ECOLOGICAL MODELS OF FEMALE SOCIAL RELATIONSHIPS IN PRIMATES: SIMILARITIES, DISPARITIES, AND SOME DIRECTIONS FOR FUTURE CLARITY

by

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Summary

Several models have been proposed to explain the variation that exists in female social relationships among diurnal primate species. While there are similarities among them, notably in the ecological cause of agonistic relationships among females within groups, their differences are most useful in testing which of the models most accurately reflects the real world. These include the question of whether competition is an inevitable cost of living in groups and whether female philopatry is a consequence of the costs of dispersal or the benefits of forming coalitions with female kin. We discuss in detail these similarities and differences, and attempt to integrate the models' divergent views into some guidelines for use in testing between models that will lead to the next generation of models.

Introduction

Primates exhibit a wide variety of social systems. They range from species whose members live solitarily to species whose members live in large social groups, some of which are fluid in space and time. Despite this variability,

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a striking feature of primates compared to other taxa is their strong tendency to live in cohesive groups. Depending on the species and local ecological and social conditions, these groups can range from very small to very large. The composition of groups can also vary, particularly in the numbers of males that associate with groups of females. Primates also differ in the stability of their group membership; in most species, males disperse at sexual maturity, but in many of these species, females also disperse. Between groups, aggression can be rare or it can be frequent. Within primate groups, interactions range from virtual non-interaction to hierarchical aggression, resulting in variation in social relationships within groups.

This diversity directs the kinds of questions primate behavioral ecologists ask. Over the past 40 years, indeed, since field primatology's infancy, questions have centered around issues of sociality because primates are, on the whole, more gregarious than other mammals. The main questions have been

1. Why live in groups?
2. What determines the number of females in a group?
3. What determines the number of males in a group?
4. Why does infanticide occur?
5. What determines the nature of female relationships within groups?
6. What determines the nature of female relationships between groups?
7. What determines which sex disperses?

Although we have some tentative answers, these questions are still far from resolved after 40 years, but irresolution does not mean the questions are insoluble. As more research is done, it becomes more evident that one of the 'hallmark' features of humans, behavioural flexibility in the face of varying ecological and social conditions (Fleagle, 1999), is in fact shared by many other primates. We mention the current state of primate behavioral ecology to provide a sense of where the main focus of this paper, female relationships in group-living primates, lies in primate behavioral ecology. For a broader review of the 'big questions' in primate behavioral ecology, we refer the reader to the recent excellent review by Janson (2000).

In this paper, we focus on the latter three questions, which can be expanded to include questions such as these:

1. What are the causes and consequences of intragroup agonism and dominance?

2. What are the causes and consequences of female aggression between groups?
3. What drives female philopatry and dispersal?

Several models have been developed in recent years that attempt to identify the ecological and social conditions that favor particular behavioral responses. These models underplay the influence of phylogeny on behavioral outcomes, perhaps because phylogeny tends to constrain rather than enhance behavioral variation (Struhsaker, 1969; Di Fiore & Rendall, 1994). These models predict behaviors that are expected to be largely independent of phylogeny *per se*, although they recognize the potential for phylogenetic niche conservatism (Harvey & Pagel, 1991; Westoby *et al*., 1995). In this paper, we briefly review these models, point out their similarities and differences, and suggest guidelines for future research. It is clear that different models make different predictions, and that all current models are still very much open for improvement.

Three basic models

The first to explicitly attempt a comprehensive model of the ecological bases of female social relationships in primates was Wrangham (1980) in his classic model of female-bondedness. Following the lead of ornithologists, theoreticians, and other mammalogists (*e.g.* Hamilton, 1964; Trivers, 1972; Jarman, 1974; Bradbury & Vehrencamp, 1977; Clutton-Brock & Harvey, 1977; Emlen & Oring, 1977) he used an ecological framework of resource availability to describe the conditions under which group living in primates evolved, and under which two types of female social relationships evolved (Fig. 1). Using the limited amount of information about primate social systems available in the late 1970s, Wrangham suggested that when foods were spatially clumped and of high quality, females would be philopatric and exhibit strong intergroup aggression because such foods would be defensible. If those high-quality clumped foods were also variable in quality, females would have 'differentiated relationships', which included strong, linear, stable dominance hierarchies within groups, rank-related grooming, and maternal inheritance of rank (Table 1). These primates he called 'female-bonded'. Conversely, he suggested that 'non-female-bonded' species would evolve when foods are either uniformly distributed or in small, high quality clumps, and that such species would exhibit female transfer, weak aggression

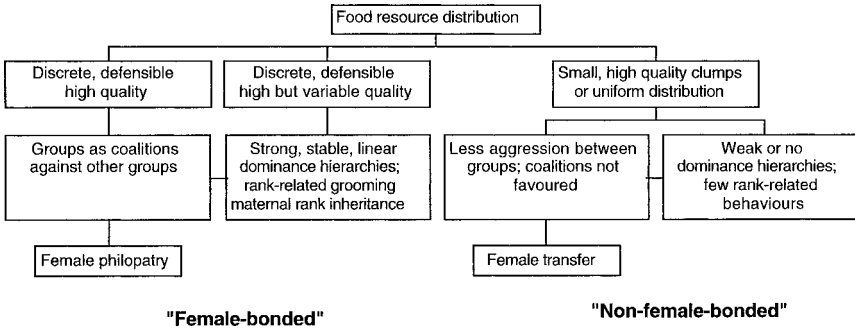

Fig. 1. Schematic of Wrangham's (1980) model of female-bondedness in group-living primates.

among groups, weak or absent dominance hierarchies within groups, and few rank-related behaviors (Table 2).

