dispersers becoming established away from their natal ground may be greatly reduced. Where this is not the case, the inclusive fitness benefits of dispersal will be reduced if many non-related dispersers can usurp resources in the natal area.

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9

Inbreeding, kinship, and the evolution of natal dispersal

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Abstract

Using analytical tools from game theory, we investigate the relevance of a series of hypotheses concerning natal dispersal, focusing in particular on the interaction between inbreeding and kin competition, as well as on the components of mating and social systems that are likely to interfere with these phenomena. A null model of pure kin competition avoidance predicts a balanced equilibrium in which both sexes disperse equally. Inbreeding costs have the potential to destabilize this equilibrium, resulting in strongly sex-biased dispersal. This effect is mostly evident when the peculiarities of the mating system induce asymmetries in dispersal and/or inbreeding costs, or when kin cooperation counteracts kin competition. Inbreeding depression, however, is not the only possible cause for sex biases. The relevance of our results to empirical findings is discussed, and suggestions are made for further empirical or modelling work.

Keywords: competition, cooperation, inbreeding, kin selection, mating systems

Chapter aims and structure

The role of inbreeding avoidance in dispersal remains highly controversial. Some authors consider it to be central, and others irrelevant. Part of the problem stems from the fact that arguments usually remain purely verbal. Moreover, potential causes are too often considered as alternatives rather than as interacting forces. Inbreeding is likely to interfere with several other selective forces behind dispersal, and the whole story is too complex to be accounted for fully by verbal models. Rather than a review of empirical data, the present chapter is an attempt to bring models and arguments into a common mathematical framework. Our purpose is to provide a formalization of the interactions between inbreeding, kinship, and dispersal, in order to evaluate the importance of inbreeding relative to other selective forces.

The concept of inbreeding itself may be confusing, as it is often used in different contexts and with different meanings (e.g. Jacquard 1975; Templeton and Read 1994). Thus, the chapter starts with some definitions and basic empirical information. It then makes a brief excursion into the verbal arguments that have been invoked when attempting to link dispersal and inbreeding. The second part, which constitutes the core of the chapter, develops an evolutionary modelling approach. After introducing the analytical framework and assumptions, we investigate the relevance of a series of hypotheses concerning natal dispersal, focusing in particular on the interaction between inbreeding and kin competition, as well as on the components of mating and social systems that are likely to interfere with these phenomena.

Some definitions, and a few words about the context

What is inbreeding?

At the individual (behavioural) level, inbreeding designates a process, that of mating with a relative. Any offspring born from such a mating is likely to carry genes that are identical by descent, and is said to be inbred. In that sense, inbreeding is a universal and inescapable feature of finite sexual populations. Population biologists, however, usually refer to inbreeding in a relative sense, as may be quantified through Wright's fixation indices. If mating partners in a population are, on average, more related than expected by chance, then observed heterozygosity (H_i) will be lower than the Hardy–Weinberg expectation (H_p). Wright's (1921) *inbreeding coefficient*:

$$F_{ip} = \frac{H_p - H_i}{H_p} \qquad (1.1)$$

measures this deficit in heterozygotes relative to random-mating expectation. A null value does not imply absence of mating among relatives, but only that mating partners are, on average, no more related than would be expected by chance. Therefore, in the following, the term 'inbreeding' will be used in its relative sense, as measuring the genetic similarity among mating partners *in excess of random-mating expectation* (or, equivalently, the probability that the two copies of a gene in any offspring are identical, *relative to random copies* from the population).

The most likely cause of inbreeding is population structure. If dispersal is low, individuals mate with neighbours, who are likely to be closer relatives than average individuals in the population. A convenient way to formalize spatial structure is to assume that populations consist of local groups of related individuals, genetically differentiated from other such groups. Genetic similarity among patch mates can be measured by their *co-ancestry*:

$$F_{gp} = \frac{H_p - H_g}{H_p} \qquad (1.2)$$

building on the fact that, because some genetic variance occurs among groups, the variance within groups (H_g) is lower than total variance (H_p). The co-ancestry between two individuals measures the probability that their gametes carry identical alleles, relative to gametes taken randomly from the population. By this definition, co-ancestry among partners equals the inbreeding coefficient of their offspring, and co-ancestry with self is $(1 + F_{ip})/2$. Co-ancestry among patch mates as a proportion of self co-ancestry measures their *relatedness*:

$$r = \frac{2F_{gp}}{1 + F_{ip}} \qquad (1.3)$$

If patterns of effective migration among groups are known, inbreeding and co-ancestry coefficients can be worked out by deriving the equilibrium conditions of a set of difference equations. This has been done in particular for situations that allow one to account for the peculiarities of breeding systems (sex-biased dispersal and degree of polygyny; Chesser 1991a,b; Sugg *et al.* 1996). A low dispersal results in significant differentiation among groups ($F_{gp} > 0$) but, if sex-biased, it also creates an excess of heterozygotes at the group level:

$$F_{ig} = \frac{H_g - H_i}{H_g} < 0 \qquad (1.4)$$

F_{gp} and F_{ig} may actually diverge drastically in polygynous mating systems with male-biased dispersal (Dobson *et al.* 1997). However, as implied by equations (1.1), (1.2), and (1.4), these coefficients are linked by the constraint:

$$(1 - F_{ip}) = (1 - F_{ig})(1 - F_{gp}) \qquad (1.5)$$

so that divergences may cancel out in such a way that inbreeding vanishes (i.e. $F_{ip} = 0$). Thus inbreeding (in its relative sense) is not a necessary consequence of population structure.

Why avoid inbreeding?

Inbred individuals often display phenotypic abnormalities, resulting in a loss of fitness through lower viability or fertility. Although *inbreeding depression* could be defined as the decline, with increasing homozygosity, in the mean phenotype of any trait (Lynch and Walsh 1998), we will refer to it as a decline in fitness. Consistent with our definition of inbreeding, the *cost of inbreeding* will be the fitness loss of an inbred mating *relative to* a random mating (Fig. 9.1).

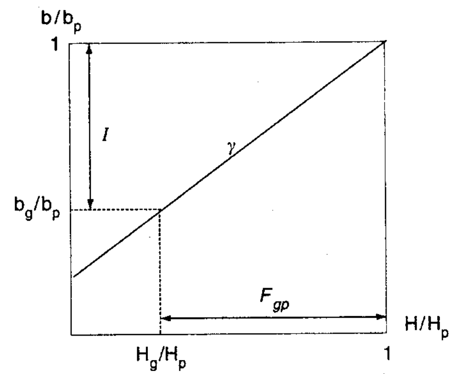

Figure 9.1. Relative fecundity of partners in a pair (b/b_p) as a function of their relative genetic dissimilarity (H/H_p). F_{gp} is the co-ancestry among partners stemming from the same patch. I the inbreeding cost of their mating, and γ the marginal decrease in relative fecundity with co-ancestry.

Inbreeding depression can occur only if alleles at a locus do not act additively. Dominance or over-dominance (heterozygote advantage) is needed. Little evidence exists for the impact on inbreeding depression of over-dominance, although it might be quite important (Lynch and Walsh 1998). In the dominance model, recessive alleles are assumed to be deleterious to various degrees. As inbreeding increases homozygosity (including that of recessive deleterious alleles), it decreases fitness. The number of recessive deleterious alleles in a population is referred to as the *genetic load*, and is quantified here as the marginal change in relative fitness with a change in relative homozygosity (Fig. 9.1).

This genetic load may actually be purged by recurrent inbreeding. If the recessive alleles are strongly deleterious, then inbred individuals carrying them are likely to die. After a few generations of inbreeding, the frequency of deleterious alleles in a group may have diminished drastically. This process, however, requires that groups must be able to cope with a high mortality rate for some generations, and that deleterious alleles are problematic enough to cause death (otherwise they might become fixed in small groups because of drift). It also implies some isolation, since newcomers are likely to bring new deleterious alleles. Social species living in closed groups might be good candidates (e.g. Reeve *et al.* 1990; Keane *et al.* 1996).

Inbreeding depression has been demonstrated repeatedly in mammals (including humans), other vertebrates, invertebrates, and plants (including, surprisingly, selfing species; Agren and Schemske 1993). It has been reported in the laboratory (e.g. Brewer *et al.* 1990; Keane 1990) and, more importantly, in the field (Chen 1993; Bensch *et al.* 1994; Jimenez *et al.* 1994; Keller *et al.* 1994; Madsen *et al.* 1996; Olsson *et al.* 1996; Keller 1998; Westemeier *et al.* 1998; reviewed by Lynch and Walsh 1998). Cases of strong inbreeding depression seem often to be linked to unusual situations such as recent habitat fragmentation (e.g. Madsen *et al.* 1996; Hitching and Beebee 1998) which isolates previously outbred populations and thereby exposes high genetic loads to selection.

A few cases showed no sign of inbreeding depression (e.g. Gibbs and Grant 1989; Reeve *et al.* 1990; Keane *et al.* 1996), which might be due to the purging of deleterious mutations. Whether such situations are common is difficult to estimate for obvious reasons of publication bias. Inbreeding might even be beneficial under some circumstances (see below).

Did dispersal evolve to avoid inbreeding?

