DIFFERENTIAL COSTS OF LOCATIONAL AND SOCIAL DISPERSAL AND THEIR CONSEQUENCES FOR FEMALE GROUP-LIVING PRIMATES

by

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Summary

Individuals that disperse may leave familiar conspecifics (social dispersal), a familiar home range (locational dispersal), or both. Social and locational dispersal are not necessarily coincident in group-living animals. Here we differentiate among some potential costs of both social and locational dispersal in group-living mammals, including aggression from strangers and unfamiliarity with new habitats. As an example of the utility of distinguishing between social and locational dispersal, we examine patterns of female transfer in Old and New World anthropoid primates. The results suggest that in Old World primates, female transfer is more likely to be frequent in populations without female aggression between groups. In anthropoid primates, female transfer is more likely to be frequent in populations in which home ranges of groups overlap extensively with those of other groups. Female

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transfer between groups in Old World, but not New World, primates appears to be more common when females suffer few or no costs of social and locational dispersal. We suggest that when there are few, if any, costs of social and locational dispersal (inferred from moderate to extensive home range overlap and the absence of aggression between groups of females), female transfer in Old World anthropoids will be obligate when groups of females cannot be monopolized by a single male and conditional upon the behavior of individual males when groups of females can be monopolized by a single male. When costs of social and locational dispersal exist (inferred from minimal home range overlap and aggression between groups of females), female transfer will be conditional upon competition with other females in their groups.

Introduction

Research on dispersal in mammals initially focused on dispersal as a behavior of solitary individuals, *i.e.* individuals travelling and foraging without other adults (*e.g.* Howard, 1960; Lidicker, 1975; Shields, 1982; Anderson, 1989). Among solitary animals, dispersal often involves leaving both familiar conspecifics (minimally, the mother) and familiar areas (minimally, the natal home range) (Waser & Jones, 1983). For solitary dispersers a new social environment is usually (though not always) associated with moving into a new location. With the emergence of behavioral ecology as a discipline, greater interest has developed in dispersal of group-living animals, including the social context of dispersal. Discussions of dispersal in group-living mammals have implied or stated specifically that dispersal can include either movement away from a familiar area *or* movement away from relatives or other familiar conspecifics (*e.g.* Greenwood, 1980; Pusey & Packer, 1987a; Clutton-Brock, 1989). These two kinds of dispersal are usually coincident in territorial populations of group-living species. They are not necessarily coincident, however, in non-territorial populations of group-living species. When the home ranges of different groups overlap, it is possible for dispersing animals to move into a new social environment while remaining in a familiar area (*e.g.* some female gorillas (*Gorilla gorilla*): Harcourt, 1978; some female chimpanzees (*Pan troglodytes*): Nishida, 1989). Similarly, entire groups of animals may leave a familiar area while remaining in a familiar social environment. For example, groups of vervet monkeys (*Cercopithecus aethiops*) moved into unfamiliar areas when they shifted their home ranges away from deteriorating habitats or other groups (Isbell *et al.*, 1990).

Dispersal from a familiar social environment and dispersal from a familiar location have not been clearly distinguished. Here we label permanent movement away from familiar conspecifics 'social dispersal' and permanent movement away from a familiar area 'locational dispersal'. Both social and locational dispersal are subsumed under the general term, 'dispersal'. We define transfer, a term used frequently in primatological literature, as social dispersal with immigration into another group.

The costs of dispersal should vary depending on the extent to which individuals disperse socially and locationally. The costs are expected to be greatest when individuals cease to interact with familiar conspecifics and begin to live in an unfamiliar area at the same time. Perhaps the most frequently documented cost of social dispersal is aggression from strangers. Dispersers generally face more aggression than non-dispersers because, as strangers, they tend to evoke more aggression from conspecifics than do familiar individuals (reviewed in Ydenberg *et al.*, 1988; vervet monkeys: Cheney, 1981; Cheney & Seyfarth, 1982; olive baboons (*Papio anubis*): Packer, 1979; Japanese macaques (*Macaca fuscata*): Packer & Pusey, 1979; black-tailed prairie dogs (*Cynomys ludoviciarius*): Garrett & Franklin, 1988; yellow-bellied marmots (*Marmota flaviventris*): Armitage & Johns, 1982; wild horses (*Equus caballus*): Berger, 1986, p. 159, 1987). This cost can be substantial. Female toque macaques (*Macaca sinica*) who joined a neighboring group were subordinate to the females they joined, and suffered lower reproductive success and greater mortality than those females (Dittus, 1987). Gray wolves (*Canis lupus*) that disperse from their social groups may be killed by conspecifics (Fuller, 1989). Other potential costs of social dispersal may include loss of alliances with relatives or other familiar conspecifics (reviewed in Gouzoules & Gouzoules, 1987) and loss of time and energy involved in establishing new relationships (Kummer, 1979; Stamps, 1991).

Costs of social dispersal may be reduced by first establishing relationships with the group to be joined (*e.g.* vervets: Cheney, 1981; chacma baboons (*Papio ursinus*): Hamilton *et al.*, 1975; Cheney & Seyfarth, 1977; olive baboons: Packer, 1979; Ransom, 1981), by dispersing with familiar conspecifics (*e.g.* vervets and baboons: Cheney, 1983; Cheney & Seyfarth, 1983; dwarf mongooses (*Helogale parvula*): Rood, 1987), or by assessing social opportunities in a neighboring group before dispersing (olive baboons: Ransom, 1981; Strum, 1987).

Although costs of locational dispersal are usually assumed to be substantial (Anderson, 1989), documentation is rare (Johnson & Gaines, 1990). One potential cost of locational dispersal is loss of knowledge about the locations of food. Dispersing red howler monkeys (*Alouatta seniculus*) had a poorer diet, with less protein and phosphorus, and more fiber, than non-dispersers (Pope, 1989). Whether this had a negative effect on survival is unknown. Mortality in a population of translocated humans (*Homo sapiens*) may have been due to the ingestion of a poisonous plant species that looked similar to an edible plant in the former habitat (Gadd *et al.*, 1962).