This was a bold attempt to both provide a general ecological model of primate social behavior and categorize living primates into types based on covariance in their social behaviors. It remains the benchmark paper in its field. Wrangham's model led to myriad field (and theoretical) examinations. Although the relative importance of food competition and predation in the evolution of group living and group size is far from being settled (Isbell, 1994), Wrangham's emphasis on food remains central to our models of how females interact within and between groups.

Wrangham's model came under reevaluation from two directions. First, as more and more primate species were studied, it became apparent that the simple dichotomy between female-bonded and non-female-bonded was not a clean one. For example, there were species with both female philopatry and weak or unstable dominance hierarchies [(*e.g.* patas monkeys (*Erythrocebus patas*) and blue monkeys (*Cercopithecus mitis*)]. There were species with strong intergroup aggression, but weak or unstable dominance hierarchies (*e.g.* patas monkeys and blue monkeys). In other words, the covariance in behavioral traits was more complex than had originally been thought. Second, there was the growing suspicion that separating the effects of intra- and inter-group contest and scramble competition might be important (*e.g.* Janson & van Schaik, 1988). Scramble competition is indirect competition by which an individual reduces the resources for others simply by consuming those resources. Contest competition often involves overt agonistic behavior, but it can also involve other behaviors that give higher-ranking animals preferential access to resources. As a result, it is not always obvious which type

TABLE 1. *Suggested ecological causes of female behavior according to each model*

	Wrangham[a]	van Schaik & colleagues[b,c,d]	Isbell & colleagues[e,f,g,h]
Behavioral expression:			
Female-female aggression (or avoidance) between groups:	discrete, defensible, high quality food patches (clumped distribution)	predation risk low; food occurs in defensible clumps[b]; limited food abundance, defensible[c]	food abundance limits female reproductive success
Highly expressed dominance hierarchies within groups:	variable quality, discrete, defensible food distribution	clumped, defensible food distribution[b]; limited food abundance, defensible[c]	clumped food distribution[e]; FSDT[f]
Female philopatry:	coalitions with kin against other groups	coalitions with kin within groups, primarily; no infanticide[d]	costs of dispersal outweigh costs of staying[g]
Coalitions within groups:	variable quality, clumped food distribution	clumped food distribution	greater success in usurping food[h]

[a] Wrangham (1980); [b]van Schaik (1989); [c]van Hooff & van Schaik (1992); [d]Sterck *et al.*, (1997); [e]Isbell (1991); [f]Isbell *et al.* (1998); [g]Isbell & Van Vuren (1996); [h]Isbell & Pruetz (1998).

of competition is operating. For example, initially it might seem a clear-cut case of scramble competition when some females arrive at food sites and begin to eat earlier than other females. Is it still scramble competition if those early-arriving females are higher-ranking females? If higher-ranking females gain earlier access because lower-ranking females are inhibited from going first (*e.g.* Whitten, 1983; Isbell *et al.*, 1999), it might instead be a case of contest competition.

Two groups working independently came up with new models that attempted to accommodate the greater diversity of primate social patterns and incorporate more complex combinations of intra- and inter-group scramble and contest competition. These second-generation models represent improvements that are both more explicit and more general, but that also leave

TABLE 2. *Syndromes of female relationships according to current models and the behaviors or conditions associated with them*

Wrangham (1980):

1. '*Female-bonded*': highly expressed, stable dominance hierarchies; frequent rank-related grooming and coalitions; male dispersal; female philopatry.
2. '*Non-female-bonded*': weakly expressed, unstable dominance hierarchies; grooming and coalitions rare; female transfer.

van Schaik (1989):

1. '*Type A*' (strong within-group scramble only): weakly expressed, unstable, weakly linear dominance hierarchies; female philopatry/transfer variable; high predation. Except for the emphasis on predation, corresponds to Wrangham's non-female-bonded classification.
2. '*Type B*' (strong within-group contest only): highly expressed, stable, linear dominance hierarchies; coalitions; inheritance of maternal rank; female philopatry; grooming bonds; high predation. Except for the emphasis on predation, corresponds to Wrangham's female-bonded classification.
3. '*Type C*' (strong within-group scramble and between-group contest): weakly expressed dominance hierarchies; coalitions against other groups only; grooming bonds; female philopatry; intermediate to high predation.
4. '*Type D*' (strong between-group contest only): weakly expressed dominance hierarchies; coalitions; inheritance of maternal rank; grooming bonds; female philopatry; low predation.

