

DISPERSAL IN PRIMATES

VARIATION IN PATTERNS AND CAUSES

PABLO POLO RODRIGO

In the animal kingdom, dispersal represents a critical decision as it affects survival and reproductive success, and is also an important component of population dynamics. This article looks at dispersal pattern variation in primates and some of the underlying reasons, both proximate and root causes.

Keywords: intra-group competition, mate choice, infanticide, inbreeding depression.

The spatial distribution of organisms is not usually random, but reacts to biotic and abiotic factors in the environment. This distribution, which may be either aggregate or disperse, is the result of individuals moving towards the location they occupy at any given moment. In this respect, the concepts of migration and dispersal describe the general characteristics of certain types of displacement. Migration refers to the movement of a large number of individuals belonging to the same species between two different habitats. Migration may be cyclical (with diverse periodicity, for example, daily or annual) or one way only, which gives rise to different migration patterns. Dispersal refers to the movement of individuals away from their natal areas and/or their parents and relatives. Dispersal can be undertaken by an individual alone or by small groups, and it can be active or passive. Dispersal is an essential characteristic of populations because it provides genetic links among them and significantly influences demographic processes and population dynamics. This article focuses on dispersal movements in primates.

■ DISPERSAL IN PRIMATES

The Primate order, to which the human species belongs, is comprised of highly social species that live in groups, often throughout their lifetime. In this respect, dispersal in primates – and in social species in general – has two facets: the ecological (spatial dispersal) and social (social dispersal) (Isbell and Van

Vuren, 1996). During spatial dispersal, individuals move to an unknown home range, while in social dispersal individuals move into new social groups. These two aspects of dispersal can occur together or not, depending mainly on the social organisation of the group. In species comprising territorial groups such as chimpanzees, dispersal of individuals often combines both aspects. In other species, such as gorillas or hamadryas baboons, the home ranges of different social groups overlap, so the dispersal of individuals generally has a social component, but not an ecological one. Finally, spatial dispersal in the absence of social dispersal would involve the displacement of the whole social group to a different home range. Dispersal of this type is often the result of changes in habitat, affecting resources or factors vital for species survival, prompting the group to seek new ranges with better conditions. Although we have considered this type of displacement as a case of spatial dispersal, it could also be considered as a non-seasonal migration process.

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■ WHY ABANDON ONE'S FAMILIAR BIRTHPLACE?

Joining a new social group often implies the loss of cooperative social relationships established with the previous group and the need to establish new social bonds, with the consequent expenditure of time and energy. Furthermore, this takes place in a generally hostile social environment, in which group members (or some of them) attack the newcomers, chasing them

	Intragroup competition for food resources	Intrasexual competition for breeding mates	Inbreeding avoidance
Stage of sexual maturity	Unclear relationship	During or after sexual maturity	Before or during sexual maturity
Gender bias	Possible	Possible	Yes
Inbreeding avoidance behaviour before dispersal	No	No	Yes
Aggression	Yes	Yes, Among members of the same sex	No
Discrimination in access to resources between individuals that disperse and those that do not	Individuals that disperse have limited access to food resources	Individuals that disperse have limited access to breeding mates	Unclear relationship
Relationship between dispersion and seasonality	Yes, related to seasonality of food resources	Yes, related to reproductive seasonality	Unclear relationship
Characteristics of the host group	Smaller groups with a greater proportion of resources/size	Groups with more numerous or better quality breeding mates	Groups with breeding mates that are not relatives

Adapted from Table 2 in Field and Guatelli-Steinberg, 2003.

Table 1. Characteristics of dispersal patterns and their possible relationship with the three main root causes of natal dispersal.

away from feeding sites and trying to prevent their integration. Also, if dispersal is to an unknown area, the individual may be more vulnerable to attack by predators and suffer certain setbacks, such as those arising from ignorance of where food resources are located. Although there are strategies to minimise these setbacks or costs, such as dispersing in the company of relatives or establishing relationships with the new group before joining it, dispersal is clearly a costly process for the individuals involved, which prompts the question why do individuals exhibit dispersal behaviour?