There is more extensive documentation that increased vulnerability to predation can be a cost of locational dispersal. Movement of vervet monkeys into unfamiliar areas was associated with increased predation by leopards (*Panthera pardus*) (Isbell, 1990; Isbell *et al.*, 1990). Dispersing male white-tailed deer (*Odocoileus virginianus*) were more likely to die of predation than philopatric (and orphaned) males, and most of the predation occurred outside or on the edge of the males' home ranges, *i.e.* in areas that were less familiar to them (Holzenbein & Marchinton, 1992). Most mortality of translocated mule deer (*Odocoileus hemionus*) was caused by predators, human hunters, and vehicles, none of which the deer had encountered in their former habitat (O'Bryan & McCullough, 1985). Dispersing yellow-bellied marmots suffered higher mortality, all attributable to predation, than philopatric marmots (Van Vuren & Armitage, 1994). Eastern chipmunks (*Tamias striatus*) experimentally placed in unfamiliar areas took twice as a long and travelled twice as far to find refuge from approaching humans compared with when they were in familiar areas (Clarke *et al.*, 1993). For some species, vulnerability to predation during locational dispersal may result more from movement itself than from lack of familiarity with the area (Snyder *et al.*, 1976; Van Vuren, 1990).

The reluctance of individuals to abandon their home ranges and the efforts of translocated animals to return to their original home ranges also suggest that animals benefit from being in a familiar area. For example, a group of Nilgiri langurs (*Presbytis johnii*) did not abandon its home range until the last tree in its home range was destroyed (Poirier, 1970).

Similarly, groups of vervets did not abandon their home ranges until they lost all but one adult and apparently could no longer defend their home ranges effectively (Hauser *et al.*, 1986; Isbell *et al.*, 1991). Translocated individuals often attempt to return home, and many succeed (Gentry, 1964; Bovet, 1984).

Costs of locational dispersal may be reduced by dispersing through gradual, incremental home range extension or by first making exploratory excursions to increase familiarity (meadow voles (*Microtus pennsylvanicus*): Madison, 1980; Johnson, 1989; Belding's ground squirrels (*Spermophilus beldingi*): Holecamp, 1984; yellow-bellied marmots: Van Vuren, 1990; oryx (*Oryx leucoryx*): Stanley-Price, 1989).

The distinction between social and locational dispersal is important to make because variation in costs of dispersal is likely to influence decisions by individuals about whether to disperse, and if so, when to disperse. It may be especially useful to make this distinction for primates, a taxonomic order in which a majority of species live in groups (Wrangham, 1987) and dispersal patterns vary. Many group-living primates are typical of many other group-living mammals: males disperse socially and perhaps locationally around sexual maturity whereas females tend to remain in their natal groups and natal home ranges throughout life (Greenwood, 1980; Wrangham, 1980; Pusey & Packer, 1987a).

In several primate species, however, transfer from one group to another is the norm for females, and in other species, female transfer may be less common but still may occur occasionally. A number of attempts have been made to find consistent patterns in female transfer (Wrangham, 1980; Moore, 1984; Pusey & Packer, 1987a; Clutton-Brock, 1989) but so far no one explanation seems to predict in which species female transfer should be frequent, occasional, or absent. Little information currently exists about whether individuals who disperse socially also disperse locationally (but see Pope, 1989; Glander, 1992).

Males apparently disperse in most species (at least socially) despite the costs of dispersal. Given that males are limited in their reproductive success by access to females (in addition to access to food), males should maximize the number of females available to them as mates. One way to do this is by moving away from close female relatives (who are likely to refuse matings: Moore & Ali, 1984) and moving into groups with more female

:latives. In contrast, given that females are generally limited in their
luctive success more by access to food than by access to mates,
reproductive success is likely to be affected more by knowledge of
me range and the presence of female competitors than by the presence
se male relatives. Although genetic consequences of female transfer
so important to consider, patterns of female transfer from one group to
er may be better understood by first viewing female movements from
erspective of what is more directly important to female reproductive
ss.

cause the potential outcome of any individual's decision to disperse
ely to depend on current ecological and social conditions (Emlen,
; Isbell *et al.*, 1993), we expect that not all individuals will gain by
rsing. We assume, nonetheless, that when female dispersal (social
cational) is frequent in a species, reproductive success is greater, on
ige, for dispersing females than for philopatric females. The means by
h dispersing females increase their reproductive success have been dis-
:d in several reviews (Harcourt, 1978; Moore, 1984; Pusey & Packer,
a). It is not our goal to contrast costs with benefits of dispersal (for
a review, see Pusey & Packer, 1987a) but to emphasize the distinction
een social and locational dispersal.

this paper we examine statistically some potential costs of social and
ional dispersal both separately and together to detect patterns that may
predict when female transfer should be frequent, occasional, or absent
nthropoid primates.

ods

rst reviewed the literature in search of studies that reported male and female dispersal
ns in cohesive, multi-female groups of primates and that gave either quantitative or
ative information about potential costs of social or locational dispersal. Cohesive,
-female groups are defined as those species in which females consistently travel and
with at least one other adult female. Males were included to contrast with females. Our
y included only those studies of female dispersal in populations in which presence or
ice of factors related to costs of either social or locational dispersal were also mentioned
Moore, 1984; Pusey & Packer, 1987a for other studies of female dispersal in which
were not mentioned). Most studies reported aggression from strangers as the sole cost
spersal; these are presented in a separate column in Table 1. We treated aggression
simple dichotomous variable (present or absent); the quality of reports on aggression
d from anecdotal to quantitative, and we could not justify any greater precision in

categorization for statistical analyses. Because males typically disperse at least socially, aggression from strangers included aggression from resident males within female groups to immigrant males or to resident males of other female groups. For females, most of whom do not disperse either socially or locationally, aggression from strangers was expressed by aggression between females of different groups. Smuts *et al.* (1987: appendix A-1) was used to verify that all species for which there are data on female dispersal patterns, and presence or absence of costs of either form of dispersal, were represented in the database by at least one population. Table 1 summarizes the data on male and female aggression toward non-group members, extent of home range overlap, and female dispersal (both social and locational) in 47 populations from 35 species in 13 genera.