Sterck *et al*. (1997):

1. '*Resident-nepotistic*': highly expressed, stable dominance hierarchies; formal signals of submission; coalitions; inheritance of maternal rank; female philopatry. Corresponds to Wrangham's female-bonded and van Schaik's Type B classification.
2. '*Resident-nepotistic-tolerant*': highly expressed, stable, linear dominance hierarchies; coalitions; inheritance of maternal rank; female philopatry; access to food and social partners allowed. Differs from van Schaik's Type D classification in the degree to which dominance hierarchies are expressed; no analog in any other model.
3. '*Dispersal-egalitarian*': weakly expressed, unstable dominance hierarchies; coalitions rare or absent; female transfer; infanticide. Corresponds to Wrangham's non-female-bonded and van Schaik's Type A classification.
4. '*Resident-egalitarian*': weakly expressed, unstable dominance hierarchies; coalitions within groups rare or absent; female philopatry. Corresponds to van Schaik's Type C classification.

Isbell (1991), Isbell & Van Vuren (1996), and Isbell & Pruetz, 1998:

1. *Contest and scramble competition for food both within and between groups*: highly expressed, stable, linear dominance hierarchies; maternal inheritance of rank; coalitions; female philopatry. Corresponds to Wrangham's female-bonded classification; differs from van Schaik's Type B and Sterck et al.'s resident-nepotistic classifications in excluding predation as a condition.

TABLE 2. *(Continued)*

2. *Contest and scramble competition for food between groups; little or no contest or scramble food competition within groups*: weakly expressed, unstable, non-linear dominance hierarchies; little inheritance of maternal rank; female philopatry. Differs from van Schaik's Type C and Sterck *et al.*'s resident-egalitarian classifications in excluding predation as a condition.
3. *Little or no contest or scramble competition for food within or between groups*: weakly expressed, unstable, non-linear dominance hierarchies; female transfer, with timing dependent on males. Corresponds to Wrangham's non-female-bonded classification; differs from van Schaik's Type A, and Sterck et al.'s dispersal-egalitarian classifications in excluding predation as a condition.

room for improvement. We summarize the approaches and main points of these models below.

Van Schaik (1989) first excluded intergroup scramble competition as having no explanatory value. Second, he created eight possible combinations of intragroup scramble competition and intragroup and intergroup contest competition. Third, using *a priori* reasoning, he eliminated those combinations he considered impossible or subordinate to others, leaving four (Table 2). He then reasoned how each of these combinations should arise from certain ecological conditions to produce particular patterns of female relationships (Fig. 2). Last, he offered examples of which primate species might best represent these types. Later, this model was modified to more explicitly incorporate predictions about the effect of infanticide by males on female philopatry (Sterck *et al.*, 1997) (Table 2).

Using empirical data to produce and test a different model, Isbell (1991) elucidated the covariation among behavioral indices of contest and scramble competition within and between groups (Table 3). Three empirical 'syndromes' of female relationships in group-living primates were revealed by this analysis (Table 2). Isbell then inferred causative correlations between these syndromes and the feeding ecology of the species expressing them (Table 1). She also later examined female philopatry and dispersal in detail (Isbell & Van Vuren, 1996) and characterized four patterns of female dispersal (although still three types of female relationships) after taking into account the effect of males on females that are not apparently food-limited (Fig. 3).

Each reported 'test' of any of these models is usually merely the observation of a pattern of primate social behavior that is consistent (or not) with

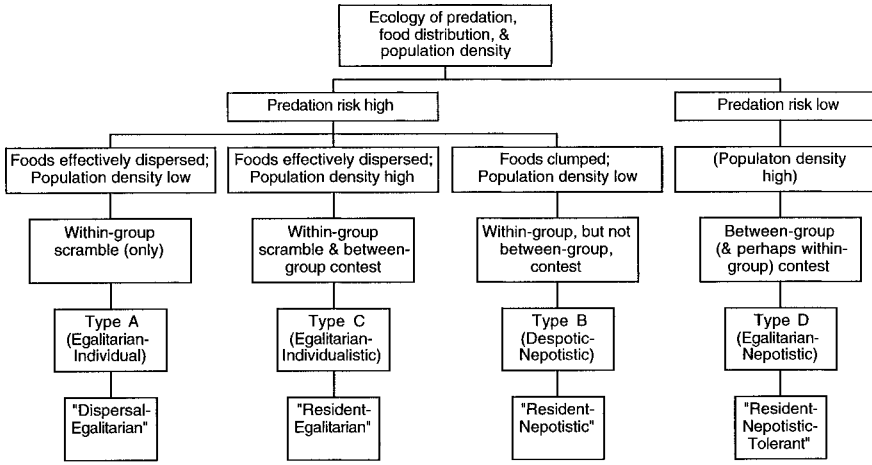

Fig. 2. Schematic of van Schaik's (1989) and Sterck *et al.*'s (1997) models of female social relationships in group-living primates, based on *a priori* reasoning about the kinds of competition that should exist and covary. Although this schematic implies a hierarchical set of causative factors, in the models food distribution, predation risk, and population density are treated in a variety of ways. For example, van Schaik's model maintains that predation precedes food distribution in determining social relationships, whereas Sterck *et al.*'s model treats them as co-equal. In addition, van Schaik suggests that Type D species (egalitarian-nepotistic) species have no intragroup contest competition, whereas Sterck *et al.* maintain that 'resident-nepotistic-tolerant' species have 'potentially high' intragroup contest competition. We have assumed equivalence of the two sets of behavioral syndromes, although the authors suggest differences between them.

the referenced model (*e.g.* Mitchell *et al.*, 1991; Borries, 1993; Barton *et al.*, 1996; Sterck *et al.*, 1997; Koenig *et al.*, 1998; Boinski, 1999; Koenig, 2000; Steenbeek & van Schaik, 2001). The same observation is sometimes consistent with all three models.