Dispersal may intuitively appear as an obvious means to avoid inbreeding depression. The pervasive importance of dispersal in general, and of sex-biased dispersal in particular, has often been interpreted as the direct consequence of inbreeding avoidance (Johnson and Gaines 1990). Indeed, incestuous matings (defined as parent–offspring or sib–sib pairing) are rare in the field (normally less than 2% according to Ralls *et al.* 1986; Harvey and Ralls 1986). Such low levels clearly could not be achieved without dispersal (in interaction with kin recognition mechanisms when these exist).

This, however, does not imply that inbreeding avoidance is the ultimate cause of dispersal, which might evolve primarily as a response to other selective pressures such as non-equilibrium population dynamics, competition for resources, or competition for mates (Johnson and Gaines 1990). These and other causes may generate sufficient

dispersal to prevent inbreeding anyway, in such a way that inbreeding avoidance itself plays only a marginal role.

Furthermore, the selective pressure induced by inbreeding may often not suffice to drive dispersal:

- Inbreeding might even be favoured, for at least two reasons. First, outbreeding may dismantle genetic co-adaptations built up locally through linked gene complexes (Shields 1982, 1983; Bateson 1983; Templeton 1986; Wiener and Feldman 1993). Second, inbred matings bring direct benefits to males (and inclusive benefits to females through increased reproductive output of related males), as long as they do not forfeit other breeding opportunities (Parker 1979, 1983; Waser *et al.* 1986).
- The costs of dispersal may outweigh those of inbreeding (e.g. Pärt 1996). The dispersal-induced mortality rate sometimes exceeds 50% (Johnson and Gaines 1990). High costs may force individuals to be philopatric, and the ensuing inbreeding history may largely purge deleterious mutations from populations, a process that would further reinforce philopatry.
- Other ways to avoid or limit inbreeding costs exist (Harvey and Ralls 1986; Blouin and Blouin 1988), including kin recognition (McGregor and Krebs 1982; Fletcher and Michener 1987; Keane 1990), promiscuity and multiple paternity (Brooker *et al.* 1990; Stockley *et al.* 1993), extra-group copulations (Sillero-Zubiri *et al.* 1996), and divorce (Kempenaers *et al.* 1998).

As a consequence, much debate has resulted over the exact role of inbreeding in the evolution of dispersal. Some authors consider inbreeding avoidance as a central cause (Bengtsson 1978; Packer 1979, 1985; Harvey and Ralls 1986; Pusey 1987; Wolff 1992; Wolff and Plissner 1998). Among the arguments presented are sex biases in dispersal and negative correlations between male and female dispersal (Pusey 1987). Others consider inbreeding to be only marginally important. Waser *et al.* (1986) argue that inbreeding depression should select for female-biased dispersal in polygynous mating systems, while the opposite is usually observed. Dobson (1982) concludes from his review that competition for mates is the primary reason for male-biased dispersal in mammals. Some authors even see inbreeding as totally irrelevant (Moore and Ali 1984), an extreme position that seems hardly tenable: in addition to clear-cut empirical evidence (e.g. Dobson 1979; Packer 1979, 1985; Cockburn *et al.* 1985; Clutton-Brock 1989; Wolff 1992), there are good logical arguments to expect inbreeding to play a significant role in dispersal. The question is not whether inbreeding affects dispersal or not, but how and by how much.

A modelling approach

Whatever the causes driving dispersal, optimal decisions are likely to depend on partners' behaviour, so that a game-theoretical approach is required. Furthermore, any consideration of the role of inbreeding has to incorporate kin selection arguments, simply because inbreeding itself cannot arise without kin structures. But its role must also be clearly differentiated from that of kin competition avoidance. For this reason our model has two starting points. The first considers a stable, structured population with no genetic load, in which local competition is the only cause affecting dispersal. The second starting point assumes a population free of any sort of competition (but not of genetic load), which will allow us to delineate the direct and indirect (kin-selected) effects of inbreeding. The interaction of both causes (a more general and realistic situation) will then be considered, before we investigate the possible influence of mating systems and social structures. However, several of the reasons why inbreeding avoidance may not drive dispersal (such as outbreeding depression, purging, or kin recognition) will not be investigated here.

Our model organism is diploid and annual, the sex ratio is even at birth, and dispersal precedes mating and is under offspring control. For analytical tractability we assume an infinite island model. Even though isolation by distance might constitute a more realistic framework, it would encumber analysis without adding much to the understanding of the basic principles delineated below.