We also solicited responses to surveys from 33 researchers about the accuracy of our assessments from the literature (see personal communications in Table 1). We received responses from all but three. In addition to verifying the data, we asked about 1) the timing of female dispersal relative to the beginning of the study (early, midway, or late) to determine whether observers might have inadvertently caused unhabituated females to disperse, 2) the duration of the study to determine whether dispersal is more likely to be observed in longer studies, and 3) whether dispersing females transferred to groups that overlapped minimally, moderately, or extensively with their natal groups (see below).

Information about home ranges of former and new groups is required for accurate identification of locational dispersal. Since this information was not generally available through either the literature or the surveys (dispersers were identified most often when they immigrated into study groups from unknown groups), we used, as a first approximation of the likelihood of locational dispersal, the frequency of female transfer and the general extent of home range overlap for any given group. Both qualitative and quantitative statements were taken from the literature: female transfer could be absent ('none' in Table 1), occasional ('some'), or frequent ('common') as reported by the investigator. Home range overlap could be 'minimal' (operationally defined as 0-25% overlap), 'moderate' (26-43% overlap), or 'extensive' (44-100% overlap). In many species, data from different populations did not differ in either extent of female transfer or home range overlap, and we treated each of those species as a single data point. In some species, however, the extent of female transfer or home range overlap varied between populations. In two species (*Papio ursinus* and *P. anubis*) female transfer was absent in one population and occasional or frequent in another. In seven species (*Cercopithecus ascanius*, *C. mitis*, *Macaca radiata*, *M. sylvanus*, *P. ursinus*, *Colobus badius*, and *Presbytis entellus*), home range overlap varied among populations. Because of this variation and because social and locational costs of dispersal are likely to vary between populations of the same species depending on local ecological conditions, we treated the populations from these seven species as separate data points during the relevant statistical analyses. Species in which adult female associations are characteristically variable over time were excluded (*e.g.* chimpanzees: Goodall, 1986; Wrangham & Smuts, 1980) and spider monkeys (*Ateles* spp.: Fedigan *et al.*, 1988; Symington, 1988, 1990). Species in which adult females typically move and feed solitarily in their own home ranges or core areas were also excluded, *e.g.* orang-utans (*Pongo pygmaeus*: Rodman, 1984).

The analysis was restricted to anthropoid primates because information on group-living prosimians was found for only two species (*Lemur catta* and *Propithecus verreauxi*). Inclusion of these two species might obscure any potential differences between prosimians and anthropoids due to phylogeny. New World and Old World primates were treated both together and separately in the analyses since there is growing evidence that social and ecological conditions may differ between them (Strier, 1990; Isbell, 1994; see also below). We excluded from the analyses populations in which female transfer was associated with events that might involve unusually high levels of social instability, such as fusions and fissions. We carried out G-tests except where noted. Populations were excluded from relevant analyses when they could not be placed into a single category.

Results

Underlying patterns of female transfer, aggression, and home range overlap

The data in Table 1 reveal several general patterns. First, variation in female transfer, aggression, and home range overlap occurs within superfamilies, within families, within genera, and even among populations of the same species, suggesting that these traits are labile.

Second, 80% of species (28 of 35) at least occasionally exhibited extensive (44-100%) home range overlap. In many of these species, the opportunity arises for females to disperse socially without dispersing locationally. In such circumstances, dispersing females may risk incurring some costs of dispersal, but not others.

Third, female transfer and extensive home range overlap tend to occur less often in Old World primates than in New World primates. Sixteen of 27 (59%) populations of Old World primates exhibited extensive home range overlap. In contrast, all eight classifiable (89%) populations of New World primates in this survey showed extensive home range overlap ($G = 7.08$, $p = 0.03$, $N = 35$). Female transfer occurs at least occasionally in 54% ($N = 26$) of Old World primate populations *vs* 88% ($N = 9$) of New World primate populations ($G = 2.70$, $p = 0.26$, $N = 35$). However, among species that are aggressive, Old World anthropoids are significantly less likely than New World anthropoids to transfer at all (38% *vs* 100%; $G = 12.32$; $p = 0.002$, $N = 22$). This difference between Old and New World primates in female transfer patterns has been suggested before (Strier, 1990).

Finally, male social dispersal is the norm for most species despite the fact that aggression toward immigrant males is common in almost all species. Apparently, social costs that prevent female dispersal are not sufficient to keep males from dispersing socially (see above).

TABLE 1. *Primate studies for which data are available on the extent of home range overlap (usually the cumulative overlap of all groups on one), male aggression toward immigrant males or resident males of other female groups, female intergroup aggression, and female social and locational dispersal*

1	2	3	4	5	6	7	8	9	10
Alouatta palliata									
La Pacifica, Costa Rica, 23 yr	Extensive	Yes	Yes	Common		Yes	Yes		Glander, 1980, 1984, 1992, pers. comm.
A. seniculus									
Hato Masaguaral, Venezuela, 2.8 yr	Moderate to extensive (28-63)	Yes	Yes	Common	Throughout	Yes	Rare; females usually form new groups with other extra-group animals	Poorer food quality; higher rate of injury; reduced reproductive success	Sekulic, 1982a, b, c; Crocket, 1984, pers. comm.; Crocket & Pope, 1988, 1993; Pope. 1989.
Brachyteles arachnoides									
Montes Claros, Brazil, > 11 yr	Extensive (46)	Yes	Yes	Common			Yes		Strier, 1987, 1990, 1991, pers. comm.: Strier *et al.*, 1993.
Cebus albifrons									
Manu, Peru, 4 yr	Extensive	Yes	No	None	NA[a]	NA	NA		Terborgh, 1983; Janson, 1986, pers. comm.; Robinson & Janson, 1987.