Examining areas of agreement can be useful (*e.g.* Whitten, 1983; Phillips, 1995; Barton *et al.*, 1996; Saito, 1996; Sterck & Steenbeek, 1997; Isbell & Pruetz, 1998; Pruetz & Isbell, 2000; see also below). However, if the goal is to determine which model more accurately reflects nature, tests must address key differences among these models, not their similarities. Each predicts combinations of behaviors and corresponding ecological causes that the others do not. Of course, as we will discuss at the end, what is really needed is a new generation of models that incorporates the strengths of previous models and addresses their weaknesses.

TABLE 3. *Behavioral indicators of different kinds of competition used by Isbell (1991)*

Behavior	Considered indicative of:
Strong, linear dominance hierarchies	Intragroup contest competition
Agonism (or avoidance) between females of different groups	Intergroup contest competition
Longer daily travel distances in larger groups	Intragroup scramble competition
Larger home ranges in larger groups	Intergroup scramble competition

The behavioral indicators were used to reveal covariation of scramble and contest competition for food in known primate populations. In each case, the presence or absence of the behavior is considered evidence for the presence or absence of the relevant kind of competition. A question unresolved: Are these behaviors appropriate indicators of competition?

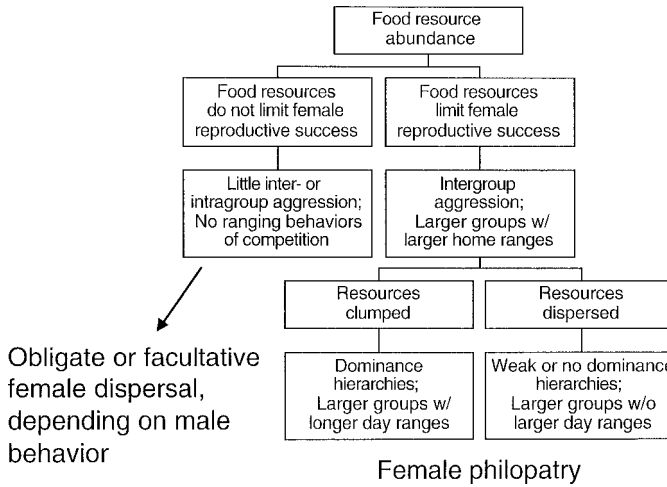

Fig. 3. Schematic of Isbell's (1991) and Isbell and Van Vuren's (1996) models of female relationships in group-living primates, based on empirical evidence about the kinds of competition expressed in known populations of primates.

Similarities among models

Primacy of ecological factors

There are at least three areas of agreement among these models. First, all three acknowledge the primacy of ecological factors as the underlying bases for the evolution of female social relationships, although they differ in

what those ecological factors are. Wrangham emphasized food distribution, whereas van Schaik and colleagues emphasized predation primarily and food distribution, population density, and male behavior secondarily. Finally, Isbell and colleagues emphasized food abundance, food distribution (or food-site depletion time, FSDT; see below), and the costs of dispersal (Table 3).

Food distribution and dominance hierarchies

Second, all these models propose causative correlations between food distribution and their behavioral syndromes, in particular, that clumped foods generate contest competition within groups. This agreement among models is nice, but it is a bit embarrassing that we do not really know yet what we are talking about. What exactly is meant by 'clumped' and 'patchy'? These qualities of foods are rarely measured in the field, and when they are, quantitative measures are extremely scale-dependent (*e.g.* Leighton & Leighton, 1982; Shopland, 1987; Whitten, 1988; Mitchell *et al.*, 1991; Barton, 1993; Chapman *et al.*, 1995; Barton *et al.*, 1996; Sterck & Steenbeek, 1997; Koenig, 2000; Pruetz & Isbell, 2000). The models make arguments about patch sizes across a wide range of spatial scales, but it is not clear what scale is appropriate for different kinds of competition.

Recognizing this, Isbell and colleagues have attempted to examine more specifically the operational aspects of food distribution as they affect competition (Isbell & Pruetz, 1998; Isbell *et al.*, 1998; Pruetz & Isbell, 2000; Mathy & Isbell, 2001). It appears that the patchiness of foods *per se* is not what matters. Rather, it is the measurable behavioral consequences of that patchiness that matter. Monopolizability, a term commonly used to describe the ability of an individual to hold onto food, is not necessarily a measurable consequence of patchiness because it requires no interaction between individuals (see below). In contrast, 'usurpability' denotes the behaviors that are recorded in agonistic interactions and is thus a measurable consequence of patchiness. A food site is *usurpable* if it can be taken from a lower-ranking individual. Isbell and colleagues have proposed that it is the usurpability of these resources that makes them contestable, and that the determinant of this usurpability is food-site depletion time (FSDT). If a food site takes a long time to deplete, then that site can be contested by other (higher-ranking) individuals. Conversely, if a food site can be depleted rapidly, that site cannot

