Oecologia (Berlin) (1986) 69:626–627

Oecologia
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Short communications

Sex-biased philopatry and dispersal in mammals

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The young males of many species of mammals move away from their parents and settle in new home ranges before starting to breed, while females are likely to stay for life near their places of birth (Greenwood 1980; Packer 1979; Dobson 1982; Waser and Jones 1983). The dispersal of some juveniles has often been interpreted as a mechanism for the avoidance of inbreeding, a view that is reinforced by recent evidence of the high costs of inbreeding in wild and captive populations (Greenwood et al. 1978; Packer 1979; Ballou and Ralls 1982). Because female mammals generally invest more in each of their reproductive attempts than do males (Trivers 1972), the costs of inbreeding should fall most heavily on them (see Greenwood 1980), and there is evidence from several species that, given the opportunity, females are less inclined than males to mate incestuously (see Packer 1979 and references therein, Hoogland 1982). We should therefore expect young females to be more likely than young males to disperse; why then are males so often the dispersing sex?

Previous arguments

Because male-biased dispersal is most characteristic of polygynous mammals (Dobson 1982), most attempts to explain it have postulated a relationship between the dispersal of young males and the strategies adopted by adult males to accumulate matings. Greenwood (1980) suggested that where adult males compete for matings by defending females (as is common in mammals), rather than by defending resources attractive to females, they will gain little by being philopatric and will therefore be more inclined than females to disperse. In contrast, males who defend territories to attract females (as often happens in birds) will probably do so most effectively on familiar ground close to male relatives and should therefore tend to be philopatric. Greenwood offered this hypothesis to account for the prevalence of female dispersal and the philopatry of males in birds (see also Baker 1978), together with the converse pattern in mammals. However Waser and Jones (1983) point out that there are a sufficient number of species of mammals in which male dispersal and territoriality are associated to cast serious doubt on Greenwood's argument.

Moore and Ali (1984) argued that the avoidance of inbreeding has been of minor importance in the evolution of dispersal, and suggested instead that the aggression of older males forces young subordinates away from home. This view discounts the greater difficulties that young males will face in attempting to re-establish themselves elsewhere, and cannot be satisfactorily applied to the many species in which the dispersal of young males is not initiated by aggression from older males (Clutton-Brock and Harvey 1976; Packer 1979, 1985). In *Antechinus stuartii* and *A. swainsonii* young males disperse at a time of the year when all of the adult males are dead (Cockburn et al. 1985).

Packer (1979) suggested that male dispersal in polygynous mammals arose from the tendency of adult males to move into temporary concentrations of sexually active females. In olive baboons *Papio anubis*, for example, adult males who transfer from one troop to another usually move into troops containing more sexually active females than were present in the troops they abandoned (Packer 1979). The fact that adult males may transfer several times in their lives must diminish the force of selection for philopatry in young males. Packer's argument can explain the dispersal of young males in gregarious species where different groups have regular contact so that males can appraise mating opportunities in troops other than their own, but it is less useful when applied to solitary species, within which males are still more likely than females to disperse (Waser and Jones 1983).

A more general relationship between inter-male competition for mates and dispersal by juvenile males has been proposed by Dobson (1982), who pointed out that opportunities for mating are scarcer for young males than for young females in polygynous species: young males may therefore be obliged to diperse in search of mating opportunities. However, there are several ways in which one can argue that intense mating competition between males could favour philopatry among young males. First, since dispersing males are likely to face rigorous competition from other males wherever they go, they could under some circumstances make greater gains in reproductive success by waiting patiently in the home area, ready to seize opportunities for increasing their social status and usurping dominant males. Second, any male who avoided the energetic costs of dispersal would thereby retain a valuable competitive advantage over dispersing males. Third, since females are likely to compete with one another to some extent for the resources essential to reproduction they might sometimes gain by dispersing and, if they compete less potently than males, might find it easier to settle after moving and therefore be more predisposed to leave home. Any path that a male of a polygynous species takes is likely to lead him to a more extreme outcome than a female might expect, but this fact alone should not necessarily result in a general tendency towards dispersal among polygynous males. Indeed, two of the three species of non-human primates in which males are regularly philopatric – the red colobus monkey *Colobus badius* (Strushaker and Leyland 1979, Marsh 1979) and the hamadryas baboon *Papio hamadryas*

(Sigg et al. 1982; Kummer 1984) – are actually more polygynous, as judged by degrees of sexual dimorphism and socionomic sex ratios (Clutton-Brock et al. 1977), than are most primates.

An alternative hypothesis

I assume that there are circumstances under which dispersal benefits juveniles of both sexes, and ask whether the costs of dispersal differ consistently between the sexes.