TABLE 1. (*Continued*)

1	2	3	4	5	6	7	8	9	10
C. apella Manu, Peru, 6.5 yr	Extensive	Yes	Yes	Some	Early and late		Yes		Terborgh, 1983; Robinson & Janson, 1987; Janson, pers. comm.
C. capucinus Barro Colorado, Panama, 7.7 yr	Extensive	Yes	Yes	Some	Late		Yes		Oppenheimer, 1982; Robinson & Janson, 1987; Mitchell, 1989, pers. comm.
C. olivaceus Hato Masaguaral, Venezuela, > 15 yr	Extensive (100)	Yes	Yes	Some	Throughout		Yes		Robinson & Janson, 1987; Robinson, pers. comm.
Saimiri oerstedi Corcovado, Costa Rica, 3-4 yr	Extensive	Yes	No[b]	Common			Yes		Boinski, 1987a, b, pers. comm.; Mitchell *et al.*, 1991.
S. sciureus Manu, Peru	Extensive		No	None		NA	NA		Mitchell *et al.*, 1991.

TABLE 1. (*Continued*)

1	2	3	4	5	6	7	8	9	10
Cercopithecus aethiops Amboseli, Kenya, 13 yr	Moderate (26-42)	Yes	Yes	Some	Late	Yes	No[c]; Yes	Increased predation[d]; lower social rank	Cheney, 1987; Isbell *et al.*, 1990; Hauser *et al.*, 1986.
C. ascanius Kibale, Uganda, > 10 yr	Minimal to moderate	Yes	Yes	None	NA	NA	NA		Struhsaker & Leland, 1979; Struhsaker & Pope, 1991; Struhsaker, pers. comm.
Kakamega, Kenya, > 4 yr	Minimal	Yes	Yes	None	NA	NA	NA		Cords, 1987a, b, pers. comm.
C. mitis Kibale, Uganda, 6 yr	Minimal	Yes	Yes	None	NA	NA	NA		Struhsaker & Leland, 1979; Butynski, pers. comm.
Kakamega, Kenya, > 4 yr	Moderate	Yes	Yes	None	NA	NA	NA		Cords, 1987a, b, pers. comm.

TABLE 1. (*Continued*)

1	2	3	4	5	6	7	8	9	10
Erythrocebus patas									
Laikipia, Kenya, 2 yr	Moderate to extensive	Yes	Yes	None	NA	NA	NA		Chism *et al.*, 1984; Cords, 1987a; Pusey & Packer, 1987a; Chism & Rowell, 1988; Chism, pers. comm.
Cercocebus albigena									
Kibale, Uganda, 1.3 yr	Extensive (72)	Yes	Yes	None	NA	NA	NA		Struhsaker & Leland, 1979; Waser, pers. comm.
Macaca fascicularis									
Ketambe, Sumatra, 4 yr	Minimal to extensive	Yes	No	Some	Early and midway		Yes		van Noordwijk & van Schaik, 1985; van Schaik, pers. comm.
M. fuscata									
various, Japan	Minimal to extensive (10-50)	Yes	Yes	None	NA	NA	NA		Kawanaka, 1973; Takasaki, 1981.
M. mulatta									
Cayo Santiago, Puerto Rico, 34 yr	Extensive	Yes	Yes	Some	Late		Yes		Hausfater, 1972; Cheney, 1987; Berard, pers. comm.

TABLE 1. (*Continued*)

1	2	3	4	5	6	7	8	9	10
M. radiata									
Mundanthurai, India	Extensive	Yes		Some			Yes		Ali, 1981.
Bangalore, India	Minimal	Yes	Yes	Some			Yes		Rahaman & Pathasarathy, 1969.
M. sinica									
Polunnaruwa, Sri Lanka	Extensive	Yes	Yes	None	NA	NA	NA		Dittus, 1986, 1987.
M. sylvanus									
Ghomara, Morocco, 2 yr	Extensive (68)	Yes	Yes	None	NA	NA	NA		Mehlman, 1985, 1986, pers. comm.; Mehlman & Parkhill, 1988.
Djurdura, Algeria, 10 yr	Minimal to extensive		No	None	NA	NA	NA		Ménard & Vallet, 1993; Ménard, pers. comm.
Papio anubis									
Ishasha, Uganda, > 5 yr	Moderate	No	No	Some	Midway		Yes		Rowell, 1966, 1969, pers. comm.
Gombe, Tanzania, 26 yr	Moderate	Rare	Yes	Some[d]	Early[d]		Yes		Ransom, 1981; Packer, pers. comm.

TABLE 1. (*Continued*)

1	2	3	4	5	6	7	8	9	10
P. cynocephalus									
Mikumi, Tanzania, 19 yr	Extensive	Yes	Yes	Some[d]	Early[d]		Yes		Rasmussen, 1981; Rhine, pers. comm.
Amboseli, Kenya	Extensive	Yes	Yes	None	NA	NA	NA		Altmann & Altmann, 1970; Shopland, 1982.
P. ursinus									
Suikerbosrand, S. Africa, 7 yr	Extensive (52)	Rare	No	Common	Throughout	Yes	Yes		Anderson, 1981, 1987, pers. comm.
Kuiseb, Namibia	Minimal (10-18)	Yes	No	None	NA	NA	NA		Hamilton *et al.*, 1975, 1976; Hamilton, 1985.
Okavango, Botswana, 17 yr	Minimal	Yes	No	None	NA	NA	NA		Bulger & Hamilton, 1987; Hamilton, pers. comm.
P. hamadryas									
Erer Gota, Ethiopia	Extensive (50) (bands)	Yes	Yes	Some			Yes		Kummer, 1968: 104; Sigg & Stolba, 1981; Sigg *et al.*, 1982.
Colobus badius									
Tana River, Kenya	Moderate	Yes	No	Common		Yes	Yes		Marsh, 1979a, b.