be contested (in quadrupedal primates, a food site has been defined as being separated from other food sites by hindlimb locomotion; Isbell *et al.*, 1998). While it might be assumed that more highly clumped foods have longer FSDTs, this need not be the case, depending on the size of the individual food item and on inter-individual distances. Thus far, FSDT has been found to be important to food usurpability among brown capuchins (*Cebus apella*; Janson, 1990), vervets (*Cercopithecus aethiops*), patas monkeys (Isbell *et al.*, 1998; Pruetz & Isbell, 2000), yellow baboons (*Papio cynocephalus*; Post *et al.*, 1980; Shopland, 1987), and rhesus macaques (*Macaca mulatta*; Chancellor & Isbell, in prep.). Food-site depletion time has the added advantage of being a measure that is primate-driven rather than primatologist-driven. In other words, it does not rely on our ability to judge what represents a food patch and what does not. It is also quantifiable across individuals, populations, and species, making comparisons much more manageable. In this context, 'usurpability' is essentially a temporal trait.

In contrast, monopolizability is a spatial trait: an area is *monopolizable* if a dominant animal can prevent lower-ranking individuals from usurping any foods within that area. Small areas will be monopolizable by higher-ranking animals independent of how long it takes to deplete the foods within that area. Larger areas will be increasingly difficult to monopolize until a critical size occurs beyond which a dominant animal can no longer effectively exclude subordinates. Unfortunately, virtually no studies have determined the zone of monopolizability around individuals within a primate group. In an experimental study, Schaub (1995) found that subordinate long-tailed macaques (*Macaca fascicularis*) were less likely to obtain foods when the dominant animals were closer to them, but he could only test them at distances of 30 cm and 100 cm. A recent study of captive rhesus macaques (Mathy & Isbell, 2001) suggests that 100 cm is well within the zone of monopolizability of higher-ranking animals when there is no physical barrier between the animals, as was the case in Schaub's experiment. In Mathy and Isbell's study, group-living individuals were provided with two apple pieces simultaneously. As the apple pieces became more spatially separated, dominant animals were progressively less able to exclude others from both pieces. At interfood distances of five or more meters, even the most dominant animals were unable to exclude any others from both apple pieces, regardless of the size of the food. Similar experiments are currently being conducted to determine whether aggression is used as an immediate deterrent to

competitors or as a way to discourage competition in the future (Chancellor & Isbell, in prep.). It is clear, however, that much more work needs to be done to tease apart the critical characteristics of foods that cause intragroup feeding competition.

Dichotomous expressions of dominance

Third, all models agree that a fundamental dichotomy exists in the expression of dominance relationships within groups. Some species are characterized as having 'female-bonded relationships' (Wrangham, 1980) or 'resident-nepotistic relationships' (Sterck *et al.*, 1997) whereas other species have 'non-female-bonded relationships' (Wrangham, 1980), or 'dispersal-egalitarian relationships' (Sterck *et al.*, 1997). Avoiding novel labels, Isbell and colleagues (1991; Isbell & Van Vuren, 1996; Isbell & Pruetz, 1998) simply described dominance hierarchies as either 'strong, stable, and linear' or 'weak or undiscernable, unstable, and non-linear'. It is not altogether clear, however, what is meant operationally by any of these distinctions. We suggest that there are several separate quantifiable traits that create 'female-bonded' or 'nepotistic' social relationships or 'strong' dominance hierarchies:

1. Rate of expression

In a 'strong dominance hierarchy' or in 'female-bonded' or 'nepotistic' social relationships, agonistic interactions (particularly over food) are relatively common, and take the form of supplants at feeding sites, or aggression during feeding. In a 'weak or undiscernable' dominance hierarchy or in 'non-female-bonded' or 'egalitarian' social relationships, agonistic interactions are rare (*e.g.* Mitchell *et al.*, 1991; Sterck & Steenbeek, 1997; Isbell & Pruetz, 1998). For example, in concurrent studies of vervets and patas monkeys, 410 observation hours were needed to place all female vervets confidently into a dominance matrix that persisted beyond that time, whereas about 760 hours were needed to do the same for the patas (Isbell, unpub. data). This still held after controlling for the number of females in each group vervets: 46 hr/female ($N = 9$); patas: 51 hr/female ($N = 15$). Interactions that were crucial to determining the dominance matrix (those that occurred closest to one side of the diagonal) were observed at a higher rate in vervets

(16 hr/interaction; $N = 25$) than in patas (54 hr/interaction; $N = 14$). Quantitative measures of the 'latency to detection' of dominance hierarchies such as these might well reveal a continuum in the rate of expression of agonistic interactions among primates. Those at either end of the continuum might be most accurately described as having 'highly expressed' and 'weakly expressed' dominance hierarchies.

