeding territory individually. Variation in the availability of medium-to-large carcasses killed by lions leads to variation in WGC associated with variation in gregariousness (Mills 1989; Owens and Owens 1996). Females breed communally, and have despotic dominance relationships but whether they are nepotistic is not known (Owens and Owens 1996). Perhaps because of the absence of cooperative BGC, eviction of females is seen.

Female coatis (*Nasua narica*) on Barro Colorado Island form coalitions with relatives, but apparently do not form nepotistic hierarchies, or form hierarchies at all (Gompper et al. 1997). Females also transfer between bands. Band females sometimes cooperatively displace males from small, high quality food patches (Gompper 1996); this may be an equivalent to BGC. This combination of nepotism without despotism, high BGC, and female transfer has no exact equivalent in primates.

In general, then, we see many common elements with primates and more careful evaluation of the factors that are unique to carnivores may well produce a more encompassing model that would explain both primates and social carnivores.

Ungulates

Group living equids resemble DE primates in some respects (Watts 1994, 1996). Dispersal is not costly to fe-

males (Berger 1986; Rutberg 1990; Monard and Duncan 1996), and female transfer is common. Inbreeding avoidance may be the main explanation for natal transfer (Rutberg and Kuiper 1993; Monard et al. 1996), but female residence may sometimes partly depend on male protection against harassment by extra-band males (Berger 1986; Rubenstein 1986; Stevens 1990). Females often do not form dominance hierarchies; even when hierarchies are identifiable, WGC over food is low (e.g., Rutberg and Greenberg 1990; Monard and Duncan 1996). As in DE primates, adult females do not structure their daughters' agonistic relationships (Monard and Duncan 1996).

In group-living ruminants, decided dominance relationships are found in some species, and dominance may affect female reproductive success. However, a review by Meydam (unpublished work) found some major differences with primates. First, clear dominance relations and linear dominance hierarchies are not limited to species with female philopatry as found in primates. Second, there is no species in which females form coalitions with relatives and show the rank inheritance characteristic for RN primates. There is no straightforward explanation for these contrasts, although the flexibility of grouping and cognitive constraints on coalition formation are both possible candidates.

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