TABLE 1. (*Continued*)

1	2	3	4	5	6	7	8	9	10
Kibale, Uganda, 16 yr	Extensive	Yes	No	Common	Throughout		Yes		Struhsaker, 1975; Struhsaker & Leland, 1979; Struhsaker, pers. comm.; Isbell, pers. obs.
Abuko, Gambia	Extensive	Yes	No	Common		No?[e]	Yes		Starin, 1981.
C. guereza									
Kibale, Uganda	Extensive (74)	Yes	Yes	None	NA	NA	NA		Oates, 1977a, b; Struhsaker & Leland, 1979.
Nasalis larvatus									
Tanjung Puting, Indonesia, > 3 yr	Extensive (groups) (95-99)	Rare	Yes	Some	Midway to late		Variable; also join extra-group males		Yeager, 1991, 1992, pers. comm.
Presbytis cristata									
Kuala Selangor, 1.5 yr	Minimal	Yes	No	None	NA	NA	NA		Bernstein, 1968; pers. comm.
Presbytis entellus									
Mt. Abu, India, 9 yr	Minimal to moderate	Yes	Yes	Some			Yes		Hrdy, 1977, pers. comm.; Moore, pers. comm.
Dharwar, India	Extensive	Yes	Yes	Some			Yes		Yoshiba, 1968.

TABLE 1. (*Continued*)

1	2	3	4	5	6	7	8	9	10
Kanha, India	Extensive (50)	Yes		Some			Yes		Newton, 1987.
P. johnii Nilgiri Hills, India, 1 yr	Extensive	Yes	No	Some			Yes		Poirier, 1969, 1970, pers. comm.
P. melalophos Kuala Lompat, Malaysia	Extensive (79)	Yes	No	Some			Yes		Bennett, 1983, 1986.
P. pileata Madhupur, Bangladesh	Extensive	Yes	No	Some			Yes		Stanford, 1991, 1992.
P. rubicunda Sepilok, Sabah, 1.5 yr	Minimal	Yes	Yes	Some or common	Not early (animals were habituated)		Join extra-group males		Davies, 1984, 1987, pers. comm.
P. senex Polonnaruwa, Sri Lanka, 1.8 yr	Minimal	Yes	No	Some or common	Midway and late		Variable; also join extra-group males		Rudran, 1973, pers. comm.; Manley, 1984; Hladik, 1977.

TABLE 1. (*Continued*)

1	2	3	4	5	6	7	8	9	10
Gorilla gorilla Virunga Mts., Rwanda, 26 yr	Extensive	Yes	No	Common	Throughout	No[f]	Yes		Harcourt *et al.*, 1976; Fossey & Harcourt, 1977; Harcourt, 1978; Watts, pers. comm.

Columns: 1. Species, study site and duration of study; 2. Home range overlap (%); 3. Male-male aggression? 4. Female-female aggression between groups? 5. Extent of female emigration; 6. Female movements in relation to duration of study; 7. Movement to new location? 8. Movement to new female group? 9. Other documented costs of dispersal; 10. Sources.

Table does not include data from all species in which females have been observed to transfer; it does attempt to include all populations for which data are available on patterns of female dispersal patterns and either extent of home range overlap or female aggression during intergroup encounters. Movements as a result of fusion and fission are excluded.

[a] NA = not applicable.

[b] No aggression observed but groups avoided each other.

[c] Cost associated with movement of entire groups into unfamiliar areas.

[d] Females that transferred were not habituated and probably disperse as a result of human presence; categorized as 'none' in statistical analyses.

[e] Individuals noted as tending to remain in areas that overlapped with their former groups even after transferring to another group.

[f] Natal females transfer directly to groups which share home ranges with the natal group; secondary movements can be to groups with non-overlapping home ranges.

Female transfer relative to costs of social dispersal

Among anthropoid primates in general, female aggression toward females of other groups is common, but not universal (Table 1). Females are aggressive toward other groups in 23 of 38 populations (60%). Female intergroup aggression is often considered a causal factor in restricting female transfer (Wrangham, 1987; van Schaik, 1989). This is not strongly supported by the combined data from Old and New World primates. Frequent female transfer apparently occurs only somewhat less in populations with female aggression than in populations with no female aggression (9% *vs* 28%; $G = 2.28$; $p = 0.32$, $N = 36$). This lack of significance is driven primarily by New World primates. Among New World monkeys, female transfer is significantly *more* likely to occur in populations with female aggression than in populations with no female aggression (Fig. 1).

Although females are aggressive between groups in six of nine populations of New World primates, female transfer occurs frequently in two of these six populations despite the potential cost of aggression and not at all in two of three populations without female aggression between groups ($G = 7.64$, $p = 0.02$, $N = 9$). In contrast, among Old World primates, female transfer is significantly *less* likely in populations with female aggression between groups (Fig. 1). Female transfer is not common in any population that shows female aggression between groups ($N = 16$) but it is common in three of 11 populations that do not show aggression between groups ($G = 7.30$, $p = 0.03$, $N = 27$). This suggests that female dispersal patterns are more influenced by the potential costs of social dispersal in Old World anthropoids than in New World anthropoids. Even in Old World species, however, the fact that females still do not frequently disperse in a majority of populations in which females show no aggression suggests that additional costs of dispersal exist to prevent them from dispersing.

