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Is There No Place Like Home? Ecological Bases of Female Dispersal and Philopatry and Their Consequences for the Formation of Kin Groups

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In L. Frank Baum's century-old tale *The Wizard of Oz*, Dorothy, a female primate, disperses with an ally from her natal home range and group to an unfamiliar area. While in this new area, she encounters unfamiliar plants, potential predators, and aggressive strangers, dangers she never faced at home. Dorothy succeeds by establishing relationships with new allies. Despite her successes in the new area, Dorothy has an overwhelming desire to return home. Baum did send Dorothy home eventually, and back to her kin group. Had she stayed in Oz, she would have left her home range as well as her kin group. Decisions about dispersal from the natal home range are important for understanding the evolution of kin groups, but they are not addressed in two widely recognized models that have been developed to explain the evolution of kin groups.

These two models focus on the benefits of grouping with kin. They are the intergroup competition model, in which inclusive fitness benefits are gained by forming groups of relatives in competition against nonrelatives for food (Wrangham 1980), and the predation/intragroup competition model, in which groups evolve in response to predation and females remain in their natal groups for the inclusive fitness benefits that are gained by forming coalitions of relatives within groups for competition for food (van Schaik 1989). Both of these models assume that group living is inherently costly and that cooperation with relatives outweighs this cost.

A third model contrasts with these models in its focus on the costs of dispersal and their effects on kin grouping. In the dispersal model, high costs of dispersal cause reproductive daughters to stay in the home range. Kin groups then form by default when there is an advantage to living in groups (Isbell 1994, Isbell & Van Vuren 1996). In this model, inclusive fitness benefits of helping kin in intergroup competition are a secondary advantage of living in groups with kin.

These three models are built largely on assumptions, some more so than others, because data are still in short supply. Some of these assumptions may eventually prove to have real-life support, but it is important to be cognizant of each assumption and to be cautious in accepting any without critical examination. To compare the relative merits of the models, it is useful to identify their assumptions, some of which were carried over from previous influential works. Thus, I begin with a chronological overview of the salient points of the models as they pertain to the evolution of kin groups. I then extend the dispersal model by focusing on the ecological bases of dispersal and philopatry from the mother's perspective. The result is the dispersal/foraging efficiency model, which describes the evolution of kin groups as a series of small, incremental steps that happen as individuals attempt to maintain or improve their foraging efficiency.

I focus on females because when kin groups form, they usually form around females and because female reproductive success is affected more than male reproductive success by ecological influences. Nonetheless, because there are times when male dispersal decisions affect female decisions to remain in or leave the natal group, I discuss males when appropriate, mainly but not entirely in the context of sex-biased dispersal. Phylogeny may play a role in dispersal patterns (Di Fiore & Rendall 1994, Isbell & Young 2002), but I emphasize the ecological influences on dispersal. I limit discussion to dispersal from the natal group or home range, because natal dispersal breaks up kin groups whereas subsequent movements simply maintain nonkin groups.

A Brief History of Group Living, Female Kin Groups, and Dispersal

The evolution of kin groups has spawned a lively debate since Alexander (1974) challenged the prevailing view that group living is inherently beneficial to all group members. Alexander uncompromisingly stated that "there is no automatic or universal benefit from group living. Indeed, the opposite is true: there are automatic and universal detriments, namely, increased intensity of competition for resources, including mates, and increased likelihood of disease and parasite transmission" (p. 328). Recognizing that there must be benefits that offset the disadvantages of group living, Alexander maintained that three advantages could be gained: (1) reduced susceptibility to predation through cooperative defense, dilution, or selfish herd effects (Hamilton 1971); (2) improved ability to get food, through either group hunting or better detection of scattered foods; and (3) shared use of a large and highly restricted resource such as a location for sleeping sites. These three advantages would not necessarily promote similar kinds of social groups, however. Individuals attempting to reduce predation or improve food finding might be attracted to others, whereas individuals needing a sleeping cliff might aggregate and yet still not be attracted to others. Alexander ruled out all but predation as the selective force favoring grouping in primates because (1) primates do not hunt in groups (with the exceptions of modern humans [*Homo sapiens*] and chimpanzees, [*Pan troglodytes*]); (2) they do not seem to use each other to locate food (although there is now evidence that in some primates, for example rhesus macaques [*Macaca mulatta*] and chimpanzees, individuals alert others to the locations of rich food sources [Hauser & Wrangham 1987, Hauser & Marler 1993, Hauser et al. 1993]); and (3) they do not have sufficiently restricted and critical resources (even including the sleeping cliffs of hamadryas baboons [*Papio cynocephalus hamadryas*] to force them to aggregate.

Alexander contributed the assumption that group living is inherently costly and that the only benefit that outweighs the cost of living in groups is predation. The assumption that group living is inherently costly has been repeated often and by now permeates our views of primate sociality (e.g., Wrangham 1980, Terborgh & Janson 1986, Janson & van Schaik 1988, van Schaik 1989, Isbell 1991, Sterck et al. 1997). It has been questioned only recently (Isbell & Young 2002). More intensively debated has been the importance of predation as the selective factor that favors group living.

The evolution of group living became closely linked with the evolution of kin groups when Wrangham (1980) proposed that groups evolved in response to food competition, not predation. He argued that when animals are faced with large, clumped, and defendable foods, individuals that cooperate with others can outcompete those that do not cooperate. All else being equal, the best ones with whom to cooperate are kin because helping kin can increase one's inclusive fitness whereas helping nonkin cannot. According to Wrangham, kin groups evolved in the context of intergroup competition. For females living in nonkin groups, Wrangham suggested that male harassment of females favors aggregations of females around protective males (figure 4.1).

Partly because it could explain both the evolution of grouping and the evolution of kin groups, Wrangham's scenario was attractive. It was appealing also because it used the

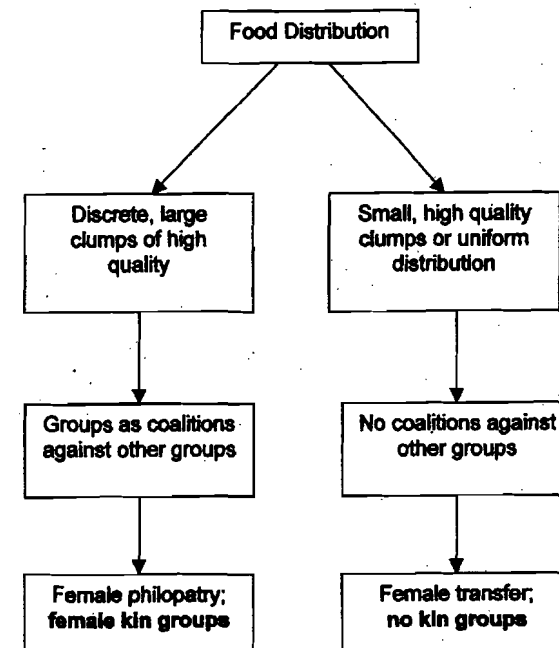


Figure 4.1. A schematic representation of the factors leading to female kin group according to the intergroup competition model (Wrangham 1980).

same theoretical reasoning previously applied to bats (Bradbury & Vehrencamp 1977) and birds (Emlen & Oring 1977) that since female reproductive success is most limited by food (Trivers 1972), females should act in ways that maximize their access to food. The intergroup competition model was not based on information from all primates, however; 23 of 29 species (79%) in the model were catarrhine primates, and 16 of the 23 catarrhines (70%) were cercopithecines, a reflection of the emphasis at that time on studies of Old World primates. It also suffered from a lack of information on female movements. At the time of the model's publication, females were known to breed in their natal groups in only four species, all of them cercopithecines. To overcome the lack of direct evidence, Wrangham used male dispersal as indirect evidence of female residence in the natal group because the two appeared to be closely associated, and indeed they are in cercopithecines. In a few additional species, no information existed on dispersal patterns of males and females. Interactions between females within groups that involved grooming, huddling together, coalition formation, and agonistic interactions were then considered to be representative of female kin groups. A near absence of data thus tied male dispersal to female philopatry and female kin groups to clearly delineated female relationships within groups, that is, easily determined, or strong, dominance hierarchies. Studies since then have shown, however, that females and males both disperse in many primate species (Moore 1984; Strier 1994, 1999), and that in some species, females have dominance hierarchies that are difficult to detect even though they live in kin groups (Isbell & Pruett 1998, Cords 2000).

Wrangham's model was challenged by van Schaik (1983), who argued against intergroup competition and in favor of predation as the primary selective factor favoring group living. Following Alexander's assumption that group living is always costly, and extending it by assuming that living in larger groups is always costlier than living in smaller groups, van Schaik examined infant/adult female ratios across 14 species (27 data points). He specifically restricted his analysis to those species that were thought at the time to live in female kin groups so that he could test the intergroup competition model. He found that in most cases the number of infants decreased as group size increased, a pattern that would not be expected if the benefits of intergroup competition outweigh the cost of intragroup competition. He interpreted this as evidence against the intergroup competition hypothesis for the evolution of group living, and as support for the predation hypothesis.

As was the case for Wrangham (1980), van Schaik's (1983) approach was undermined by lack of information about female movements. Most important, females in three genera that comprised nearly half of the data points (12 of 27) in van Schaik's analysis are now known to disperse regularly (*Alouatta*) or at least occasionally (*Presbytis* and *Trachypithecus*), substantially weakening the purpose of the analysis as a test of the intergroup competition model. In addition, while fewer infants per female in larger groups may be a real phenomenon, other factors, such as infanticide, can also plausibly explain van Schaik's results (Isbell 1991, Crockett & Janson 2000, Steenbeck 2000). Interestingly, infanticide is now being considered one of the main factors influencing female dispersal decisions, particularly in *Alouatta*, *Presbytis*, and *Trachypithecus* (Isbell 1991, Isbell & Van Vuren 1996, Sterck et al. 1997, Crockett & Janson 2000, Sterck & Korstjens 2000).

