

Dispersal in primates: advancing an individualized approach

Preface

As a universal aspect of natural history, dispersal is important to multiple disciplines within the natural sciences, including behaviour, ecology, evolutionary biology, genetics and conservation biology. Who disperses when, where and how (behaviour and ecology) can lead us to understand why dispersal occurs at all (evolutionary biology) and what the consequences of dispersal are for populations in the short term (e.g., degree of genetic differentiation) and in the long term (e.g., population viability). It is important, then, to document the natural history of dispersal if we are to gain greater understanding of these broader perspectives. Unfortunately, documenting dispersal has turned out to be exceedingly difficult, for several reasons. First, not every individual disperses, and for those that do disperse, it is often a once-in-a-lifetime event. What are the chances that this event will be witnessed by scientists? Second, studies are often not sufficiently long to document beyond anecdotal information on dispersal, and anecdotes are currently difficult to publish. Finally, the circumstances faced by animals before and after they disperse are often only documented when collecting such data does not interfere with the main purpose of the study. Focusing on dispersal in a grant proposal is likely to be as risky as dispersal itself! The difficulties are even more challenging for those studying long-lived animals, which are typically slow to mature.

What do we know about dispersal? Beyond its universality in the natural world, we know that dispersal is indeed risky, fraught with danger from many angles (Pusey & Packer, 1987; Isbell & Van Vuren, 1996). Animals that move into unfamiliar areas (locational dispersal) may die from predation because they lack knowledge about predators in those new areas (e.g., the types of predators, their densities, and their habits) and because they lack knowledge of the locations of safe places. Dispersers may die of starvation because they may move to a place where their nutritional needs cannot be met, or where they are prevented from eating as much as they need by others in the

area. Dispersers that leave home and begin to interact with strangers (social dispersal) are susceptible to injury and possibly death as a result of increased aggression from those strangers (Isbell & Van Vuren, 1996). Finally, we must not forget accidents; how many animals killed on the road are individuals in the process of dispersing? The high risk of dispersal makes its universality all the more puzzling evolutionarily. The benefits must be exceedingly high in order to outweigh the high cost of dispersal.

Normally, one might expect to find very little information on dispersal in such long-lived mammals as primates, but there are certain primate characteristics that lend themselves to the study of dispersal. While studies of nocturnal primates still often rely on indirect or non-visual observations and the capture/recapture techniques common to studies of other nocturnal mammals, the majority of primates are diurnal, which makes it easier to observe individually recognizable animals. Some primatological studies have also become multi-generational in regard to both subjects and observers, finally accumulating data on dispersal that are now more than anecdotal. Employment of an individual-based, multi-year focus is making it possible to begin to identify the circumstances surrounding who disperses when, where, how and why. This special issue of *Behaviour* reveals that there is much more variation in the causes of dispersal than was originally thought.

This Special Issue arose from an invited symposium at the XXIInd Congress of the International Primatological Society in Edinburgh, Scotland, UK, 3–8 August 2008. The symposium, titled *Should I Stay or Should I Go Now? Dispersal Opportunities, Individual Decisions, and Consequences for Wild Primates*, enabled primatologists to present the gains in our knowledge since this topic was last tackled in special journal issues (2003–2004 *Primate Report* and 1992 *International Journal of Primatology*). Together these two special issues presented 13 papers that covered theoretical aspects of dispersal (4 papers) and presented data on some of the better-studied primates, namely baboons (2 papers), macaques (3 papers), howler monkeys (2 papers), langurs (1 paper) and ring-tailed lemurs (1 paper). While the 2003–2004 special issue examined dispersal from a broad perspective, investigating the proximate and ultimate causes of primate dispersal (Jones, 2003), the 1992 issue emphasized two key points: female life history strategies drive dispersal and dispersal is a coevolutionary process between the strategies of females and the strategies of males (Smith & Sprague, 1992).

Since these publications, long-term studies have gotten longer, more long-term studies have become established, some of the lesser known species are

now being studied, and technological tools for studying genetic relationships non-invasively have become available. The key point we would like to make here is that dispersal strategies are often highly individualized, dynamic and flexible. While Pusey & Packer (1987), in their classic review of the topic, noted that primate dispersal showed high levels of both inter- and intra-specific variation, we are only now beginning to understand the extent of this variability. This variability exists because individuals face circumstances that are unique to them, particularly in the social realm, and these circumstances can affect the decision to stay in the natal home range or group or to leave. The word 'Now' in the title of the symposium is highly meaningful here as it underscores the dynamic nature of such decisions.