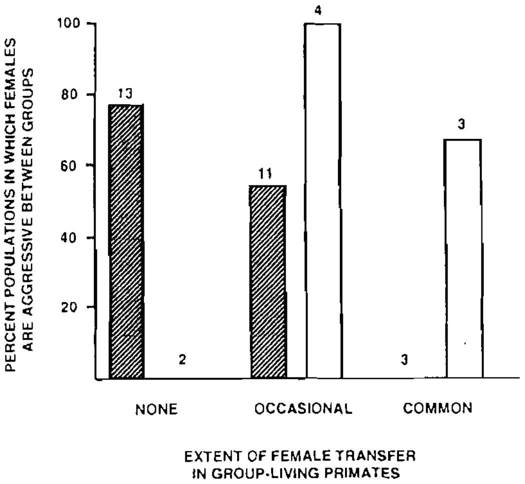

Fig. 1. Extent of female transfer in anthropoid primates relative to aggression between groups of females (see methods for definitions). Filled bars are Old World primates; open bars are New World primates. Sample sizes are above the bars.

Female transfer relative to costs of locational dispersal

It has been suggested that females are more likely to transfer between groups when home range overlap is extensive (Ali, 1981) because females would not then lose knowledge of the locations of foods (Ali, 1981) or predators (*e.g.* Isbell *et al.*, 1990) as a result of transferring. The data in Table 1 indicate that female transfer is not a common phenomenon even when there is extensive home range overlap. Although 24 of 37 populations of anthropoid primates have extensive home range overlap (73%), female transfer is frequent in only six of those 24 populations (25%).

On the other hand, female transfer is never frequent in populations with minimal home range overlap. Among Old World primates alone, all four populations with frequent female transfer also have moderate to extensive home range overlap (Fig. 2). Among New World primates, all three populations with frequent female transfer also have extensive home range overlap. This suggests that lack of knowledge of novel areas may assist in keeping females from transferring to other groups most of the time.

It is possible that female aggression reduces the extent of home range overlap and that lack of female aggression increases the extent of home range overlap, thus causing social and locational costs of dispersal to co-vary. This is not the case for Old World anthropoids (it could not be examined in New World anthropoids). Although six of 11 (54%) Old World anthropoid populations without female aggression have extensive home range overlap, nine of 16 (56%) populations with female aggression also have extensive home range overlap ($G = 0.02$, $p = 0.99$, $N = 27$).

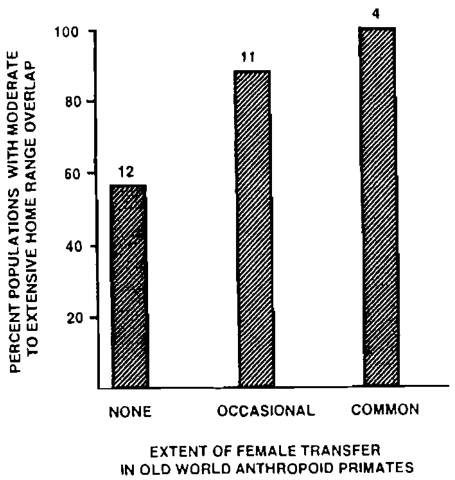

Fig. 2. Extent of female transfer in Old World anthropoid primates relative to the extent of home range overlap (see methods for definitions). New World primates were not included because they showed no variation in the extent of home range overlap. Samples sizes are above the bars.

This suggests that some of the costs of social dispersal vary independently from some of the costs of locational dispersal.

Is female transfer more likely when costs of social and locational dispersal are both low?

Although costs of social or locational dispersal by themselves may not be sufficient to prevent female transfer in some species, together they may have a stronger effect in reducing the frequency of female transfer. Conversely, when few costs of social and locational dispersal exist, females should be more likely to transfer. These conditions might arise when females are not aggressive and when home ranges of groups overlap. Among Old World anthropoids, this appears to be the case. Among species without female aggression, female transfer is absent in two of three populations with minimal home range overlap and it is occasional or frequent in all eight populations with moderate or extensive home range overlap ($G = 12.9$, $p = 0.05$; $N = 11$).

These patterns of female social and locational dispersal are not a consequence of observer bias. For example, observers may cause females to leave their groups in the early stages of studies when animals are not yet habituated, thereby overestimating the extent of dispersal. On the other hand, studies of short duration may not be sufficiently long to detect dispersal that occurs only occasionally, thus underestimating the extent of dispersal. Responses to the surveys indicate, however, that neither was a problem in these analyses. Only two of nine observers who reported occasional transfer also reported transfer occurring early in the study when females were not well habituated (both observers studied baboons). Similarly, there was no statistically significant difference in the length of studies without female social dispersal and those with occasional female social dispersal (Mann-Whitney U-test: $N_1 = 10$; $N_2 = 11$; $U = 44$; $p > 0.20$; 2-tailed).

Discussion

These results are preliminary. More data are needed on multiple groups and multiple populations of more species. The extent of female transfer in any species may, in fact, be labile and dependent upon local ecological conditions such as the intensity of female-female competition (which is itself dependent on the abundance and distribution of foods), the density of groups (which affects the extent of home range overlap), and the intensity of male-male competition (see below).

Does locational dispersal occur when social dispersal occurs?

We have suggested that overlapping home ranges allow social dispersal without locational dispersal. What is the evidence that this occurs? Unfortunately, in species with frequent female social dispersal, patterns of locational dispersal are not well-documented. Groups of red colobus (*Colobus badius*) in Kibale Forest, Uganda, have extensive home range overlap and females often transfer to neighboring groups (Struhsaker, 1975; Struhsaker & Leland, 1979). In Gambia, female red colobus who transferred tended to stay in the part of their new group's home range which overlapped with that of their former group, even when their new group moved beyond the area of overlap (Starin, 1981). However, female red colobus at the Tana

River, Kenya, apparently did transfer to groups with non-overlapping home ranges (Marsh, 1979a).

In Volcanoes National Park, Rwanda, female gorillas transferring for the first time moved to groups whose home ranges overlapped extensively with those of their former groups (Fossey & Harcourt, 1977; Harcourt, 1978). On the other hand, secondary movements of females were often to distant groups whose home ranges did not overlap with those of the females' most recent groups (Harcourt, 1978).