The renewed emphasis on predation as the ultimate selective pressure favoring group living provided the opportunity for alternative models for the evolution of female kin groups. If, as van Schaik (1983) argued, intergroup competition was not an important positive force in the evolution of group living, then female kin groups must have evolved for other reasons.

In van Schaik's (1989) predation/intragroup competition model, female kin groups ultimately evolved because predation forces females to live in groups, and the inevitable intragroup competition that occurs with group living favors coalition formation by kin when foods are clumped and therefore monopolizable (figure 4.2). Here van Schaik (1989) agreed with Wrangham (1980) that females form coalitions with kin because they gain inclusive fitness benefits by doing so. Van Schaik (1989) differed from Wrangham (1980), however, by proposing that coalition formation with kin depends not only on the distribution of foods, but also on the intensity of predation. Moreover, coalitions were argued to occur largely within groups rather than between groups in response to monopolizable foods (figure 4.2). Van Schaik (1989) allowed intergroup competition to favor coalitions and therefore kin groups only in rare situations where low predation risk allows females to live in less spa-

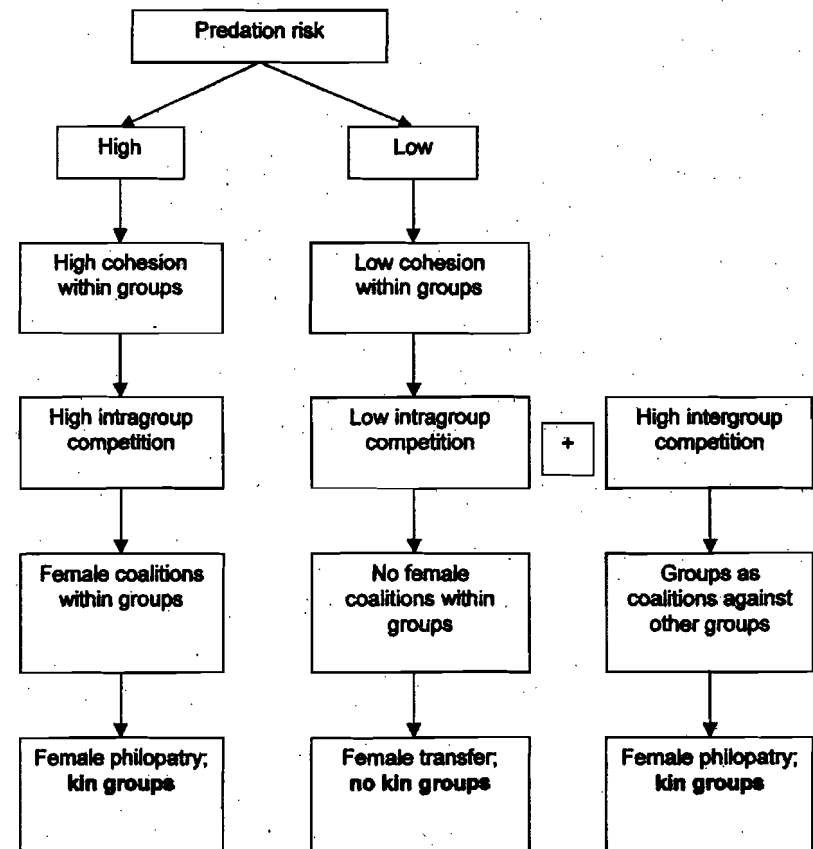


Figure 4.2. A schematic representation of the factors leading to female kin groups according to the predation/intragroup competition model (van Schaik 1989, Sterck et al. 1997).

tially cohesive groups. Increased interindividual distances would decrease intragroup competition to such an extent that it would become less important than intergroup competition (figure 4.2).

Eight years later, Sterck et al. (1997) modified the predation/intragroup competition model to incorporate the growing evidence of female dispersal in species with male dispersal. Though earlier van Schaik (1989) had criticized the intergroup competition model for being unable to explain why females that disperse from their natal groups nonetheless live in groups, Sterck et al. (1997) now converged with it by suggesting that such groups evolve in response to a selective pressure other than the one that favors female kin groups. Whereas the intergroup competition model held that nonkin groups evolve because females benefit from aggregating around males that can protect them from harassment, the modified predation/intragroup competition model proposed that nonkin groups evolve because females benefit from aggregating around males that can protect them from infanticide. Thus, both models agree not only that female kin groups form because of the benefits of coalitions (of one kind or another), they also agree that nonkin groups form because of the benefits of aggregating around males.

Isbell (1991) and colleagues (Isbell & Van Vuren 1996, Isbell & Pruett 1998, Isbell, Pruett, & Young 1998, Pruett & Isbell 2000, Isbell & Enstam 2002, Isbell & Young 2002, Mathy & Isbell 2002) have been working on an alternative model that differs from both the intergroup competition model and the predation/intragroup competition model. Analyzing quantitative data, Isbell (1991) found that species in which groups of females are aggressive toward other groups also expand home ranges with increasing group size (and likewise decrease them with decreasing group size). In nearly all catarrhine species surveyed, females that display intergroup aggression typically remain in their natal groups, a finding consistent with expectations of the intergroup competition model. She suggested that females are aggressive toward other groups because aggression helps to minimize losses of food resources to groups that would otherwise expand into their home ranges. Though her conclusion was consistent with Wrangham's emphasis on intergroup competition for the evolution of kin groups, it differed in the ecological basis for intergroup competition. The combination of home range expansion with increasing group size and invariable female aggression between groups suggested that food abundance, as opposed to food distribution, affects female reproductive success in most species. This inference has subsequently been supported by data from hanuman langurs (*Semnopithecus entellus*) at Ramnagar, Nepal (Koenig 2000) and squirrel monkeys (*Saimiri* spp.: Boinski et al. 2002).

Among populations of females apparently constrained by food abundance, Isbell (1991) found that daily travel distance increases with increasing group size in primates that feed extensively on fruits but not in those that feed extensively on leaves or arthropods (see also Janson & Goldsmith 1995). Nearly all species surveyed that increase daily travel distance with group size also have strong female dominance hierarchies within groups, whereas nearly all species that do not adjust daily travel distance to group size have much less obvious dominance hierarchies. Because fruits are thought to be clumped, and leaves and arthropods ubiquitous or dispersed, she inferred, as did Wrangham (1980) and van Schaik (1989), that the spatial distribution of food resources determines competitive relationships within groups. In fact, more recent investigations of the ecological determinants of variation in competitive relationships among females within groups suggest that the critical characteristic is temporal rather than strictly spatial. Larger food size or, more important, longer

feeding site depletion time makes foods more usurpable than do shorter distances between foods (i.e., more clumped distributions; Shopland 1987, Janson 1990, Isbell & Pruett 1998, Isbell, Pruett, & Young 1998, Mathy & Isbell 2002).

These results disconnected female philopatry from strong dominance hierarchies for the first time. Isbell's model described a type of female that the intergroup competition model did not recognize and that the predation/intragroup competition model recognized only after changing predation pressure, intragroup competition, and intergroup competition. Isbell's model was more parsimonious than the predation/intragroup competition model in that the existence of this type of female required only a change in the usurpability of food among females limited by food abundance. These species are represented by patas monkeys (*Erythrocebus patas*) and at least two other species of African guenon (blue monkeys [*Cercoptes mitis*] and redtailed monkeys [*C. ascanius*]). Patas monkeys have female philopatry, intergroup aggression, large interindividual distances within groups, dominance hierarchies that are difficult to detect, and spatially dispersed foods, but they also have heavy predation (Chism et al. 1984, Chism & Rowell 1988, Isbell & Pruett 1998, Isbell, Pruett, & Young 1998, Pruett & Isbell 2000, Isbell & Enstam 2002). Their heavy predation is contrary to what the predation/intragroup competition model predicts, making them more accurately described by Isbell's (1991) model than the predation/intragroup competition model.

In a few species, for example red colobus (*Procolobus badius*), Isbell (1991) found no behavioral indicators of competition, that is, no significant changes in home range size and daily travel distance with group size and little aggression between females either within or between groups. The lack of behavioral indicators of competition led Isbell to begin to question the assumption that increased competition is inherent in group living.

Like Sterck et al. (1997), Isbell and Van Vuren (1996) investigated the growing reports of greater variability in female dispersal patterns but again from a different perspective, that of differential costs of locational and social dispersal to individuals. Locational dispersal involves movement away from a familiar place, whereas social dispersal involves movement away from familiar conspecifics. The main potential costs of locational dispersal are increased risk of predation and poorer access to foods through lack of knowledge about the new environment. The main potential cost of social dispersal is increased aggression, coming from strangers. For group-living animals, there are three potential combinations of dispersal: locational dispersal without social dispersal, locational dispersal coupled with social dispersal, and social dispersal without locational dispersal, each of which has a different set of costs. Only the last two types have an impact on the evolution of kin groups.

Isbell and Van Vuren (1996) found that for catarrhine primates, regular female dispersal from the natal group to another group (transfer) is most likely when the costs of dispersal are minimal, that is, when there is little aggression between females of different groups and females are able to remain in much, if not all, of their natal home ranges when they transfer (e.g., Kibale red colobus and mountain gorillas [*Gorilla gorilla beringei*]). In some catarrhine species (e.g., banded leaf monkeys [*Presbytis melalophos*] and capped langurs [*Trachypithecus pileata*]), female transfer is "occasional," that is, not regular but occurring more often than can be called exceptional (see Isbell & Van Vuren 1996 for quantitative cutoffs for regular, occasional, and exceptional transfer). In these species, females also face little aggression from females of other groups and so face minimal costs of social dispersal. They often also have extensively overlapping home ranges with neighboring groups and so face minimal costs of locational dispersal (Isbell & Van Vuren 1996).