2. Reversals against the hierarchy

In a 'strong' dominance hierarchy or in 'female-bonded' or 'nepotistic' social relationships, observations below the matrix diagonal, *i.e.* interactions against the hierarchy, usually account for less than five percent of observations [*e.g.* baboons (Hausfater, 1975; Hausfater *et al.*, 1982; Smuts, 1985; Barton & Whiten, 1993; Ron *et al.*, 1996), macaques (Missakian, 1972; Silk *et al.*, 1981), and vervets (Seyfarth, 1980; Cheney *et al.*, 1981; Isbell & Pruetz, 1998)]. In contrast, in a 'weak or undiscernable' dominance hierarchy or in 'non-female-bonded' or 'egalitarian' social relationships, as much as 15% of agonistic interactions may be reversals [*e.g.* blue monkeys (Rowell *et al.*, 1991; but see Cords, 2000) and patas monkeys (Isbell & Pruetz, 1998)].

The percentage of reversals is often included as a measure of linearity. We recommend, however, that the standard use of linearity measures be abandoned. Linearity was meant to identify intransitive relationships in dominance matrices, where A > B and B > C, but C > A (Lehner, 1996). Such 'circular' dominance relations are virtually unheard of in primates, however. Reported cases of mathematical non-linearity in primates are often mainly a measure of the number of empty cells in the matrix, not intransitive relationships (*e.g.* Rowell *et al.*, 1991; Isbell & Pruetz, 1998). In contrast, the frequency of reversals against the hierarchy is worth documenting because it seems to correlate with stability, another important descriptor of dominance hierarchies.

3. Stability

In a completely stable dominance hierarchy, dominance matrices produced during one period of time are identical to dominance matrices during another period of time. They are considered less stable as dominance matrices for the two time periods become more different (*e.g.* yellow baboons; Samuels

et al., 1987; Hanuman langurs (*Semnopithecus entellus*); Borries, 1993). Often, when a group becomes unstable, it has a high frequency of agonistic interactions and a high percentage of reversals. This form of instability is caused more by the high frequency of reversals, however, and not necessarily a high frequency of agonistic interactions, which could occur even in stable groups.

Do these three measures of 'strong' *vs* 'weak' dominance hierarchies covary across primate groups and do they interact with relationships of females between groups to produce what we have recognized as different types of female social relationships? In other words, are there two types of female dominance hierarchies within groups, that when coupled with interactions between groups, result in two types of female social relationships (Wrangham, 1980), or might we need to expand them to three (Isbell, 1991) or even four (van Schaik, 1989) or more to take into account all possible combinations of these measures (Table 2)? Since these are all quantitative traits, where is the line drawn between the end points? What other traits consistently correlate with these measures (*e.g.* grooming, coalition formation, inheritance of maternal rank, rank-related access to food, or reproductive success)? These questions are open to quantitative statistical inquiry.

Disparities among models

Do group-living primates always incur a cost of food competition?

There are also some fundamental differences between the two second-generation models, of which we will highlight two. First, van Schaik and colleagues assume, along with many other primate behavioral ecologists, that all group-living primates experience a cost associated with living in groups (*e.g.* Alexander 1974; Dunbar 1988; Janson & van Schaik, 1988). 'Within-group competition . . . is a virtually inevitable and universal cost of group living' (Sterck *et al.*, 1997). In contrast, Isbell's analysis revealed a syndrome in which known behavioral expressions of competition between females are apparently weak or non-existent. This syndrome may represent situations when female reproductive success is limited by factors other than food abundance, such as disease, predation, infanticide, density-independent events, or time (Isbell, 1991; Stanford, 1995; Yeager & Kirkpatrick, 1998). These are often colobines. In some places, colobines occur in extraordinarily large

groups (*e.g.* Yunnan snub-nosed monkey (*Rhinopithecus bieti*): Kirkpatrick *et al.*, 1998; Angolan black and white colobus (*Colobus angolensis*): Fimbel *et al.*, 2001). Fimbel *et al.* (2001) suggested that female Angolan black and white colobus in Nyungwe Forest, Rwanda, may not be food-limited because they feed heavily on mature leaves. Female red colobus (*Procolobus badius*) at Gombe National Park, Tanzania, appear to be limited more by predation than by food (Stanford, 1995).

In colobines and some other largely folivorous primates (*e.g.* mantled howlers (*Alouatta palliata*); Milton, 1984), food progresses through the gut relatively slowly, requiring the animals to rest while digesting their food (Bauchop, 1978; Parra, 1978; Kay & Davies, 1994; Kirkpatrick *et al.*, 2001). If females cannot process their foods quickly enough, they may run out of time in a day before they run out of food. Reproductive success could then be more time-constrained than food-constrained. This is not to say that food is unimportant for female colobines. Indeed, the positive correlation between colobine biomass and food quality (Davies, 1994) suggests that colobine populations are food-limited. Even female red colobus in Kibale National Park, Uganda, which show no behavioral expressions of competition (Struhsaker & Leland, 1987; Isbell, 1991; but see Gillespie & Chapman, 2001), range in ways that are predictable by their foods (Struhsaker, 1975; Isbell, 1983; Gillespie & Chapman, 2001). However, although all females need sufficient food in order to give birth, sufficient food does not always keep their offspring alive. It has been estimated, for example, that 38-61% of infant mortality in gorillas occurred as a result of infanticide over a 15-year period (Fossey, 1984). In Thomas's langurs (*Presbytis thomasi*) and red howlers (*A. seniculus*), larger groups are more likely to attract infanticidal males, and it has been suggested that infanticide, as opposed to limited food abundance, is responsible for the typically small group sizes in these two species (Crockett & Janson, 2000; Steenbeek & van Schaik, 2001). Infanticide reduces recruitment and may cause females to either exclude other females from their groups or disperse. Indeed, the pattern found by van Schaik (1983) of fewer infants per female in larger groups of primates and interpreted as evidence of food competition could have well been caused instead by higher rates of infanticide in larger single-male groups of such time-constrained species (Isbell, 1991; Crockett & Janson, 2000). In these species, food competition may occur on occasion but not to the extent that it affects female reproductive success (Watts, 1985,