Squirrel monkeys (*Saimiri oerstedi*) in Corcovado, Costa Rica, have extensive home range overlap (Boinski, 1987a, b) but whether dispersing females in this species transfer to groups with overlapping home ranges is unknown.

According to home range maps and data on individual transfers (Anderson, 1981, 1987) female chacma baboons at Suikersbosrand, South Africa, may disperse both locationally and socially. Anderson suggested that female dispersal patterns in this population differed from those of other populations because there were no predators in the study area until recently. This is an idea that is consistent with expectations based on the costs of locational dispersal suggested here.

Mantled howler monkeys (*Alouatta palliata*) and red howler monkeys are the only primate species reported thus far in which females commonly disperse socially and locationally (Crockett, 1984; Pope, 1989; Glander, 1992). Female red howlers at Hato Masaguaral, Venezuela, moved up to six home range diameters away from their natal home ranges (Pope, 1989).

The social system of hamadryas baboons (*Papio hamadryas*) illustrates the importance of distinguishing between social and locational dispersal. In hamadryas baboons the band is made up of several clans, and the clan is made up of several one-male units (Stammbach, 1987). The band is the basic foraging unit; each band maintains its own home range and daily foraging direction (Sigg & Stolba, 1981). Females commonly transfer between one-male units and between clans within bands (Sigg *et al.*, 1982). When females transfer at maturity to different one-male units, however, they encounter neither a novel home range nor a social environment of novel aggressive females. Most female hamadryas baboons remain throughout their lives in their natal home ranges along with their female relatives. In this respect, hamadryas baboons are similar to other female-resident species (see also Dunbar, 1988) in that female movements do not involve the risk of incurring costs of locational and social dispersal. The same may be true for proboscis monkeys (*Nasalis larvatus*) (Bennett & Sebastian, 1988; Yeager, 1991, 1992).

Our understanding of the social system of chimpanzees may also benefit from considering the distinction between social and locational dispersal. Chimpanzees are organized into communities which include multiple males and females that often travel and feed independently of one another (Goodall, 1986; Nishida & Hiraiwa-Hasegawa, 1987). Various combinations of social and locational dispersal may occur. A female may (1) remain in her natal home range with her natal community (philopatry), (2) remain in her natal home range but associate with males of a different community (social dispersal), or (3) expand into the home range of another community and associate with males from both communities (social and locational dispersal) (Pusey, 1979; Uehara, 1981, cited in Kawanaka, 1984; Nishida, 1989). Further subtleties are introduced when females have distinct natal home ranges or core areas within the community (Wrangham, 1979a, b); they may disperse socially and locationally to some extent within their own 'community' when they expand their ranges at sexual maturity (Goodall, 1986). Among New World primates, the social system of black spider monkeys (*Ateles paniscus*) appears to be similar in many ways to that of chimpanzees (Symington, 1988; 1990).

Why are Old and New World primates apparently different in their responses to potential costs of social dispersal (Fig. 1)? One possibility is that Old and New World primates may have evolved fundamentally different responses to similar social and ecological problems (see also Dunbar, 1991; Strier, 1990), or, they may face fundamentally different social and ecological problems. For example, although there are avian predators of primates in the Old and New Worlds, there is apparently no New World equivalent of the leopard as a major predator of primates (Isbell, 1994; E.A. Herre, pers. comm.). The historic biogeographic ranges of leopards and Old World primates overlap extensively (Ewer, 1973; Wolfheim, 1983). Unlike other mammalian predators, leopards commonly climb trees and can prey heavily even on arboreal primates (reviewed in Isbell, 1994). Leopard predation can be especially severe when individuals are in unfamiliar areas; thus, leopard predation may have favored the evolution and maintenance of site fidelity in vervets (Isbell, 1990; Isbell *et al.*, 1990, 1993). New World primates, which have no major mammalian ambush predators and often have extensive home range overlap, may not suffer the costs of locational dispersal to the extent that dispersing Old World primates may suffer. As suggested by the results, the combined costs of locational and social dispersal may more strongly influence the evolution and maintenance of group fidelity among some primates than costs of either alone.

Patterns of female transfer: some predictions

The decision to disperse or remain in the natal group may involve a cost-benefit analysis by the potential disperser, depending on the circumstances surrounding the decision; the individual disperses if fitness prospects are better elsewhere (Van Vuren & Armitage, 1994). Such a cost-benefit analysis may explain patterns of female transfer in primates. Our results suggest that among Old World species, females may be free to transfer when they do not incur many of the presumed costs of social and locational dispersal. Female transfer is expected to be frequent in these species because females (1) face no intergroup aggression from other females, (2) have undifferentiated relationships within groups (*i.e.* female dominance hierarchies within groups are weak or not discernable; see below), and (3) have overlapping home ranges with other groups. We further predict that such females will have no energetic costs of daily travel as group size increases. These are hypothesized to be traits associated with populations in which female reproductive success is not limited by food abundance (Isbell, 1991). Nonetheless, it is reasonable to ask why females transfer at all.

Once the costs of social and locational dispersal are removed and females are free to transfer, we expect that males will be free to become philopatric. Whether males disperse or remain philopatric in such situations will depend on the defensibility of females; this will then determine female transfer patterns in species without costs of dispersal for females. If one male cannot monopolize access to all females in the group (*e.g.* red colobus in Kibale Forest, Uganda), males will be philopatric (the presence of male relatives within groups will reduce competition among males within groups but will not reduce competition among males between groups). Female transfer will be obligate to avoid incestuous matings. On the other hand, if one male can monopolize access to all females in the group (*e.g.* gorillas, Tana River red colobus; many langurs (*Presbytis* spp.) are also predicted to fit this pattern), many males will disperse at least socially and female transfer will be conditional upon strategies of individual males. Females should transfer if, by doing so, they can avoid incestuous matings or infanticidal males, or when they have failed to reproduce for other reasons in their current group (Harcourt, 1978; Marsh, 1979a; Watts, 1990). Such 'male-conditional' female transfer is expected to occur less frequently than 'obligate' female transfer.