Dispersal by individual females in species with regular and occasional female transfer was suggested to be heavily dependent on the chances of successful reproduction in their natal groups. These females are the same as those catarrhines suggested by Isbell (1991) to not be limited in their reproductive success by food abundance and by Wrangham (1980) and Sterck et al. (1997) as aggregating around males for protection from harassment or infanticide. Isbell and Van Vuren (1996) suggested that female reproductive success in these species depends less on food abundance than on attributes of individual males. Such females would be expected to leave their natal groups when their reproductive success is threatened by infanticidal males or incestuous matings with fathers and brothers. Females would also be expected to leave if they fail to reproduce for reasons unrelated to male behavior, however, because there are additional causes of reproductive failure in females, for example hormonal insufficiency or fetal damage (e.g., Albrecht et al. 2000).

Isbell and Van Vuren (1996) suggested that in those catarrhine primates with only exceptional female dispersal at most, for example vervets (*Cercopithecus aethiops*) and macaques (*Macaca* spp.), females are philopatric because aggression from strangers and/or movement into unfamiliar areas make dispersal too costly. These exceptional cases of female dispersal occur only in unusual situations when females fail to reproduce or are very unlikely to reproduce compared to others in their current groups.

In contrast to catarrhines, platyrrhine females are actually more likely to disperse from their natal groups despite aggression from strangers (costs of locational dispersal could not be examined in New World primates because all the species meeting the criterion for inclusion, that is, cohesive multifemale groups, had no variation in home range overlap, the measure used to estimate costs of locational dispersal). In the absence of more inclusive data, Isbell and Van Vuren (1996) speculated that although both catarrhine primates with female philopatry and platyrrhine primates have costs of social dispersal, platyrrhines might have lower costs of locational dispersal than catarrhines with female philopatry, making dispersal costs lower overall and thus making dispersal more likely in platyrrhines. They suggested that the potential for lower costs of locational dispersal among platyrrhines might exist because extensive home range overlap minimizes unfamiliarity with new areas and there were no reports of platyrrhines experiencing a New World equivalent of the leopard (*Panthera pardus*), a mammalian predator that can decimate primate groups in a short period of time (e.g., Isbell 1990, Isbell & Enstam 2002).

The focus on costs of dispersal to individuals questions the scenario that inclusive fitness benefits from helping kin defend food resources from nonkin (within or between groups) was the selective advantage behind kin group formation. Given that the costs of dispersal would have been sufficient to keep solitary foraging females in the natal home range, Isbell and Van Vuren (1996) suggested that kin groups would have formed by default once there was an overall advantage to living in groups. Inclusive fitness benefits would be gained as a secondary advantage of living in groups.

This model, like the others, was hindered by insufficient information. Gaps existed particularly in the natural history of New World primates, Malagasy prosimians, and colobines. The long debate over the selective pressures favoring kin groups has, fortunately, helped to generate studies of some of the less well known taxa, providing an opportunity for further modification and refinement of models. In the next section, I summarize the dispersal model from the usual perspective of the disperser and then extend it by taking the mother's perspective and adding data from hitherto underrepresented taxa.

Dispersal from the Offspring's Perspective

Because primates are mammals, male reproductive success is ultimately dependent on females: if females fail to reproduce, males also fail. Males are constrained to react to, rather than determine, female decisions to disperse. When costs of social and locational dispersal exist, individual females should attempt to remain philopatric, but only as long as those individuals can reproduce successfully at home. If a female cannot reproduce where she is, she should take her chances with the potential costs of dispersal in her current social and ecological milieu and leave. Sometimes no costs of dispersal exist that are strong enough to affect reproductive success. Nonetheless, the same bottom line applies: a female should disperse when her chances of reproducing are better elsewhere. This bottom line also applies to males, but because the causes of reproductive failure are more numerous in females, female dispersal is more complex than that of males.

Solitary foraging is generally viewed as the ancestral mammalian foraging/social system (Charles-Dominique 1978, Eisenberg 1981). To understand the evolution of kin groups, it might be profitable to examine the ecological differences between having exclusive access to one's home range (which requires dispersal of offspring) and sharing it with other reproductive females (which allows philopatry of female offspring). Surviving in the home range without reproducing can be as evolutionarily insignificant as dying while dispersing. Thus, when females face costs of dispersal and still disperse, it is likely to be because they would not have reproduced had they remained. If, however, daughters are presented with the opportunity to reproduce in the natal home range or group, they should stay. This opportunity may arise if mothers are able to share their home ranges with their daughters.

Dispersal from the Mother's Perspective

Since the reproductive success of mothers depends not only on the survival and reproduction of their offspring but also on the mother's own ability to obtain sufficient food for future reproduction, mothers are expected to share their home ranges with their reproductive daughters only when both the costs of dispersal make it unlikely that their daughters will reproduce in a new area and they can maintain their own reproductive output. If mothers can expand their home ranges to accommodate their reproductive daughters, their own reproductive success is expected not to be diminished. Primate mothers appear to differ, however, in the extent to which they are able to expand their home ranges to accommodate their reproductive daughters. Five different types of mothers can be distinguished on the basis of home range overlap and expansion: stingy mothers, generous mothers, incomplete suppressors, facilitators, and indifferent mothers.

"Stingy Mothers": Female Dispersal Required

From the perspective of dispersal, there is little difference between females that are traditionally considered solitary, females that live in monogamous groups, and females that form cohesive groups with other adult, but nonbreeding, females. In all cases, only one female in a given "group" typically reproduces, and in all cases, females that do not reproduce typically disperse socially when they have the opportunity to reproduce elsewhere. In many of

these cases, reproduction is also limited to one female within a local area. Such females do not share the resources within their home ranges with other reproductive females. These females are referred to as stingy mothers here.

The most obvious examples of stingy mothers are socially monogamous species and solitarily foraging species with minimally overlapping home ranges and aggression between reproductive females. Female pottos (*Perodicticus potto*) are solitary foragers with home ranges that overlap only minimally with those of other females (Charles-Dominique 1977, Bearder 1987). Female western tarsiers (*Tarsius bancanus*) and aye-ayes (*Daubentonia madagascariensis*) also forage alone in nonoverlapping home ranges (Bearder 1987, Sterling 1993). The socially monogamous gibbons (*Hylobates* spp.), titi monkeys (*Callicebus* spp.), owl monkeys (*Aotus* spp.), indri (*Indri indri*), woolly lemurs (*Avahi*), and bamboo lemurs (*Hapalemur* spp.) are territorial, with minimally overlapping home ranges (Wright 1986, Leighton 1987, Palombit 1994, Nievergelt et al. 1998, Fuentes 2000, Kappeler 2000, Thalmann 2001, Bossuyt 2002).

Also considered stingy are females that breed to the exclusion of other females even when multiple adult females share the home range. They are stingy mothers because shared food resources are not typically converted to offspring for any but the one reproductive female. Thus, although more than one adult female may be present in family groups of tamarins (*Saguinus*), lion tamarins (*Leontopithecus*), marmosets (*Callithrix*), and pygmy marmosets (*Cebuella*), they are considered to have stingy mothers because reproduction is limited to one female, with informative exceptions (Goldizen 1987, Ferrari & Lopes Ferrari 1989, Savage 1990, Garber 1993, Rylands 1993, Soini 1993, Digby & Ferrari 1994, Goldizen et al. 1996, Savage et al. 1996). Suppression of reproduction is well documented in female marmosets and tamarins and continues until either the reproductively active female disappears from the group or the suppressed females leave (Abbott et al. 1993). It has not been considered for other stingy females, but in gibbons, if the mother disappears, the daughter will not disperse and will reproduce (Leighton 1987), suggesting a release from some sort of reproductive suppression.

Complete reproductive suppression in philopatric adult female offspring may represent a balance for mothers between the costs of sending their daughters out into the world (high risk of mortality) and the cost of sharing resources with their daughters' offspring (reduction of mothers' future reproduction). Adult daughters may "agree" to suppress their own reproduction if it means they can remain in the natal home range until an opportunity to reproduce arises either in the natal home range or in another home range as a result of the disappearance or displacement of the resident female reproducer on that home range.

Callitrichid groups can at times have more than one reproductive female (Goldizen 1987, Rothe & Koenig 1991, Dietz & Baker 1993, Digby 1995, Goldizen et al. 1996). In many of these cases, the dominant female attempts to kill the offspring of the other females (Digby 2000), a behavior that would be expected of stingy mothers. In lion tamarins (*Leontopithecus rosalia*) without female infanticide, the reproductive females were known to be mothers and daughters, and although the daughters had poorer reproductive success than their mothers, they had greater reproductive success than females that dispersed. Polygyny in lion tamarins was positively correlated with quality of home ranges and home range size (Dietz & Baker 1993), suggesting that kin groups can form at least temporarily if mothers are willing and able to expand their home ranges to accommodate their grandoffspring. This does not seem to be the norm with stingy mothers, however.

Stingy mothers do not often appear to take opportunities to expand their home ranges or they seem unable to expand their home range boundaries because of aggression by neighbors. One female potto left her home range to her daughter rather than expand it (Charles-Dominique 1977). Other female pottos did not expand their home ranges when openings arose but instead left their home ranges and moved to an entirely different home range (Charles-Dominique 1977). Similarly, groups of pygmy marmosets (*Cebuella pygmaea*) moved to new home ranges instead of expanding their old home ranges when their food resources declined (Soini 1993). Saddle-back tamarins (*Saguinus fuscicollis*) at Manu, Peru, did not pass beyond their home range boundaries into another group's home range even when the other group was away (Terborgh 1983). Home range boundaries persisted over many years in owl monkeys (*Aotus trivirgatus*; Terborgh 1983, Wright 1986, Peres 2000). For at least four years, female siamangs (*Hylobates syndactylus*) did not expand into home ranges left open when an illness went through the population (Palombit 1994). Upper limits to home range size are not restricted to primates but are common among terrestrial mammals (Kelt & Van Vuren 2001). Reluctance to expand into available areas is surprising given that expansion presumably increases access to food resources and should therefore be beneficial to mothers' reproductive success. I will suggest ecological reasons for this reluctance after I describe the four other types of mothers.