Dispersal must often be difficult and dangerous: young animals who leave home pass through unfamiliar terrain and may have to live for some time in suboptimal habitats. Dispersal by young males is associated with their differential mortality in a number of mammals (see Ralls et al. 1980), and Holekamp (1984) observed that although juvenile male Belding's ground squirrels *Spermophilus beldingi* who dispersed were significantly heavier when they left than were males of the same age who did not disperse, their body weights subsequently dropped below those of the non-dispersing males. Juvenile males and females probably find dispersal equally demanding, but if their life-time fecundity schedules typically differ the stresses of dispersal could have different consequences for their subsequent reproduction. In polygynous species of mammals, females usually start breeding as soon as they reach maturity, while mating by males is often delayed because of the control that old, dominant males exert over opportunities for mating (Ralls 1977; Alexander et al. 1979; Jarman 1983; Michener 1983; Harvey and Clutton-Brock 1985). This period of reproductive inactivity through which young adult males are forced to pass is likely to diminish the influence of juvenile dispersal on the ages at which they first breed: males have time to recover from or compensate for the energetic demands of dispersal. If, however, dispersal takes up a significant portion of a juvenile female's time or causes her to lose condition it will almost certainly delay the onset of her reproductive life. Dispersal thus imposes heavier costs on the juvenile females than on the juvenile males of polygynous species.

This hypothesis can be generalised to suggest that the sex for which juvenile dispersal causes the greater delay in age at first breeding will be the least likely to disperse; it can probably account for the general association of male-biased dispersal with polygyny.

The hypothesis predicts that differences in the dispersive tendencies of the sexes will be slight or inconsistent in species where males and females are able to begin reproducing at similar ages, and where members of each sex are potentially able to breed over more than one season. It also predicts that sex-biases in philopatry and dispersal will be most profound when the energetic demands of dispersal are most severe, as when dispersers are obliged to travel over long distances or from one island of habitat to another. Since the publication of Greenwood's (1980) review, any attempt to account for the male-biased dispersal of mammals should also be tested by its applicability to the female-biased dispersal of birds. Greenwood's explanation of the philopatry of male birds – that the establishment and defence of a territory will be most practible near the home area – is congenial with the hypothesis given here: a male bird is probably able to set up his territory and acquire a mate earlier through philopatry than would be possible if he dispersed. However, I suggest that it is the connection of male territoriality with monogamy, not territoriality per se, that sets the dispersal patterns of birds apart from those of mammals. Where the onset of reproduction by males is delayed through polygyny the significance for juvenile males of dispersal is diminished, whether or not they eventually hold territories, and dispersal becomes more costly for females than for males.

References

Baker RR (1978) The evolutionary ecology of animal migration. Hodder and Stoughton, London

Ballou J, Ralls K (1982) Inbreeding and juvenile mortality in small populations of ungulates: a detailed analysis. Biol Conserv 24:239–272

Clutton-Brock TH, Harvey PH (1976) Evolutionary rules and primate societies. In: Bateson PPG, Hinde RA (eds) Growing points in ethology. Cambridge University Press, Cambridge

Clutton-Brock TH, Harvey PH, Rudder B (1977) Sexual dimorphism, socionomic sex ratio and body weight in primates. Nature 269:797–800

Cockburn A, Scott MP, Scotts DJ (1986) Inbreeding avoidance and male-biased natal dispersal in *Antechinus* spp. (Marsupialia: Dasyuridae). Anim Behav (in press)

Dobson FS (1982) Competition for mates and predominant juvenile male dispersal in mammals. Anim Behav 30:1183–1193

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162

Greenwood PJ, Harvey PH, Perrens CM (1978) Inbreeding and dispersal in the great tit. Nature 271:52–54

Harvey PH, Clutton-Brock TH (1985) Life history variation in primates. Evolution 39:559–581

Holekamp KE (1984) Natal dispersal in Belding's ground squirrels (*Spermophilus beldingi*). Behav Ecol Sociobiol 16:21–30

Hoogland JL (1982) Prairie dogs avoid extreme inbreeding. Science 215:1639–1641

Jarman PJ (1983) Mating system and sexual dimorphism in large, terrestrial, mammalian herbivores. Biol Rev 58:485–520

Kummer H (1984) From laboratory to desert and back: a social system of hamadryas baboons. Anim Behav 32:965–971

Marsh CW (1979) Female transference and mate choice among Tana River red colobus. Nature 281:568–569

Michener GR (1983) Kin identification, matriarchies and the evolution of sociality in ground-dwelling sciurids. In: Eisenberg JF, Kleiman DG (eds) Advances in the study of mammalian behavior. The American Society of Mammalogists, Special Publication No 7

Moore J, Ali R (1984) Are dispersal and inbreeding avoidance related? Anim Behav 32:94–112

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

Ralls K (1977) Sexual dimorphism in mammals: avian models and unanswered questions. Amer Nat 111:917–938

Ralls K, Brownell RL, Ballou J (1980) Differential mortality by sex and age and mammals, with special reference to the sperm whale. Rep Int Whal Comm special issue 2:223–243

Sigg H, Stolba A, Abegglen J-J, Dasser V (1982) Life history of hamadryas baboons: physical development, infant mortality, reproductive parameters and family relationships. Primates 23:473–487

Strushaker TT, Leyland L (1979) Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. Adv Study Behav 9:159–228

Trivers RL (1972) Parental investment and sexual selection. In: Cambell B (ed) Sexual selection and the descent of man. Chicago University Press, Chicago

Waser PM, Jones WJ (1983) Natal philopatry among solitary mammals. Q Rev Biol 58:355–390

Received November 25, 1985