For those species in which females would incur costs by transferring, we predict that most females will remain in their natal groups throughout life. Infanticidal males also exist in these female-resident species (*e.g.* redtail monkeys: Struhsaker, 1977; blue monkeys: Butynski, 1982), and many females in female-resident species do not always successfully rear offspring. However, most females in female-resident species do not have the option of transferring in the face of such conditions because, by transferring, they would be more likely to incur costs of locational dispersal, social dispersal, or both, that would reduce their reproductive success even further. We expect that female transfer in many of these species will be exceptional and conditional upon competition with other females in their groups for access to food. Females are predicted to transfer in female-resident species when their energy intake cannot surpass energy output relative to other females in their groups. All else being equal in a given population, those who transfer will be the lowest-ranking females in the largest groups because they often cannot compete effectively against others in their own groups for food and they expend more energy in daily travel than the lowest-ranking females of smaller groups (Isbell, 1991). Such females will transfer to smaller groups because, although they will likely continue to be the lowest-ranking females in their new groups, they will expend less energy in daily travel than they did in their former groups. Note that this prediction only applies to those Old World female-resident species that exhibit both strong female dominance hierarchies within groups and greater daily travel distances with larger group sizes (*e.g.* rhesus macaques, olive baboons, and vervets; see Isbell, 1991). Males will then disperse despite the costs of social or locational dispersal because the costs are outweighed by greater reproductive opportunities away from female relatives. We define this type of female transfer as 'female competition-conditional' transfer.

Thus, what has been labelled in Table 1 as occasional female transfer is likely to include both male-conditional and female competition-conditional transfer. Unfortunately, the data in Table 1 are not sufficiently detailed to distinguish between these two types of female transfer. However, they should be distinguishable in the field by the following suites of characteristics:

Male-conditional female transfer is predicted to occur in populations (1) without female aggression between groups, (2) that exhibit weak female dominance hierarchies, at best, within groups (see Isbell, 1991), (3) in which larger groups do not travel farther daily distances than smaller groups, (4) with single-male, multi-female groups, and (5) more frequently than female competition-conditional female transfer. Female competition-conditional female transfer is predicted to occur in populations (1) with female aggression between groups, (2) that exhibit strong female dominance hierarchies within groups, (3) in which larger groups travel farther daily distances than smaller groups, and (4) as rare events.

There are some Old World female-resident species with female aggression between groups that do not exhibit female dominance hierarchies or greater daily travel distances in larger groups (*e.g.* patas monkeys, redtail monkeys, and blue monkeys). In these species, energy intake and output should be similar for all females within groups regardless of group size. Female transfer is predicted, therefore, not to occur at all in these species as long as their habitats are undisturbed.

Both within and between groups, patterns of female aggression covary with patterns of ranging behavior as a function of group size (Isbell, 1991). Our predictions of the extent of female transfer in Old World anthropoid primates are also associated with this covariation of female aggression and ranging behavior. It has been hypothesized that this covariation is ultimately determined by variation in food abundance and food distribution (Isbell, 1991). Our predictions are also consistent with this hypothesis. This suggests the possibility of a general unified model of primate behavioral ecology that explains patterns of female aggression, ranging behavior, philopatry, social and locational dispersal, and perhaps other traits of ecological and evolutionary importance.

The evolution of kin groups: what is cause and what is effect?

In two of the three Old World primate species in which females frequently transfer from their natal groups, females usually move directly to neighboring groups with overlapping home ranges (red colobus: Struhsaker, 1975; Starin, 1981; gorillas: Harcourt, 1978). Female relationships within groups of these species are undifferentiated, *i.e.* grooming relationships are weak, female-female coalitions are rare, and dominance hierarchies are weak or poorly defined (Wrangham, 1980; van Schaik, 1989; Isbell, 1991). Females should find it easier to transfer if affiliative relationships are not an integral part of living in groups because the benefits of such relationships are not theirs to lose.

This is a reversal of the argument that weak bonds in female-transfer species are a consequence of the fact that unrelated females are less affiliative than related females (Wrangham, 1980). In support of that argument, related female gorillas are more frequently affiliative with one another than with unrelated females (Stewart & Harcourt, 1987; Watts, 1994). On the other hand, females in other species (*e.g.* blue monkeys: Rowell *et al.*, 1991) that have only weakly differentiated female relationships nevertheless still do not transfer. Even related females may not have particularly strong affiliative relationships with one another.

The apparent constraining effects of costs of social and locational dispersal on female movements in Old World anthropoids suggest that kin groups did not necessarily evolve as a direct result of inclusive fitness benefits gained by helping relatives in defense of food resources (see Wrangham, 1980, 1982; van Schaik, 1989). The food defense hypothesis implies that individual females initially lived near both relatives and non-relatives, and that when cooperation became beneficial, females chose to live with relatives. Inclusive fitness benefits gained through joint defense of food resources are viewed in the food defense hypothesis as a cause and primary advantage of living in groups with kin.

For other group-living mammals it has also been suggested that group living evolved through retention of daughters within the maternal home range because of the costs of dispersal (ground squirrels: Armitage, 1981; lions: Pusey & Packer, 1987b). Our investigation suggests that this may also be the case for most species of Old World primates. An alternative scenario for the evolution of kin groups in Old World primates is that once cooperative defense of food resources became beneficial, kin groups then would have formed by default because of the costs of locational and social dispersal to individual females (see also Emlen, 1984; Wolff, 1994). Inclusive fitness benefits gained through joint defense of food resources are viewed in this scenario as a consequence and an additional advantage of living in groups with kin rather than a cause and primary advantage.

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