"Generous Mothers": More Options for Reproduction

Contrasted with stingy mothers are populations in which solitarily foraging reproductive females have overlapping home ranges and thus share food resources in the common area. These are referred to here as generous mothers. To share their home ranges with their adult daughters, mothers must be willing and able to expand their home ranges beyond what they need for their own reproduction. The prevalence of shared home ranges among solitarily foraging mammals (Waser & Jones 1983) suggests that this is often achieved, but in solitarily foraging primates, it appears to be less common than exclusively used home ranges (table 4.1). Female galagos and bush babies (*Galago*, *Galagoides*, and *Otolemur*) and mouse lemurs (*Microcebus murinus*) have extensively overlapping home ranges (Charles-Dominique 1977, Bearder 1987, Radespiel 2000, Eberle & Kappeler 2002), which indicates that they share their resources to some degree. Co-inhabitants of the shared home ranges are expected to be daughters in most cases. Reproductive female galagos share the mothers' home ranges and therefore, their food (Charles-Dominique 1977, Bearder 1987). Close genetic relatedness among female mouse lemurs that have extensive home range overlap has also been confirmed (Wimmer et al. 2002).

"Incomplete Suppressors": Limited Tolerance of Reproduction in Multifemale Groups

Incomplete suppressors are defined here as females that live in home ranges sufficiently large to enable other females to reproduce, but only up to a point. They are similar to stingy mothers in having home ranges with minimal overlap, but they differ in that multiple females defend the same home range. Incomplete suppressors are different from generous mothers in that multiple females often travel together in their shared home range. Though females living in multireproductive female groups have overcome complete reproductive

suppression, they will, like stingy females with complete suppression, disperse if their chances of reproducing in their natal groups are poor.

Among incomplete suppressors, female red howlers (*Alouatta seniculus*) that succeed in reproducing in their natal group do not disperse; females that disperse have not yet reproduced. Female red howlers that disperse are frequently targets of aggression by unrelated female group mates before they disperse (Crockett 1984; Pope 2000a, b), and the process of targeted aggression eventually results in groups consisting of single matriline (Pope 2000b). There are reports of targeted aggression in some group-living Malagasy prosimians (e.g., *Lemur* and *Propithecus*) in some populations, and females targeted with aggression also disperse from their groups (Vick & Pereira 1989, Pereira 1993, Wright 1999). Targeted aggression and dispersal of targeted females may be a mechanism for reducing food competition caused by increasing group size in species that have fixed home ranges. Unlike many other species in which the size of the home range changes with changes in group size (see below), home ranges of ring-tailed lemurs (*Lemur catta*) and Milne-Edwards's sifakas (*Propithecus diadema*) have been extraordinarily stable in size for up to three decades and counting, regardless of changes in group size or population density (Wright 1995, Jolly & Pride 1999).

Targeted aggression with eviction may be a characteristic of incomplete suppressors. Unfortunately, incomplete reproductive suppression makes it impossible to determine what a dispersing female's reproductive success would have been had she remained. In captivity, where home ranges cannot possibly expand and the option to disperse is nonexistent without human intervention, the poorer reproducers are often those that are recipients of aggression (Silk et al. 1981, Wasser & Barash 1983, Silk 1988, Vick & Pereira 1989, Pereira 1993). Without human intervention, targeted aggression can even become fatal in captivity (McGrew 1997). In the wild, females that stay in their groups despite being targeted with aggression could suffer the same fate. Given such dire odds, targeted females may be better off taking their chances with dispersal. At worst, dispersers that die would break even and at best, dispersers that survive would eventually reproduce. Even if their reproductive success is lower than that of females that stay, it is likely to be greater than if they themselves had stayed.

"Facilitators": Greater Tolerance of Reproduction in Multifemale Groups

In some species, mothers do not normally target females in their groups with aggression but allow them to stay and may even facilitate their reproduction through preferential treatment (Fairbanks 2000). Such mothers are called facilitators here. Female yellow baboons (*Papio cynocephalus cynocephalus*) and macaques live in groups of related matriline; females rarely disperse in these species (Pusey & Packer 1987a, Isbell & Van Vuren 1996). These are equivalent to the species called female-bonded by Wrangham (1980). These are also the species in Isbell's (1991) model for which home range size increases with larger group size. Expansive home ranges are difficult to keep exclusive. Thus, facilitators differ from stingy mothers and incomplete suppressors by having overlapping and indeterminately growing home ranges. Costs of daily travel do not limit home range expansion in these species because daily travel distance and home range size are independent (Isbell 1991). Facilitators

differ from generous mothers by invariably traveling within sight of other adult females in the shared home range.

"Indifferent Mothers"

Because it has become so ingrained in the literature that females are limited in their reproductive success by food (Trivers 1972), it may be difficult by now to imagine females that are not limited by food. The fifth type of mother appears, however, to be less responsive than the other four types to differences in food resources.

In these species, females appear more indifferent than concerned about the presence of other females. They neither force dispersal nor facilitate philopatry. Such females are referred to as indifferent mothers here. In many colobines, such as red colobus, capped langurs, banded leaf monkeys, Thomas's langurs (*Presbytis thomasi*), and Nilgiri langurs (*Trachypithecus johnii*), females commonly or at least occasionally disperse, and they emigrate without aggression from other group members. They can either transfer directly to an existing group or create a new group by joining a male (Struhsaker 1975, Marsh 1979, Stanford 1991, Starin 1991, Bennett & Davies 1994, Oates 1994, Steenbeek et al. 2000). Females also experience little aggression from neighboring groups when they immigrate. Colobines often, though not always, have extensively overlapping home ranges, and females often disperse to groups whose home ranges overlap extensively with those of their natal groups (Isbell & Van Vuren 1996). Aggression from strangers and unfamiliarity with new areas, the main costs of dispersal, thus appear to be minimal for indifferent females. Low costs of dispersal may also reduce pressure on mothers to provide a place in their own home ranges for their daughters.

Although most female red colobus at Abuko, Gambia, leave their natal groups, they often stay within their former group's home range (Starin 1981, 1991). During a five-year study of olive colobus (*Procolobus concolor*) at Tai National Park, Ivory Coast, at least 8 of 16 females changed groups (Korstjens 2001, Korstjens & Schippers 2003). One female whose dispersal history was well documented left her group when the group followed the resident male as he moved back into the home range (but not the group) from which he had come. She returned to her former home range as a solitary female but joined the group again when the male returned with the rest of the group. The only other adult female in the group also left during the shift in range use, but her fate was unknown (Korstjens 2001, Korstjens & Schippers 2003). Site fidelity may be more important than group fidelity in colobines. Similarly, mountain gorillas (*Gorilla gorilla*) have little female aggression within or between groups, extensive home range overlap, and female transfer (Harcourt 1978, Watts 1990, Yamagiwa & Kahekwa 2001).

Table 4.1 provides a summary list of primate genera (sometimes species when they appear to differ) for which there are data to classify them into the five types discussed above using information first and foremost on the extent of home range overlap with other reproductive females, followed by (1) female social dispersal, (2) targeted aggression, and (3) presence or absence of contest competition among females between groups.

With few exceptions, it is fairly easy to classify genera as long as sufficient data are available. The genus *Pan* is a difficult one to classify largely because great individual variation exists in female ranging behavior. For example, in the same population, some female

Table 4.1. Genera Categorized as Stingy Mothers, Generous Mothers, Incomplete Suppressors, Facilitators, and Indifferent Mothers^a

Stingy Mothers	Generous Mothers	Incomplete Suppressors	Facilitators	Indifferent Mothers
<i>Avahi</i> ^b	<i>Microcebus</i>	<i>Eulemur</i>	<i>Cebus</i>	<i>Brachyteles</i>
<i>Cheirogaleus</i>	<i>Galago</i>	<i>Hapalemur</i>	<i>Saimiri (boliviensis)</i>	<i>Saimiri (oerstedii)</i>
<i>Daubentonia</i>	<i>Galagoides</i>	<i>Lemur</i>	<i>Cercopithecus</i>	<i>Nasalis</i>
<i>Eulemur</i>	<i>Otolemur</i>	<i>Propithecus</i>	<i>Erythrocebus</i>	<i>Presbytis</i>
<i>Hapalemur</i>	<i>Pongo</i> ^c	<i>Varecia</i>	<i>Macaca</i>	<i>Pygathrix</i>
<i>Indri</i>	<i>Pan</i> ^c	<i>Alouatta</i>	<i>Mandrillus</i>	<i>Trachypithecus</i>
<i>Lepilemur</i>			<i>Papio</i>	<i>Simias</i>
<i>Perodicticus</i>			<i>Theropithecus</i>	<i>Colobus</i>
<i>Phaner</i>			<i>Semnopithecus (Rammagar)</i>	<i>Procolobus</i>
			<i>Pongo</i> ^c	<i>Gorilla</i>
<i>Varecia</i>			<i>Pan</i> ^c	
<i>Tarsius</i>				
<i>Alouatta</i>				
<i>Aotus</i>				
<i>Callicebus</i>				
<i>Callithrix</i>				
<i>Cebuella</i>				
<i>Leontopithecus</i>				
<i>Saguinus</i>				
<i>Hylobates</i>				
<i>Pan</i> ^c				

^aSee text for the criteria used in classifying each category. Varying contributions of goal-directed travel and wandering are predicted to determine the extent to which mothers can expand their home ranges to accommodate reproduction by their daughters. Although phylogenetic niche conservatism probably plays a major role in establishing the relative contributions of goal-directed travel and foraging behavior in most cases, the potential exists for females in different populations within a species to express different types because travel and foraging behavior may also be affected by local conditions. Similarities in energetic constraints make it more likely that when a genus is listed under two types, the combination will be stingy mothers and incomplete suppressors (e.g., *Varecia variegata* and *Alouatta pigra*) or generous mothers and facilitators (e.g., *Pongo*). Additional references not in text: *Avahi*: Thalmann 2001; *Cheirogaleus*: Fietz 1999; *Eulemur*: Overdorff 1996; *Hapalemur*: Nievergelt et al. 1998, Mutachler et al. 2000; *Lepilemur*: Thalmann 2001; *Tarsius*: Gurin 2000; *Microcebus*: Fietz 1999; *Mandrillus*, *Theropithecus*: Stambach 1987; Isbell & Van Vuren 1996; *Brachyteles*: Printes & Strier 1999; *Colobus*: Fashing 2001; *Nasalis*, *Pygathrix*, *Simias*: Yeager & Kool 2000.