When trying to answer this question, we must distinguish between the proximate causes, which refer to the mechanisms involved in the expression of behaviour, and the root causes, which are related to the adaptive consequences of behaviour and, therefore, to the reason for its selection and evolution. Possible proximate causes for dispersal in primates are: the attraction to members of other groups, physiological factors, nutritional status of the individual, interaction between group members (including aggression or sexual interaction), coercion, or response to environmental disturbance. Regarding

the root causes of dispersal in primates, four broad categories have been proposed. First, individuals may leave their group to avoid competing for food resources with other members, especially relatives. Second, individuals may leave their group in response to intrasexual competition for breeding partners, especially that occurring between relatives. Third, females could use dispersal as a strategy against infanticide. Infanticide is an adaptive strategy, practised by males that are unrelated to the offspring, as it shortens the postpartum infertility period of the mother, speeding up the reproductive rate. Fourth, individuals who leave the natal group could benefit from mating with unrelated individuals and thus avoid the negative effects of inbreeding on the survival of offspring (i.e., inbreeding depression).

These four benefits of dispersal are not mutually exclusive, since, although the primary cause of dispersal may be to avoid intragroup competition for food resources, for example, the dispersal of one gender resulting from this selective pressure might, in turn, reduce the risk of inbreeding or competition for mates. Studying dispersal patterns and specifically determining which individuals disperse, when

they disperse and their dispersal mode, can help us determine the root causes of dispersal in each case (Table 1). Furthermore, the place or group to which individuals disperse is also important, as reflected in some of the examples presented below. Thus, for example, when female dispersal is not associated with sexual maturity but rather with increased intrasexual aggression within the group, and females move to less densely populated groups or a better home range in terms of food resources, we can postulate that the most likely cause of dispersal is competition for food within the group.

■ DISPERSAL PATTERNS

Who disperses?

In most mammals there is a gender bias in dispersal patterns, with the male being the one to leave the natal unit. This is due to the differences in parental investment common to mammals (females invest more than males) and this affects potential reproductive rates (the number of offspring each sex can produce per time unit if reproduction were not limited by the availability of mates), and the factors limiting reproductive success in males and females (Trivers, 1972). On the one hand, if females remain in their home range they have access to known food sources, and food sources are a limiting factor for reproduction. The formation of cooperative relationships between related and unrelated individuals is also favoured (when males disperse, so-called matrilineal relationships are established), having a positive impact on female survival and reproduction. On the other hand, although males may also benefit from remaining in their home environment, their reproductive success is limited by the number of available mates, so the costs of dispersal could be compensated by joining units where availability of mates is optimised.

There are several species of primates corresponding to this general pattern of dispersal (Table 2). One example of male dispersal associated with competition for mates is the Hanuman langur (Figure 1) (Koenig and Borries, 2001). This species, which belongs to the family Cercopithecidae or Old World monkeys, can live in groups comprising one adult male and several females (unimale-multifemale) or in multimale-multifemale groups. In the former, the males usually leave the group on reaching sexual maturity, although they may be



Daniele Colombo

Figure 1. The picture shows two Hanuman langurs (*Semnopithecus entellus*) in India. This Asian species of Cercopithecidae (Old World monkey) forms groups numbering 15 to 54 individuals among which are one or more breeding males. Males disperse prompted by competition for breeding partners.

driven out sooner if the dominant male (possibly the father) is replaced by another individual from outside the group. By contrast, in multimale-multifemale groups, males tend to remain longer in their home units before dispersing. In both cases, competition for breeding partners is thought to be the main cause for dispersal. In unimale-multifemale groups, one male expels the other competitors whereas in the multimale-multifemale group, the dominant male monopolises mating and fathers most offspring. Meanwhile, displaced males tend to disperse and form male-only groups, waiting to form or join a group in order to mate.