1994; Steenbeek & van Schaik, 2001) or results in behavioral expressions of competition (Isbell, 1991).

In addition, competition may not inevitably *increase* with group living. Consider that solitarily foraging adult females often share extensively overlapping home ranges (*e.g.* galagos (*Galago* and *Galagoides* spp.): Bearder, 1987; orangutans (*Pongo pygmaeus*): Rodman & Mitani, 1987; Delgado & van Schaik, 2000), a social system thought to be ancestral in mammals (Charles-Dominique, 1978). Now consider the case where these same females start foraging together. If the same numbers of females forage over the same area in both cases, there is no reason to expect scramble competition to always be greater for the group-living females than for the solitarily foraging females. On the contrary, foraging together could actually decrease costs of scramble competition by eliminating travel to places where feeding has already occurred (Cody, 1971; Altmann, 1974; Rodman, 1988). This, coupled with good evidence (see above) that dispersed foods, or those with small FSDTs, are associated with minimal contest competition, suggests again that increased competition may not always be a consequence of living in groups.

The disparity between the assumption that all group-living primates experience some form of food competition that is behaviorally expressed and exacts a reproductive cost, and the data that suggest that some primate populations do not experience it is part of a broader disparity. The quantitative data compiled in Isbell (1991) indicate that contest and scramble competition consistently covary both within and between groups, whereas the *a priori* reasoning of van Schaik and colleagues allows contest and scramble competition to vary independently. This disparity presents an opportunity for future research. Do all females experiencing intragroup contest competition also experience intragroup scramble competition? Is the same true of intergroup competition? How should we measure scramble competition?

Female philopatry and dispersal

A second disparity concerns female philopatry, which can be separated into two types — living in the natal area (locational philopatry), and living with natal group members (social philopatry). Wrangham (1980) and van Schaik (1989) both contend that social philopatry results from an *internal* cause — the inclusive fitness benefits of coalition formation with kin, but they disagree on the targets of coalitionary efforts. Wrangham argues that entire

groups represent coalitions against other groups, whereas van Schaik argues that multiple coalitions form within groups against each other. Isbell and Van Vuren's (1996) review of the data suggests that the evolution of kin groups was a two-step process, with the first step being the evolution of locational philopatry. The costs of dispersal, including aggression from strangers and predation, may be so high, at least for Old World primates, that females often cannot afford to leave their natal area. The second step may have involved the coalescing of females that use the same area (social philopatry). Once there was an advantage to foraging with others, groups that would have formed would be kin groups by default given that females were living near female relatives already (Waser & Jones, 1983; Pusey & Packer, 1987; Isbell, 1994). In this view, social philopatry is ultimately a consequence of *external* causes, and is *not* caused by coalition formation within groups. Coalitions within kin groups are expected to occur only if they help females obtain resources that are usurpable (Isbell & Pruetz, 1998).

Guenons are a case in point. Although female guenons are philopatric, they are not, except for vervets, like other cercopithecines in having strong dominance relationships and frequent coalitions (Cords, 1987; 2000; *cf.* Di Fiore & Rendall, 1994). Isbell and colleagues attribute their behavior to the costs of dispersal and a diet of relatively non-ursurpable foods (Isbell, 1991, 1998; Isbell & Van Vuren, 1996; Isbell & Pruetz, 1998), whereas van Schaik and colleagues suggest that their philopatry is driven, unusually for primates, by the benefits of kin in *inter*group competition rather than intragroup competition (Sterck *et al.*, 1997).

The emphasis on the evolution of female kin groups has perhaps obscured recognition that many primate species are not composed of female kin groups. As Strier (1994) and Kappeler (1999) have suggested for New World monkeys and Malagasy lemurs, respectively, female social dispersal is more common than one might expect. This is especially so for female New World primates because females of many Neotropical species commonly disperse despite aggression from females in other groups (Isbell & Van Vuren, 1996). Here is where we suspect phylogenetic history may exert an influence on female social relationships.