^bGenera are listed in most cases, unless variation has been observed at lower taxonomic levels.

^c*Pan* and *Pongo* have question marks because there is evidence that different types may be represented at the same time by different individuals in the same population.

chimpanzees might be considered generous mothers since they most often forage alone in overlapping home ranges (Williams et al. 2002). Some individuals might, however, be considered stingy mothers because about half of all natal females disperse socially and locationally (Williams et al. 2002). Yet others might be considered facilitators because daughters that do not permanently leave their natal communities return to settle in their mothers' home ranges if their mothers are still alive. In such cases, mothers and daughters also travel together in their shared home ranges (Williams et al. 2002). They can probably all be safely ruled out as incomplete suppressors because they do not travel in cohesive multifemale groups. They can also all be ruled out as indifferent mothers because female reproductive

success is positively correlated with high rank (Pusey et al. 1997), and indifferent mothers cannot be ranked. The variability of types of mothers within a single population of chimpanzees may exist partly because female chimpanzees are, unusually for primates, influenced not only by food competition but also by male aggression and the ranging behavior of sons (Williams et al. 2002). Male chimpanzees sometimes employ violent coercion of females that affects their ranging behavior (Wrangham 1979, Smuts & Smuts 1993), and mothers sometimes follow their growing sons as the sons become more involved with adult males (Williams et al. 2002).

Pongo is another genus that may be difficult to classify. Female orangutans might be considered generous mothers because females typically forage alone in overlapping home ranges (Rodman & Mitani 1987, Rodman 1988a, Singleton & van Schaik 2001). The observation of adult females occasionally traveling together (Rodman & Mitani 1987) suggests, however, that individual variation in ranging behavior may also exist in orangutans. Male harassment also occurs in orangutans (Rodman & Mitani 1987, Smuts & Smuts 1993) and affects the ranging behavior of females (Fox 2002). Perhaps male harassment contributes more to patterns of association among female orangutans than is currently recognized.

Some genera have been placed in two different types not because individual females in the same population range differently but because different types can be expressed in (1) different species within the same genus, (2) different populations within the same species, and even (3) the same group during different seasons. For example, female black howlers (*Alouatta pigra*) that live at high densities appear to be incomplete suppressors. At low densities, and when whole groups have been translocated to suitable but unpopulated habitats, females become stingy by sorting themselves into one per home range (Ostro et al. 1999, 2001). Female ruffed lemurs (*Varecia variegata*) change from stingy mothers to incomplete suppressors when they change their ranging patterns in different seasons (Moriand 1991, Rigamonti 1993).

Ecological Underpinnings of the Five Types of Mothers

Are Stingy Mothers Highly Goal-Directed Travelers?

Why stingy mothers do not take advantage of openings to expand their home ranges is an unexplored research question. One possibility is that they face energetic constraints that the other types of mothers do not face. If this is the case, the constraint does not appear to come from reliance on any particular diet. Stingy mothers include primates typically classified as frugivores (e.g., gibbons), insectivores (western tarsiers), gummivores (marmosets and pygmy marmosets), and folivores (indris and bamboo lemurs). The constraint may rather come from having a great need to minimize either time or energy in travel. In some cases, this need could arise from having a small body that requires small and frequent feedings, which appears to be the case for very small mammals, such as rodents and shrews (Zydel & Wunder 2002). Though the limited sample on basal metabolic rates for primates calls for caution, stingy mothers appear to have among the lowest basal metabolic rates for their body sizes (35–95% of the expected value; Genoud et al. 1997, Power et al. 2003). Basal metabolic rates measure the energy needed for minimal bodily maintenance, and the low basal metabolic rates that are found in stingy mothers are generally considered to be adapta-

tions for conserving energy under conditions of severe environmental stress (Jolly 1984, Müller 1985, Richard 1987, Wright 1999). Some stingy primates have specialized adaptations for locomotion compared to their closest nonstingy relatives (e.g., extreme brachiation in gibbons but not orangutans). I suggest that along with their severe energetic constraint comes a distinctive traveling style that affects the ability of mothers to expand their home ranges (figure 4.3).

Stingy mothers are often described as highly goal directed in their movements, that is, traveling directly from one food site to the next without foraging between sites (e.g., *Phaner*, *Indri*, *Callicebus*, *Saguinus*, and *Hylobates*; Rodman 1988b, Garber 1989, Wright 1994, Kappeler 2000, Garber & Bicca-Marques 2002, Schülke in press). Some of these (e.g., *Callicebus*, *Phaner*, and *Ayahi*) can even be considered trapliners (Wright 1994, Thalmann 2001, Schülke in press), which involves making repeated visits over several hours or days to sequential food sites (Garber 2000, Milton 2000). When an individual is highly goal directed, it acts as if it knows where it is going and that the food will be there. Highly goal-directed animals give the impression that they are minimizing the time or the energetic expense of travel between food sites. Movements between distant food sites are direct and efficient.

Their normal efficiency can be seen by observing individuals that do move to new surroundings or that are faced with a familiar area that has been experimentally altered. A female indri that had apparently recently established herself in a new area traveled two to three times farther to go the same horizontal distance as a female that was familiar with her home range (Pollock 1979). Experimental removal of a food tree resulted in apparent confusion in fork-marked lemurs (*Phaner furcifer*) that had traveled quickly to it (Petter et al. 1975). Golden lion tamarins (*Leontopithecus rosalia*) that had been experimentally introduced to a new area became more efficient at getting to food sites over time (Menzel & Beck 2000). Pottos took 5 to 10 days to find a new food site in their home ranges, while galagos (*Galago alleni* and *Galagoides demidovii*), which share their home ranges with other females, took only 3 to 5 days (Charles-Dominique 1977). The difference between pottos and galagos is not likely to be because pottos are slower and thus cannot cover their home ranges as quickly as galagos; indeed, unlike galagos, they seem to have no difficulty excluding others from their home ranges, a feat that appears to require a certain degree of mobility and the ability to monitor daily (or nightly in the case of pottos) their home range boundaries (Mitani & Rodman 1979). The gibbon's specialization for brachiation has been suggested as a more energetically efficient way to move in an arboreal environment than walking because it allows direct travel (Parsons & Taylor 1977).

Stingy mothers may not expand their home ranges even if given the opportunity because going into new areas requires exploring for food with uncertain success. The "downtime" that is an integral aspect of exploration may decrease foraging efficiency beyond that which highly goal-directed primates can tolerate. Stingy mothers may also be unable to share their home ranges with their daughters because additional females could reduce the predictability of food locations (if they do not feed in groups, see below). Consider the energetic cost for females relying on predictably located foods if they were to travel directly and repeatedly to those food sites after others have already reached and depleted them. Stingy mothers may simply be unable to allow their adult daughters to remain and reproduce in a shared home range without suffering a cost to their own reproductive success (figure 4.3). Finally, even if mothers could expand their home ranges to enable their daughters to reproduce in the

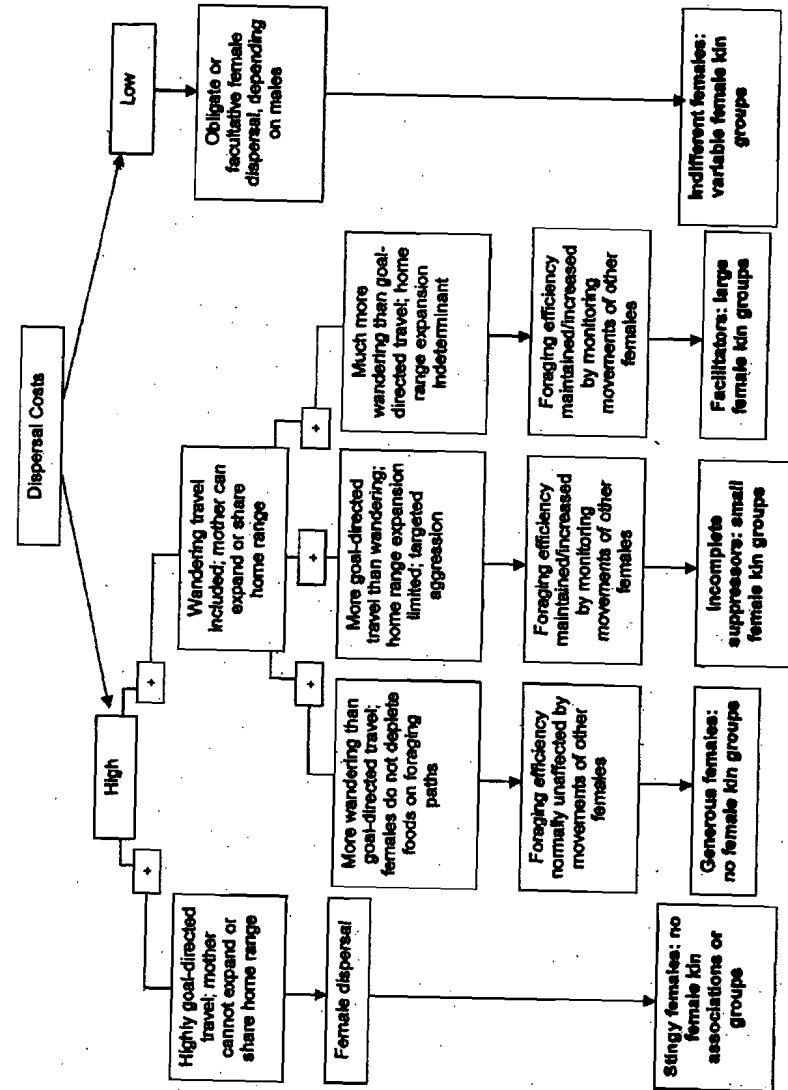


Figure 4.3. A schematic representation of the factors leading to female kin groups according to the dispersal/foraging efficiency model presented in this chapter.

natal home range, such expansion might increase the risk of infiltration by additional, unrelated females, further reducing the predictability of food locations.