However, there are several species that do not conform to this general pattern of dispersal, and the males remain while the females leave the natal unit (Table 2). In these cases, competition for food

is considered to be the most common cause underlying this pattern, although inbreeding avoidance and mate choice are also likely causes in some cases. Muriquis are a species of New World monkeys, belonging to the atelidae family, which form multimale-multifemale

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groups with fission-fusion dynamics in which females typically leave the natal group around sexual maturity. While not aggressively expelled from the group, adult females often move from feeding sites, so it is thought that the dispersal is largely due to competition for food resources (Printes and Strier, 1999). Chimpanzees, which belong to the hominid family, also have social systems following fission-fusion multimale-multifemale group dynamics (Stumpf, 2007). Males are philopatric, remaining in their natal communities, where they form alliances and cooperate in defending the territory, whereas females disperse to other groups on reaching sexual maturity. However, unlike what happens in muriquis, this dispersal seems more closely related to females becoming attracted to males from outside the group than to competition for food within the group. In this case, the proximate causes of dispersal would seem to be related mainly to inbreeding avoidance, although competition for food resources may also play a role in the process. Finally, the human species also represents an exception to the general dispersal pattern in primates because, even though both sexes may leave their natal units, dispersal is biased towards females in most societies studied (Rodseth *et al.*, 1991).

Other species do not exhibit a gender bias in their dispersal pattern, since both sexes leave their natal group (Table 2). Gorillas, which belong to the hominid family, are an example of this dispersal pattern (Figure 2). Their social groups are formed by one or sometimes two reproductive males, although there is one dominant male that monopolises matings and therefore group paternity (Harcourt and Stewart, 2007). Consequently, the major cause of male dispersal relates to reproductive competition. For females, this dispersal is related to inbreeding avoidance and choice of a mate.

Finally, it should be noted that the type of sex bias in dispersal is important, as it will determine the kinship structure within the group and influence social relationships (i.e., social structure). Generally speaking, social relationships with related group members are lost by the gender that disperses. Furthermore, the links established in the new group with individuals of the same sex are often weak or nonexistent. By contrast, the philopatric sex, the one that remains in the natal environment, forges strong cooperative links and alliances with relatives, forming

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Weesam, 2010

Figure 2. A mountain gorilla (*Gorilla berengei berengei*) in Uganda. In this species, where groups have one or two breeding males, both males and females disperse from their natal units.

the core of the social structure of the group (matrilineal or patrilineal, depending on sex). Thus, philopatry, kinship and cooperation tend to be linked. In humans, however, females tend to maintain ties with relatives, even though they separate from them, except in extreme patriarchal societies.

Likewise, they can also form cooperative ties in their new groups with females they are not related to, something less common in other primate species exhibiting female dispersal, except perhaps bonobos. Moreover, in human societies where females are philopatric, males also do not lose ties with their relatives and, in fact, these societies are often characterised by a high degree of community endogamy, as males either stay in their natal community or move to a neighbouring group, often dependent on the natal community (Rodseth *et al.*, 1991).

When to disperse? Dispersal timing and its relationship to infanticide

We can speak of two types of social dispersal depending on when it takes place. Primary (or natal) dispersal occurs around the time of sexual maturity when the individual separates from its natal group,



Predominant social organisation	Gender most prone to disperse	Examples of possible root causes for dispersal
Multimale-multifemale groups	Males	Yellow baboon: Intrasexual competition for breeding mates. Rhesus macaque: Intrasexual competition for breeding mates. Intragroup competition for resources. Inbreeding avoidance.
	Females	Muriqui: Intragroup competition for resources. Chimpanzee: Inbreeding avoidance. Intragroup competition for resources. Western red colobus: Intrasexual competition for breeding mates. Inbreeding avoidance.
	Both	Red howler monkey: Intrasexual competition for breeding mates. Intragroup competition for resources.
Unimale-multifemale groups	Males	Hanuman langur: Intrasexual competition for breeding mates.
	Females	Hamadryas baboon: Female dispersal/transfer resulting from competition or male coercion.
	Both	Gorilla: Intrasexual competition for breeding mates. Inbreeding avoidance (in natal dispersion of females).
Unimale-multifemale groups	Both	Cotton-top tamarin: Intrasexual competition for breeding mates.
Couples	Both	Lar / white-handed gibbon: Intrasexual competition for breeding mates. Competition for resources.