Both the Neotropics and Madagascar were colonized through major founding effects of 'dispersing' primates. Evidence suggests that Madagascar was invaded only once about 80-55 mya and that South America was

invaded at least once about 30 mya, with the invaders most likely coming from Africa (Klein, 1989; Fleagle & Kay, 1997; Fleagle, 1999; Martin, 2001; but see Arnason *et al.*, 2001). These large land masses would have been most successfully colonized by small-bodied primates for which social and locational dispersal by both sexes was the norm (such as occurs in pottos (*Perodicticus potto*): Bearder, 1987). This might have set up a very different evolutionary trajectory in these primates which would ultimately result in female social relationships that are fundamentally different from those of Old World anthropoids. It may be unwise to discount the importance of phylogenetic 'accidents' that might have produced founder effects in Madagascar and the New World. For good reason, however, the models focus on ecological and social explanations for variation in female relationships: variation sometimes exists even at the level of the population. Perhaps all primates share the ancestral type of dispersal by both sexes but female locational philopatry evolved in the presence of a unique selective pressure, such as a major mammalian predator that greatly increased the costs of locational dispersal. The 10 kg fossa (*Cryptoprocta ferox*) and the 40 kg leopard (*Panthera pardus*) could fill that niche for most extant Malagasy prosimians (Goodman *et al.*, 1993) and most Old World primates (Hoppe-Dominik, 1984; Isbell, 1990), respectively. There seems to be no mammalian predator in the New World as damaging to primates as leopards can be (Emmons, 1987; Isbell & Van Vuren, 1996).

Predation and dispersal are challenging to study because they occur sporadically. However, these two factors are at the heart of the differences between the models. Wrangham's model considers predation to be insignificant in causing variation in female relationships. van Schaik and colleagues consider predation to be ultimately responsible for variation in female relationships. Isbell and colleagues consider predation to be only indirectly involved in causing variation in female relationships. Further, Wrangham's model predicts that females will disperse when they gain no inclusive fitness benefits by staying to help their female relatives in food competition. van Schaik and colleagues predict that females will disperse largely to avoid, or be protected from, infanticidal males, whereas Isbell and colleagues predict that females will disperse whenever they have a better chance of reproducing somewhere else. They suggest that infanticide, incest, severe aggression from other females, reproductive suppression, and high travel costs relative to food intake may all be important because each can impinge on a female's chances of

reproducing in the natal group (Isbell & Van Vuren, 1996). Information is crucially needed on interactions between predators and prey, and the social and ecological conditions facing females before and after dispersal, in order to test between the models.

What should go into a third-generation model?

In the decade since van Schaik and Isbell proposed their second-generation models of female primate social relationships, primatologists have continued to add to the catalogue of primate populations and species for which we have detailed behavioral and ecological data. Although the current models agree that food is important in determining female relationships, they do not always agree on what aspects of food determine what aspects of female relationships. To test between the models, we will need to expend greater effort on measuring quantitative characteristics of food, such as food distribution, food-site depletion time, interfood distance, area of monopolizability, and daily travel distance and home range size relative to group size. We will also need to develop quantitative measures of competitive relationships that move beyond current descriptions of dominance matrices and the linearity of dominance hierarchies. Latency to the hierarchy's detection is one, but not the only, quantitative measure that could be added. Additionally, a focus on the dynamics of predator-prey relationships and on dispersal will help not only in testing existing models but also in solving some of primate behavioral ecology's other persistent problems. Third-generation models should rest on a firm foundation of empirical, quantitative, and even experimental research. Once quantitative and empirical evidence directs us to where the current models fall short, we can begin to build the next generation of models. What improvements can third-generation models include?

First, future models should clearly and explicitly define their terms. People in graduate seminars all over the world have asked, 'What exactly does this author mean by clumped, or differentiated, or cohesive, or strong?' Such definitions should unambiguously define measurable behavioral or ecological traits.

Second, the ideal model would be hierarchical. For example, theory suggests that both high predation rates and clumped resources should lead to lower inter-individual distances (van Schaik, 1989; van Hooff & van Schaik,

1992), but which takes precedence when these traits do not covary, as in patas monkeys? A hierarchical model would tell us. In the case of patas monkeys, data suggest that food distribution takes precedence over predation risk (Isbell & Enstam, 2002). In addition, a hierarchical model provides a logical flow chart of causative factors and their consequences. In the real world, multiple factors simultaneously impinge on animals. Multiple factors suggest more a partitioning of variance than simple hypothesis testing, and that may be a fruitful approach. However, it does require even richer data sets than simple hierarchical models in a world where data are still in short supply. An alternative to a strictly hierarchical model would be one that allows multiple factors to impinge simultaneously, but that does so in a way sufficiently explicit to at least provide a road map for sorting out conflicting causative factors. Meanwhile, we suggest that hierarchical causative models are preferred unless they prove to be inadequate.

Finally, we need even greater effort in the following four areas:

We need commitments to more long-term studies because functional explanations for variation in female social relationships, and indeed, all kinds of social behavior, require data on lifetime reproductive success of multiple individuals. The wealth and value of data that arise from long-term field studies should not be underestimated.

We need more study sites per species because primates can be exceedingly flexible in their social behavior, and much of this flexibility may be the result of local ecological and social conditions. Investigation of populations of the same species that live under different social or ecological conditions will go far to enable researchers to test and further refine proposed explanations.

We need more studies of unusual species because exceptions are one of the best ways to test rules. The extraordinary often explains the ordinary.

We need studies of unstudied species because, as well as we know primates, we still need to know more. We encourage those at the beginning of their careers to get out and explore, and create and keep, study sites. And we encourage everyone to devise tests of the models and their underlying assumptions before we accept any as a standard.

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