Many of the papers in this issue reveal just how flexible dispersal decisions can be. It is no longer accurate to state that one or the other sex disperses at sexual maturity; dispersal in primates is much more complicated than that. Whereas cercopithecine monkeys are indeed 'typical' mammals in having male dispersal and female philopatry (Greenwood, 1980; Pusey & Packer, 1987), many other primate taxa are turning out to be quite variable (Strier, 1994), and we have tried to include examples from a wide range of taxa to highlight the diversity of social systems and dispersal options in primates. The 11 papers in this Special Issue of *Behaviour* are based on long-term studies (4–38 years) with multiple representatives from the four major primate taxa. This special issue includes two species of prosimians (one nocturnal, solitary foraging species and one diurnal, group-living species, both of which have both male and female dispersal), four species of platyrrhines (one monogamous species and three group-living species, two with non-sex-biased dispersal, one with male dispersal and occasional female dispersal, and one with female dispersal in most, but not all, populations), and five species of catarrhines (all group-living species, one with male dispersal, one with female dispersal and three with both male and female dispersal).

While the majority of the papers presented here deal with natal dispersal, many (e.g., Di Fiore et al., Jack & Fedigan, Morelli et al., Robbins et al., Teichroeb et al.) do include data on secondary dispersal (defined here as further social dispersal subsequent to natal transfer). Some of the papers included in this issue were chosen to highlight the fact that in many primate species, both males and females can disperse from their natal groups, e.g., lowland woolly monkeys (*Lagothrix poeppigii*) (Di Fiore et al.), but we were surprised to find out that variability can exist even within the same species. For example, in

a study that combined behavioural observations with molecular analyses, Di Fiore et al. found that white-bellied spider monkeys (*Ateles belzebuth*) have female-biased dispersal at one site, as reported elsewhere for other species of spider monkeys (*A. paniscus*: Symington, 1987), but non-sex-biased dispersal at another site.

A common explanation for sex-biased dispersal is inbreeding avoidance (Packer, 1979, 1985; Pusey & Packer, 1987; Clutton-Brock, 1989). Interestingly, in chimpanzees (*Pan troglodytes*), which have male philopatry and (largely) female dispersal, Stumpf et al. suggest that incest avoidance is not a trigger for dispersal in their study population because most maturing female chimpanzees mate (with potential kin) in their natal group before emigrating sometime after menarche. Such a delay, however, may ultimately pose little risk of inbreeding due to a suspected period of sub-fecundity following menarche. But how do we explain dispersal by both sexes? In white-faced capuchins (*Cebus capucinus*), a species long considered to have male dispersal and female philopatry, Jack and Fedigan document that 14% of the adult females in their study groups have been immigrants. Given that dispersal is so risky, dispersal by both males and females would seem to be overkill, at least for species that live in large groups, if its only evolutionary function is in avoiding inbreeding. For species that live in small breeding groups, however, bisexual dispersal may indeed be the best way to avoid inbreeding. In Milne-Edward's sifakas (*Propithecus edwardsi*), usually only one male and one female breed per group and both males and females disperse. Morelli et al. provide behavioural evidence and genetic confirmation that incest is avoided in Milne-Edward's sifakas because maturing individuals disperse whenever a related adult of the opposite sex is present in the group. In owl monkeys (*Aotus azarai*), also, only one male and one female breed in a group, and Fernandez-Duque reports no sex bias in dispersal rate or distance, no inheritance of territory, and no reproduction between kin. Nonetheless, inbreeding avoidance is not guaranteed in such small groups. In golden-brown mouse lemurs (*Microcebus ravelobensis*), individuals forage solitarily but sleep in small groups. Radespiel et al. report that although both males and females disperse, genetic analyses reveal that inbreeding does occur on occasion because males sometimes delay dispersal.

Indeed, the timing of natal dispersal may be critical and highly individual, with many species displaying a considerable age range during which dispersal occurs. For example, dispersal may occur between 3.5 and 8 years

in Milne-Edward's sifakas (Morelli et al.), and between 10 and 15 years of age (or not at all) for female chimpanzees (Stumpf et al.). This variation in the timing of dispersal likely reflects a balance between the potential costs of leaving vs. staying. While delayed dispersal may provide some individuals with the time needed to reach a larger body size (e.g., male mouse lemurs: Radespiel et al.) or increased social and physical maturation (e.g., female chimpanzees: Stumpf et al.), others, such as male patas monkeys (*Erythrocebus patas*) and female mountain gorillas (*Gorilla gorilla beringei*) may often wait to disperse until the opportunity arises to join other conspecifics directly upon leaving their groups, as Rogers & Chism and Robbins et al. report. Individuals may also time their dispersal so that they are emigrating and/or immigrating with others (parallel dispersal). Female ursine colobus (*Colobus vellerosus*: Teichroeb et al.), male and female white-faced capuchins (Jack & Fedigan) (Fig. 1), and male humans (*Homo sapiens*: Glover & Towner) are examples of species that engage in parallel dispersal. In species with male-biased dispersal, parallel dispersal appears to be associated with the presence of coalitions, which likely makes it easier to join existing groups (Schoof et al.).