It may be informative that stingy mothers also occur among nonprimate mammals that live close to the energetic edge of death. Female voles (*Microtus*), elephant shrews (*Elephantulus*), and tree shrews (*Tupaia*) are stingy: mothers often maintain nonoverlapping home ranges or, if they share their home ranges with other females, only one female typically breeds (Jannett 1978, Rathbun 1979, Getz et al. 1993, Emmons 2000). When nest sharing does occur between reproductive female voles, it usually occurs under high densities coupled with high resource availability (e.g., prairie voles [*Microtus ochrogaster*]; Getz et al. 1993, Cochran & Solomon 2000] when it may be difficult for offspring to find their own home ranges and less costly for mothers to allow others to reproduce in the home range. When densities are low, mothers often abandon their home ranges rather than share them with maturing daughters (e.g., *M. montanus*; Jannett 1978). There is also substantial evidence that offspring of female voles are reproductively suppressed (Wasser & Barash 1983, Solomon & French 1997, but see Wolff et al. 2001). Though use of the same nests repeatedly in some of these species suggests that individuals are goal directed in their travel, the extent to which females are goal directed between food sites remains to be determined. Tree shrews, which are perhaps more closely related to primates than to other taxa (Fleagle 1999) typically eat fruit and slow-moving, hidden arthropods. Emmons (2000) provides evidence that the fruit component of their diet is critical to their survival and reproduction. When they feed on fruit, they do travel in a highly goal-directed manner.

Do Generous Mothers Wander More Than Stingy Mothers?

How might generous mothers differ from stingy mothers to allow them to expand their home ranges so that their daughters can reproduce while remaining philopatric? I suggest that generous mothers are less energetically constrained than stingy mothers. Again, although the data are sparse, generous mothers appear to have somewhat higher basal metabolic rates (84–114% of expected) than stingy mothers (Genoud et al. 1997). The relaxation of energetic constraints may afford them the opportunity to be less goal directed and more exploratory in their ranging behavior (figure 4.3). Exploratory movements involve some degree of wandering as animals forage for food. Compared to goal-directed travel, wandering involves slower travel speeds, more frequent short-term changes in direction, more stops to search for food, and less success at finding food at each stop. In the jargon of feeding ecology, animals that “forage” (as opposed to “feed”) engage in wandering as a mode of travel. Unlike goal-directed travel, which takes individuals quickly and directly to a productive food site, wandering can take individuals to places that are unproductive. Home range expansion may be possible for individuals that wander more than they engage in goal-directed travel because both wandering and home range expansion involve going into areas where productivity is uncertain.

The diet of most generous mothers appears to assist their wandering. Galagos move quickly and pursue fast-moving arthropods (Bearder 1987). Unlike plants and slow-moving arthropods, highly mobile arthropods have the ability to move quickly out of the reach of their predators. Predators of mobile prey must be able to follow their prey. By pursuing mobile arthropods, generous mothers are likely to find themselves in areas of unknown productivity.

An interesting consequence of classifying mothers by whether they share home ranges with other reproductive females is that differences in male ranging behavior become more obvious. It has always been puzzling why males of some primate species range almost entirely within a given female's home range (regardless of whether the male and female travel separately or together), when they would theoretically do better reproductively if they were to range over partial home ranges of multiple females. The latter strategy need not include an increase in their own home ranges. It is worth noting that male ranging behavior seems to be fairly well predicted by whether mothers are stingy or generous. This holds for mammals as diverse as rodents, shrews, and primates. In species with stingy mothers, the home range of a given male is almost always shared with only one reproductive female (e.g., elephant shrews, Rathbun 1979; prairie voles, Carter & Getz 1993; gibbons, Leighton 1987). By contrast, in species with generous mothers, the home range of a given male usually overlaps those of multiple females (e.g., meadow voles [*Microtus pennsylvanicus*], Madison 1980, Boonstra et al. 1993, Bowers et al. 1996; galagos, Bearder 1987). It is possible that the energetic constraints that are suggested to operate on stingy mothers also operate on male conspecifics, with similar results. Although this possibility deserves attention, further discussion is beyond the scope of this chapter.

Are Incomplete Suppressors Goal-Directed Wanderers?

How might incomplete suppressors differ from stingy and generous mothers in their movements? The interchangeability of females between stingy mothers and incomplete suppressors at a level as small as that of the group suggests that the major difference between incomplete suppressors and stingy mothers is more ecological than physiological. If this is the case, basal metabolic rates of incomplete suppressors should be similar to those of stingy mothers and different from those of generous mothers. Basal metabolic rates are available for only two incomplete suppressors (35% and 55% of expected), and it is dangerous to draw conclusions on such a small sample size. Nonetheless, since most incomplete suppressors are Malagasy prosimians, and all Malagasy prosimians that have been studied have lower basal metabolic rates than expected (Jolly 1984, Richard 1987, Genoud et al. 1997, Wright 1999), it is possible that more data will support the prediction that incomplete suppressors are more similar to stingy mothers than to generous mothers.

If incomplete suppressors are more energetically limited than generous mothers, they may be more constrained to minimize energy spent in travel. Incomplete suppressors may be able to wander more than stingy mothers but may travel in a goal-directed manner more than generous mothers (figure 4.3). More extensive wandering may enable mothers to share home ranges with their reproductive daughters, while their goal-directed travel may make it difficult for mothers to expand their home ranges indeterminately as additional daughters are born. A high degree of goal-directed travel should also result in little home range overlap with other groups as females attempt to maintain the predictability of their food locations.

Goal-directed travel has been reported for species considered here to be incomplete suppressors. Mantled howlers (*Alouatta palliata*), for example, often move directly to preferred food sites within their home ranges (Milton 1980, 2000). Ring-tailed lemurs (*Lemur catta*) have also been reported to move directly to specific food sites, at times going outside their normal home range to do so (Jolly & Pride 1999). The wandering component may be under-

reported in these species because goal-directed travel is more impressive and is often interpreted as an indication of advanced cognitive ability. Nonetheless, ring-tailed lemurs can forage in a broad front as they move (Klopfer & Jolly 1970), which suggests a kind of wandering. Groups of ruffed lemurs move more extensively over their home range during the seasons when they live together as cohesive groups and are incomplete suppressors, but restrict their movements to subranges within their group's home range when they split up into single-female units and become stingy (Morland 1991, Rigamonti 1993). The switch from incomplete suppressor to stingy is predicted to be accompanied by an increase in the percentage of goal-directed travel. The relative contributions of wandering and goal-directed travel should become clearer in the future when more studies of the micromovements of individuals are conducted.

Are Facilitators Predominantly Wanderers?

Facilitators may differ from the other mothers in being the least energetically restricted of the primates; they have the highest basal metabolic rates among the primates (114–142% of expected; Genoud et al. 1997). A lesser need to conserve energy may mean that facilitators are better able than stingy females and incomplete suppressors to spend time actively searching for food when it becomes scarce. Whereas stingy mothers (e.g., fat-tailed dwarf lemurs [*Cheirogaleus medius*] and incomplete suppressors (e.g., Verreaux's sifakas [*Propithecus verreauxi*]) may increase their resting time when food becomes less abundant (Richard 1978, 1987), facilitators (e.g., brown capuchins [*Cebus apella*]), tend to increase their time spent foraging and feeding (Terborgh 1983). Facilitators may thus be able to wander much more than the other types of mothers (figure 4.3). They may also travel in a goal-directed manner (Janson 1998, Pochron 2001), albeit to a lesser extent than the other types of mothers. A large wandering component should allow mothers to expand their home ranges so that their daughters can reproduce in the natal home range without reducing mothers' foraging efficiency and future reproductive success. Indeed, there seems to be no limit to the size of the home range; home range size typically expands with increasing group size in yellow baboons, macaques, and guenons (Isbell 1991), all of which are considered to be facilitators.

Patas monkeys provide an extreme example of the ranging behavior of facilitators. Patas have extraordinarily large home ranges, which increase as group sizes increase (Chism & Rowell 1988). They have also been described as "feeding at a steady walk" (Hall 1965), and their long stride has been interpreted as an adaptation for efficient foraging over long distances (Chism & Rowell 1988, Isbell, Pruetz, Lewis et al. 1998). Patas typically travel circuitously except when they travel to water during the dry season (Hall 1965, Isbell et al. 1999). Their locations during the day are difficult to anticipate. Indeed, of all the species that I have followed, I have found it most difficult to predict the general location of patas groups later in the day. With one possible exception (vervets), these other species (i.e., red colobus, sifakas, brown lemurs [*Eulemur fulvus*], and ring-tailed lemurs) are not facilitators.

Data from brown capuchins provide another example of facilitators' greater emphasis on wandering. At Iguazu National Park, Argentina, they spent 47% of their time in "slow foraging" (equivalent to wandering) and 6% in "fast travel" (equivalent to goal-directed

travel). Although both modes of travel occurred while the animals moved between feeding platforms (Janson & Di Bitetti 1997, C. H. Janson personal communication), wandering involved many short-term changes in direction, presumably as a result of searching for and foraging on insects, whereas goal-directed travel involved direct, nonstop movement to feeding platforms (Janson & Di Bitetti 1997, Janson 1998).