Table 2. Top dispersal patterns in primates according to the predominant type of social organisation of the species and dispersal gender bias. Several examples are provided with the most likely root cause of dispersal in each case.

while secondary dispersal constitutes a change of social unit during adulthood.

The time when individuals disperse from their natal unit can be critical to their survival but this parameter varies greatly between species and between different individuals within a species, as observed in the Hanuman langur. It is thought that dispersal timing is determined by the balance between the potential costs of remaining in the group (inbreeding depression, aggression by group members, limited access to food and social resources) and the potential costs of leaving (described above).

In some species in which the dispersal of females is secondary, the decision of when to do so is influenced by the risk of infanticide (Sterck and Korstjens, 2000). As a general rule, females change social group when they do not have any dependent

offspring so as to avoid potential infanticide by males in the new group. Secondly, in species where paternity centres on a single male or is heavily biased toward him (e.g., gorillas, Thomas langurs or red colobus) the perception of the risk that this male may be replaced by an outsider, which would represent a risk of infanticide, triggers the dispersal of non-lactating females. Sometimes females disperse to the group of the potential infanticidal male. This dispersal is interpreted as mate choice, because females seem to change social unit to seek a male that will provide them with better protection against aggression for their young.

Means of dispersion. Sexual conflict and dispersion in hamadryas baboons

As discussed above, dispersal may occur spontaneously or as a result of rejection and



Juan Genovés, *Gap*, 2013. Acrylic on canvas, 120×90 cm.



Pablo Polo

Figure 3. In hamadryas baboons (*Papio hamadryas hamadryas*) the males assault the females and carry them off. One mark of this aggressive event is a bite on the neck, known as grazing.

aggression by group members. However, in hamadryas baboons, belonging to the family of Old World monkeys, females do not disperse as a result of either, but are «kidnapped». Kidnapping is a type of sexual coercion involving the forcible removal of a female from her social unit. In hamadryas baboons this is a complex process whereby males compete for a female, and the female is assaulted by a male abductor. She is subjected to aggression in order to condition her behaviour on changing unit, which has an immediate associated reproductive cost for the female (Polo and Colmenares, 2012; Polo *et al.*, 2014) and reproductive success (Figure 3). Thus, the dispersal of females between unimale units, which is the basic social and reproductive unit in this species, is more closely related to a coercive male strategy than to a female reproductive strategy, as the group change is initiated by the male and implies costs for the female.

■ FINAL REFLECTIONS

We now have a greater understanding of dispersal patterns, having characterised a large number of species. This information also shows us there are numerous exceptions to the general patterns described. Firstly, although the root cause in male dispersal in many species is related to intragroup competition for access to females, there are also cases in which dispersal seems more closely related to competition for food among group members or inbreeding avoidance. Likewise, dispersal in females seems to be more related to competition for food within the group or the avoidance of inbreeding. However, in some species females may also leave the group in search of better mating opportunities. In fact, according to the current consensus, dispersal in primates appears to be the result of a combination of all or some of these causes, at both the interspecies and intraspecies

level. Secondly, not all individuals in a population behave according to this general pattern of dispersal. For example, in some cases, female chimpanzees do not disperse and remain in their natal groups throughout their lives. By contrast, cases have been reported where females are the philopatric sex and sometimes they are the ones to leave their natal group (for example, capuchin monkeys). These cases can be explained in terms of an individually-based dispersal phenomenon, because the costs and benefits of dispersal are not only dependent on gender and species, but also the status of each individual within the group (Jack and Isbell, 2009). So, in species with female philopatry, the balance between costs and benefits for certain females may favour leaving the group, for example due to their low position in group-dominance hierarchy, which would limit access to resources. The two features above underlie the great variability found in inter-species, intra-species and inter-individual dispersal patterns in primates. ☺

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Pablo Polo Rodrigo. Researcher in Human and Animal Behaviour at the Department of Psychobiology. Complutense University of Madrid (Spain).