Although leaving home may be accompanied by risks and individuals may take steps to mitigate those risks, under certain circumstances it might be better to leave when conditions at home have changed for the worse, and this may help to explain female dispersal in conjunction with male dispersal in species that live in larger breeding groups. One change occurs when groups become unstable in membership as a result of immigration by males or females. If the arrival of new group members is accompanied by a high risk of infanticide (by males or by females), females with young offspring may disperse rather than stay and lose their investment. Similarly, females that are targeted with heightened aggression may choose to leave rather than remain. In Milne-Edward's sifakas (Morelli et al.), ursine colobus (Teichroeb et al.), and white-faced capuchins (Jack & Fedigan), females often disperse following changes in group membership and resultant infanticide. In fact, failure to reproduce for any reason (e.g., infanticide, hormonal insufficiency, or miscarriage) might be incentive enough for some females to disperse in species with both male and female dispersal (Isbell & Van Vuren, 1996; Isbell & Young, 2002). For example, after dispersing from their natal groups and joining neighboring groups, female mountain gorillas often make secondary transfers to other groups, and one predictor of such secondary dispersal events is reproductive failure (Robbins et al.).



Figure 1. A coalitionary threat display between an adult male and a juvenile male white-faced capuchin monkey (*Cebus capucinus*). These types of coordinated threat displays are common among male capuchins and are believed to reinforce social bonds. Male capuchins frequently engage in parallel dispersal and rely on each others' support to successfully immigrate into or takeover new groups. Photo courtesy of Amanda D Melin. This figure is published in colour in our online edition that can be accessed via <http://www.brill.nl/beh>

The possibility also exists that less immediate effects on reproductive success, e.g., differential access to resources, influence the decision of individuals to disperse. Thus, in the female-dispersing chimpanzees, natal females with a higher quality diet (one rich in fruits) tend to disperse earlier in life (Stumpf et al.). Conversely, in the bisexually dispersing ursine colobus, young, nulliparous females disperse after they are targeted with aggression

from older females, but targeted aggression occurs only in larger groups, where feeding competition is thought to be greater (Teichroeb et al.). Not surprisingly, Glover and Towner's study of male long-distance dispersal in humans showed that many dispersers had little access to material wealth in their childhood homes. Surprisingly, however, some dispersers were quite wealthy. The fact that they dispersed to a booming mining town reveals that the incentives for dispersing are more complex in humans than is the case for non-human primates, because social circumstances are also more complex.

It is our hope that the papers presented in this special issue illustrate how far dispersal research in primates has come and stimulate new directions for future research on this topic. While historically studies of primate dispersal (and mammalian dispersal in general) tended to look for broad general patterns (e.g., Greenwood, 1980; Pusey & Packer, 1987), we now realize that there are many exceptions to these general patterns and that inter- and intra-specific variation in dispersal is even greater than once thought. Discovering how variable primate dispersal is has led many researchers to embrace the individually based approach, which we highlight here. As for the future of dispersal research, although we need to continue with the long-term, individualized approach, dispersal studies can be greatly advanced through the use of a number of well established technologies such as GIS/GPS tracking, socio-endocrinology, and molecular genetics. While several of the studies included in this special issue do make use of these technologies (e.g., radio-collars or tracking microchips to locate missing individuals: Di Fiore et al., Duque, Morelli et al.; glucocorticoid profiles as indicators of stress: Stumpf et al.; molecular techniques for estimating kinship, paternity and/or dispersal distances: Di Fiore et al., Morelli et al., Radespiel et al.) more widespread use will greatly aid our ability to study the dispersal process, its proximate causes, and its outcome.

KATHARINE M. JACK

LYNNE A. ISBELL

Guest Editors

E-mail: kjack@tulane.edu

References

- Clutton-Brock, T.H. (1989). Female transfer and inbreeding avoidance in social mammals. — *Nature* 337: 70-72.

- Greenwood, P.J. (1980). Mating systems, philopatry, and dispersal in birds and mammals. — *Anim. Behav.* 28: 1140-1162.
- Isbell, L.A. & Van Vuren, D. (1996). Differential costs of locational and social dispersal and their consequences for female group-living primates. — *Behaviour* 133: 1-36.
- Isbell, L.A. & Young, T.P. (2002). Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. — *Behaviour* 139: 177-202.
- Jones, C.B. (2003). The proximate and ultimate costs and benefits of dispersal in primates. — *Primate Rep.* 67: 3-6.
- Packer, C. (1979). Inter-troop transfer and inbreeding avoidance in *Papio anubis*. — *Anim. Behav.* 27: 1-36.
- Packer, C. (1985). Dispersal and inbreeding avoidance. — *Anim. Behav.* 33: 676-678.
- Pusey, A.E. & Packer, C. (1987). Dispersal and philopatry. — In: *Primate societies* (Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T., eds). University of Chicago Press, Chicago, IL, p. 250-266.
- Smith, E.O. & Sprague, D.S. (1992). Introduction: migration and dispersal. — *Int. J. Primatol.* 13: 357-360.
- Strier, K.B. (1994). Myth of the typical primate. — *Am. J. Phys. Anthropol.* 37: 233-271.
- Symington, M.M. (1987). Sex ratio and maternal rank in wild spider monkeys: when daughters disperse. — *Behav. Ecol. Sociobiol.* 20: 421-425.
-