Intriguingly, if basal metabolic rates are a measure of the degree to which primates are energetically constrained, humans and chimpanzees are well within the range for facilitators (basal metabolic rates of 128% and 141% of expected, respectively; Genoud et al. 1997).

Are Indifferent Mothers Not Limited by Food Abundance?

Colobines and mountain gorillas are fairly folivorous, with slow gut passage times that require the animals to rest while digesting their food (Bauchop 1978, Parra 1978, Kay & Davies 1994, Kirkpatrick et al. 2001). Slow digestive rates raise the possibility that most folivores may be more constrained by digestion time than by food abundance (see also Zynel & Wunder 2002 for herbivorous voles). In other words, they may run out of time in a day before they run out of food to eat. If this is the case, the presence of other females should make little difference in their ability to obtain food. When female reproductive success is limited more by digestion than by food abundance, females should either be indifferent to the presence of other females or avoid competing with them over food, particularly if it interferes with digestion.

Although a positive correlation exists between colobine biomass and leaf protein-fiber ratios (Davies 1994, Chapman et al. 2002), the correlation does not necessarily mean that food limits female reproductive success in colobine populations. If the correlation exists as a result of recruitment of infants, then food may indeed limit both female reproductive success and the size of populations. On the other hand, if the correlation exists as a result of movement of individuals to areas with high densities of food, then different factors might limit female reproductive success and populations. Consider animals that are highly mobile, such as many of the larger ungulates. Aggregation of individuals in areas of high food density could produce a positive correlation between food density and numbers of animals without any increase in infants. The same might be said for female colobines because they are less constrained to remain in a particular group than many other female primates. Without knowing details about individuals within populations, that is, their movements and their reproductive success, a correlation between food density and population size cannot be used to infer that food abundance limits reproductive success of females in those populations.

Though all females need sufficient food to give birth, having enough food is not always sufficient for keeping infants alive. This may be most obvious when female reproductive success is limited more by digestion time (or food quality) than food abundance. Under such conditions, other factors, such as infanticide, could replace food abundance as ultimately limiting female reproductive success (see Wolff 1993 for a similar argument for rodents), but these factors would remain hidden if they mirror the density dependence of food limitation. Indeed, in Thomas's langurs, infanticide is more frequent in larger groups than in smaller groups (Steenbeek 2000). More explicitly, in mountain gorillas, infanticide accounts for at least 37% of deaths of animals to age 3 (Watts 1989, see also Fossey 1984). If the frequency of predation were that high, we might have little hesitation in suggesting

that predation limits the Virunga gorilla population. Unlike facilitator females, the relative fitness of many indifferent mothers may be determined less by food than by differential ability to anticipate and respond appropriately to the risk of infanticide (figure 4.3). If so, infanticide should be a strong factor in female dispersal decisions in these species. Infanticide has, in fact, been suggested as the cause of female dispersal and small female group sizes in Thomas's langurs (Steenbeek & van Schaik 2001).

Among species in which gut passage times are not slow, female reproductive success is more likely to be limited by food abundance, and infanticide is probably less important than the mother's nutritional condition in contributing to infant mortality. For example, female patas monkeys are facilitators whose ranging behavior appears to be more finely tuned to food abundance than to other factors (Isbell & Enstam 2002). Infanticide was implicated in the death of only 1 of 85 (1.2%) infant patas monkeys over a 10-year period (Enstam et al. 2002, Isbell unpublished data).

Species in which female reproductive success is limited by non-food-related factors other than infanticide are also expected to have indifferent mothers. Squirrel monkeys (*Saimiri oerstedii*) in Corcovado, Costa Rica, and red colobus in Kibale, Uganda, and Gombe, Tanzania, may be examples of indifferent mothers whose reproductive success is limited more by predation than by food. In these species, home ranges overlap extensively, females commonly disperse, and there appears to be little competition for food either within or between groups (Struhsaker 1975, Boinski 1999), all of which are characteristics of indifferent mothers. In contrast, the risk of predation appears to be very high (Stanford 1995, Boinski 1999). Many of the behaviors of female squirrel monkeys, for example, highly synchronized births within groups, spatial associations of multiple mothers and infants, and coordinated group movements, have been interpreted as adaptations for reducing predation (Boinski 1987, 1999; Boinski et al. 2000).

The classification of Corcovado squirrel monkeys as indifferent mothers is, at first glance, questionable because they are more frugivorous than folivorous and have a congener (*S. boliviensis* at Manu, Peru) with facilitator females (Boinski 1999). Nonetheless, interbirth intervals half as long at Corcovado (one year) as at Manu (two years), despite a richer food supply at Manu (Boinski 1999, Boinski et al. 2002), suggest that different factors may indeed limit female reproductive success in these congeners. Unlike many other species with indifferent mothers, the Corcovado females appear to be limited more by predation than infanticide. Although infanticide can shorten interbirth intervals (Hrdy 1974), there have been no cases of infanticide at Corcovado (Boinski 1999) to explain their short interbirth intervals. In contrast, their high infant mortality (50% within the first six months of age) has been attributed mainly to predation (Boinski 2000).

The ecological conditions faced by females whose reproductive success is limited by something other than food abundance may make female social dispersal no more costly than philopatry (see Watts 2000 for gorillas) and perhaps more beneficial than costly. Since for indifferent females food is not as crucial as, for example, avoiding infanticide or predation, their dispersal decisions are not expected to be based on maintaining foraging efficiency (figure 4.3). Their dispersal decisions are instead expected to be determined by their ability to keep their offspring alive, staying if they succeed and leaving if they fail. Thus, although juvenile female dispersal is the norm in Corcovado squirrel monkeys, adult females also transfer between groups if their infants die (Boinski et al. 2002).

Consequences of Foraging Efficiency and Costs of Dispersal on the Formation of Female Kin Groups

The costs of dispersal may have favored the willingness of mothers to allow daughters to remain in the natal home range, the probable first step in the evolution of kin groups (Pusey & Packer 1987b, Isbell & Van Vuren 1996). If mothers could expand their home ranges without sacrificing foraging efficiency and their future reproduction, daughters would be able to stay and reproduce in the natal home range. This problem might have been solved initially by mothers acquiring larger home ranges than were required for their own maintenance and reproduction. If they could not do this, female kin groups would likely not have evolved.

Once females began to share home ranges, there would have been three alternatives available to females whose reproductive success was limited by food abundance. The alternative taken would have depended on the relative contributions of wandering and goal-directed travel, and on the mobility of the food. Two alternatives involve group living, and they differ from each other in the size that the group can become. The third alternative does not involve group living. With this alternative, females can share a common area while foraging alone. Thus, philopatry is not equivalent to feeding and traveling together in a cohesive group.

I suggest that kin groups become beneficial only when it is important to avoid feeding in places recently visited by others that share the same home range. If females must minimize foraging in areas already covered by others in order to maintain their foraging efficiency, females that feed on relatively immobile food may need to monitor the movements of their relatives in some way. Multiple senses are available for monitoring the whereabouts of others. Since primates generally are visually oriented animals, monitoring may be best done visually. Visual monitoring requires fairly close proximity. Primates that appear to be less visually oriented (e.g., the nocturnal and some of the cathemeral species), might also monitor the movements of others in the shared home range through vocal or olfactory cues. Only visual monitoring would require females to remain near each other while moving; however. Thus, the second step in the evolution of kin groups might have involved visually coordinated traveling and feeding together to enable females to avoid places already harvested by others (Cody 1971, Altmann 1974, Rodman 1988b). At this stage, they would be recognizable as groups (figure 4.3). Species differences in the modal size of groups would be determined by the extent to which home ranges could be expanded (and for incomplete suppressors and facilitators, also daily travel costs; Wrangham et al. 1993, Janson & Goldsmith 1995), which would depend to a large degree on the extent of wandering in the travel/feeding repertoire. Aggressive interactions with larger neighboring groups might also contribute to restricting home range expansion.

In some species, for example galagoes, females would not need to monitor the movements of their relatives to maintain their foraging efficiency because their food is highly mobile. Flying and hopping arthropods, which can move in and out of the paths of foraging females fairly easily, may render monitoring the movements of others in a shared home range unnecessary and perhaps even detrimental, unless the movements of others help to flush up arthropods. But unless monitoring the movements of others at least maintains foraging efficiency for mothers, mothers are not likely to sacrifice attention to their surroundings to live with

others. Such an explanation would be consistent with the absence of group foraging in female galagos even though they share their home ranges with other females (figure 4.3). Galagos often double back on their path during the night's foraging (Charles-Dominique 1977). It can be argued that if a female is willing to forage again along her previous foraging path, she does not perceive a decline in her foraging efficiency. The mobility of their food may enable female galagos to double back without reducing their foraging efficiency. By the same reasoning, foraging efficiency may not be reduced if a female were to forage in areas that have already been visited by another female. Such females would not need to live in groups although they benefit from remaining in a familiar area.

Contrary to the assumption that group living always involves a cost, the dispersal/foraging efficiency model suggests that when there is a reproductive cost to females of having others around, even kin, they do not share the home range with reproductive daughters. Home range sharing only occurs when females do not actually incur reproductive costs. When mothers allow reproductive daughters to share their home ranges, neither mothers nor daughters need incur automatic costs, because the home range will be large enough for them and their offspring. Group living becomes merely an efficient way for visually oriented primates that feed on immobile foods to share their home ranges with other individuals.

In this model, groups evolve through a series of small and incremental steps in which the predominant selection pressure is the maintenance of foraging efficiency. Kin selection is involved only to the extent that a mother tolerates or facilitates reproduction by her offspring in her home range. Intergroup competition, one of the two alternatives that have been invoked in the past as selection pressures favoring the evolution of kin groups (Wrangham 1980), is not a necessary component in the evolution of kin groups according to the dispersal/foraging efficiency model, although it might have been a relatively small step for groups that already travel and feed together to begin cooperating in keeping other groups from exploiting the foods in their home range. Success in intergroup competition is viewed by the dispersal/foraging efficiency model as an additional benefit of living in kin groups, not the primary benefit (Isbell & Van Vuren 1996). Interestingly, within the Cercopithecoidea and Ceboidea, the species with female philopatry have larger home ranges per individual than species with frequent female dispersal (see Milton & May 1976). Perhaps once facilitator females formed kin groups, they became even more acquisitive, an act that reinforces intergroup competition.

Intragroup competition and predation, the other proposed selective pressures (van Schaik 1989, Sterck et al. 1997), also have little influence on the evolution of female kin groups in this model. Intragroup competition is, instead, largely a function of the depletion time of foods. If foods are depleted slowly, they can be usurped and females will interact agonistically, even to the extent of forming coalitions, if doing so helps females usurp the foods (Isbell & Pruett 1998, Isbell, Pruett, & Young 1998, Mathy & Isbell 2002). Of course, when coalitions form to help individuals usurp food from others, they will most often form with kin to reap the benefits of inclusive fitness.

The evidence that locational dispersal increases the risk of predation relative to philopatry suggests that predation was a strong selective pressure on mothers to allow daughters to remain in the natal home range. However, although predation may have helped to set the stage for the evolution of kin groups, according to the dispersal/foraging efficiency model, no amount of predation would favor home range sharing with reproductive daughters if mothers' foraging efficiency were compromised. In this model, if foraging efficiency cannot

be maintained, kin grouping does not occur. Kin grouping occurs when there are no reproductive costs, that is, when foraging efficiency can be maintained to enable females to reproduce. Reproductive costs become apparent only after kin groups become very large and energy intake cannot keep up with the energetic cost of increasing daily travel distances. The maintenance of foraging efficiency is sufficient to explain the evolution of kin groups, and predation need not be invoked. Indeed, evidence that polyspecific groups reduce the risk of predation for group members, which are clearly not related (e.g., Noë & Bshary 1997), provides perhaps the most convincing evidence that kin groups are not required for animals to reduce their risk of predation.

Benefits of Dispersal, or Why Dispersal Is Often Sex Biased

I have focused on the costs of dispersal to explain the tendency of females to remain philopatric. Now I discuss the benefits of dispersal, because in some species females commonly or occasionally disperse, and in the long run there must be an advantage to female dispersal that outweighs its costs for such species. Some of these benefits appear to be created by males. To fully understand female decisions to disperse or remain philopatric, it is necessary to discuss male dispersal, particularly for those species in which female reproductive success does not appear to be limited by food abundance.

The benefits of dispersal are intensely debated with no real consensus yet, but the disagreement centers on inbreeding avoidance (Pusey & Packer 1987a, Clutton-Brock 1989, Pusey & Wolf 1996) and increased opportunities for breeding (Moore & Ali 1984; Moore 1988, 1992). These hypotheses are largely designed to explain sex-biased dispersal, but particularly male dispersal, because male dispersal with female philopatry has usually been considered the norm among mammals in general and primates in particular (Clutton-Brock & Harvey 1976, Greenwood 1980, Wrangham 1980, Pusey & Packer 1987a, Clutton-Brock 1989). I argue here that both advantages accrue, one for females and the other for males.

The adaptationist approach assumes that dispersal had to have a net benefit in order to evolve, but this does not mean that all individuals will always gain. Dispersers take their chances, and some succeed whereas others do not. For example, sightings of leopards or their signs are punctuated by long periods of no sightings and no disappearances of vervets and patas monkeys in Laikipia, Kenya (Isbell unpublished data), which suggests that leopards are not always a danger to them (see also Isbell 1990). If leopards had not been present and actively hunting monkeys when vervets in Amboseli dispersed to new areas, the dispersers might not have suffered higher mortality despite their ignorance of the new home ranges (Isbell et al. 1990). Anderson (1987) suggested that female dispersal in chacma baboons (*P. ursinus*) at Suikerbosrand was common because leopards had not been present in the area for over 50 years. The outcome of individuals' decisions to disperse clearly depends on the local social and ecological milieu (Emlen 1984, Van Vuren & Armitage 1994, Isbell & Van Vuren 1996).

If mothers cannot increase the size of their home ranges to accommodate their daughters, their daughters will leave their natal home ranges despite the costs of dispersal if their chances of reproducing elsewhere are greater. Because inbreeding is more costly to females than to males (Clutton-Brock & Harvey 1976), selection should favor females that minimize incestuous matings (e.g., Packer 1979). Males disperse because limited mating opportunities in their natal groups or home ranges create greater mating opportunities in other groups or

home ranges, all else being equal. Male dispersal may thus be driven not by their own avoidance of inbreeding but by reduced mating opportunities in the natal group or home range. In rare cases, males may remain when females disperse and the costs of social dispersal are so high that dispersing males have no chance of increasing their matings elsewhere. Chimpanzees may exemplify this situation.

If females are able to reproduce while remaining in their natal groups or home ranges, males then typically leave. In several species with male-biased dispersal, for example, olive baboons (*P. anubis*), yellow baboons, chacma baboons, gray-cheeked mangabeys (*Lophocebus albigena*), and Tibetan macaques (*Macaca thibetana*), males disperse to groups having more estrous females or more females than their current groups (Packer 1979, Zhao 1994, Alberts & Altmann 1995, Henzi et al. 1998, Olupot & Waser 2001). Though this does not necessarily mean more actual matings, evidence from baboons suggests that socially dispersing males do have greater mating success than philopatric males (Packer 1979, Alberts & Altmann 1995). In other species with male-biased social dispersal, for example, vervets, long-tailed macaques (*Macaca fascicularis*), and hanuman langurs, males do not disperse to groups with more females or more females in estrus (Henzi & Lucas 1980, Cheney & Seyfarth 1983, van Noordwijk & van Schaik 1985, Borries 2000). Whether this still holds when female relatives are excluded has not been considered, however. Since female relatives are largely unavailable for mating, discounting those females may well reveal that males in these species actually do disperse to groups with greater numbers of available females.

When females suffer no costs of dispersal that are sufficient to affect reproductive success (as appears to be the case for indifferent mothers), dispersal patterns are expected to be variable, and dependent upon the conditions facing individual females. Males can then influence female dispersal decisions. Males may respond by remaining philopatric unless they recognize better mating opportunities elsewhere, in which case they may also disperse. It is worth considering that the tendency for males to remain philopatric in large groups (e.g., Kibale red colobus and Costa Rican squirrel monkeys) occurs partly because they become less able to count or compare their relative breeding opportunities as numbers of females in groups increase (Hauser et al. 1996, Brannon & Terrace 1998, Wilson et al. 2001). If males remain, females will be forced to disperse socially because inbreeding depression is more costly to females than to males (Clutton-Brock & Harvey 1976).

In small to mid-sized multifemale groups in which females experience no significant costs of dispersal, only one male typically mates even if more than one remains. When most males disperse, females have more options. Some females leave their groups while others remain; hence the lower frequency of female compared to male social dispersal in single male, multifemale species with indifferent mothers. Such females should leave their groups if doing so enables them to avoid incestuous matings or infanticidal males, or to return to familiar areas (e.g., gorillas, Tana River red colobus, Thomas's langurs, and olive colobus), or when reproduction has failed for other reasons that are also unrelated to competition for food (Ibell & Van Vuren 1996, Steenbeek 2000; reviewed in Sterck & Korstjens 2000).

Testing the Dispersal/Foraging Model

The opportunity to reproduce while remaining philopatric could arise when mothers are able to accommodate their daughters by expanding their home ranges while still maintaining

their foraging efficiency. Whether mothers could do this would depend on the relative importance of goal-directed travel and wandering, with a larger proportion of wandering enabling mothers to enlarge their home ranges without sacrificing foraging efficiency. Kin groups could occur if maintenance of mothers' foraging efficiency also requires visual monitoring of daughters' movements.

The data presented here support the dispersal/foraging efficiency model, but they were not collected specifically to test the model. More direct tests of the model could be developed by collecting comparative data on the percentage of time spent wandering and in goal-directed travel. With its distinction between slow foraging and fast travel, the work of Janson and Di Bitetti (1997) on brown capuchins shows nicely that the data can be collected. Other measures of the micromovements of individuals might also be incorporated into tests of the model. For instance, a higher percentage of unsuccessful stops for food indicates that wandering is more prevalent than goal-directed travel, whereas a higher percentage of successful stops indicates that goal-directed travel is more prevalent than wandering. Stingy mothers are predicted, therefore, to have the highest percentage of successful stops for food, followed by incomplete suppressors, generous mothers, and finally facilitators (figure 4.3). Obviously, we will not gain a full sense of the biological meaning of the data until comparative data from each of these types of mothers are available. Except for stingy mothers and incomplete suppressors (whose basal metabolic rates may be similar), basal metabolic rates are expected to mirror this order, once the effects of body size, and perhaps phylogeny, are removed. Though indifferent mothers cannot be directly compared with the other four types (since their reproductive success is not as dependent on food abundance), they can still contribute to tests of the model if they can be studied sufficiently long and intensively to determine what does limit their reproductive success. As the data trickle in, the weaknesses of this model will undoubtedly become more apparent and a more accurate model will replace it. I look forward to that day.

A Storybook Ending Either Way (as Long as She Reproduces)

Had L. Frank Baum known what we know now about female primates, he might have developed another, equally happy ending for Dorothy. Consider the alternative: if Dorothy had found a mate in Oz, she might have been content to remain. Sometimes for female primates, "somewhere over the rainbow" holds the promise of reproductive success, but when reproductive success is more likely in their natal home ranges, females will respond as if "there's no place like home" whether they live in Madagascar, the neotropics, Africa/Asia, or Kansas. The opportunity and ability to reproduce in the natal home range may have been prerequisites for the formation of kin groups.

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