Local competition without inbreeding

The idea behind kin selection is that individuals gain inclusive fitness benefits from enhancing the reproduction of relatives (Hamilton 1964). Hamilton and May (1977) showed that dispersal might be selected for in stable habitats and in the absence of inbreeding depression, even if it bears survival costs. This arises from the inclusive fitness benefits of avoiding competition with kin, not from direct fitness effects. Indeed, dispersal is clearly detrimental in terms of individual fitness, because it bears dispersal costs which, in stable habitats (notwithstanding demographic stochasticity), are not compensated for by a lower level of competition in the new habitat. But relatives will benefit from the release from competition, which may improve the disperser's inclusive fitness sufficiently for some level of dispersal to be favoured. Hamilton and May (1977) considered only one sex competing for a limiting resource, but we will follow here a formalization with two sexes, in order to allow for later inclusion of inbreeding and possible biases in sex-specific dispersal.

Let us consider patches of limited size (say N breeding opportunities). Let female i in patch j disperse with probability x_{ij}, and survive dispersal with probability s ($c = 1 - s$ is the mortality cost to dispersal). In her new patch, she will compete for N breeding opportunities among $Nb(1 - x + xs)$ unrelated females, where b is the average number of daughters per female, and x is the average dispersal rate in the population. With the complementary probability $1 - x_{ij}$, this female will stay in her patch, and compete there for N breeding opportunities among $Nb(1 - x_j + xs)$ females, from which $Nb(1 - x_j)$ are related (x_j is the average dispersal rate in patch j). In case of success, this female will produce b copies of her genes, so that her total fitness may be written:

$$W_x = x_{ij}\frac{sNb}{Nb(1 - x + xs)} + (1 - x_{ij})\frac{Nb}{Nb(1 - x_j + xs)} \tag{2}$$

Selective pressures are derived using the direct fitness approach of Frank and Taylor (Taylor and Frank 1996; Frank 1997, 1998):

$$\frac{\mathrm{d}w_\xi}{\mathrm{d}\xi} = \sum_{z=x,y} c_z\left(\frac{\partial W_z}{\partial x_{ij}} + r_{xz}\frac{\partial W_z}{\partial x_j}\right) \tag{3}$$

where w_ξ is the fitness of an allele coding for female dispersal, and ξ the breeding value (expected phenotypic effect) of this allele. The sum is taken over all classes expressing, or affected by, the gene (here females and males). c_z measures the reproductive value of class z, and r_{xz} the relatedness of the focal female to individuals of class z born in patch j. Under our assumptions, males and females have identical reproductive value, and relatedness within classes equals that among classes. Coefficients c_z will therefore be omitted, and a single parameter r used to designate relatedness among offspring born in the same patch. Using equation (2) into (3) provides:

$$\frac{\mathrm{d}w_\xi}{\mathrm{d}\xi} = \frac{s}{1 - x + xs} - \frac{1}{1 - x_j + xs}\left(1 - r\frac{1 - x_{ij}}{1 - x_j + xs}\right) \tag{4}$$

The evolutionarily stable strategy (ESS) is found by setting this derivative to zero, while equating $x_{ij} = x_j = x$:

$$c = rk_x \tag{5a}$$

where $k_x \equiv (1 - x_j)/(1 - x_j + sx)$ is the probability that a breeding female is local. This simple result, first reached by Frank (1986) and Taylor (1988), has the intuitive meaning that, for an inner equilibrium, dispersal costs must meet kin competition costs. Similar reasoning for males (writing male dispersal as y) leads to:

$$c = rk_y \tag{5b}$$

where $k_y \equiv (1 - y_j)/(1 - y_j + sy)$ is the probability that a breeding male is local.

For an explicit solution to (5), one needs to express r as a function of dispersal rate and patch size. This is obtained by first writing down the difference equations for genetic variance H_i, H_g, and H_t, then substituting their equilibrium values into the equation for relatedness (1.3). The results are plotted in Fig. 9.2a in the x–y space, using Perrin and Mazalov's (1999) difference equations, which account for inbreeding depression under infinite island assumptions. (Finite island or stepping-stone models are expected to lower the evolutionarily stable dispersal probabilities by generating relatedness among neighbours.) The best-response curve of females (dashed line) is plotted as a function of male dispersal, and the best-response curve of males (plain line) as a function of female dispersal. These curves cross on the diagonal, because (5a) and (5b) are symmetrical. This joint equilibrium implies identical dispersal by both sexes, the amount of which depends on s and N. Note that at equilibrium the individual fitness of a philopatric individual exceeds that of a disperser. Because the male curve crosses the female one from above, the balanced equilibrium found here is a convergence stable strategy (CSS) (Taylor 1989; Motro 1994). Any random drift of the population away from this equilibrium creates a selective pressure on both sexes to return back to it. Convergence stability stems from the fact that an individual optimal decision depends mainly on what other individuals *of the same sex* are doing. (Here, dispersal is a means to avoid interactions with relatives of the same sex.) However, it should also be noted that, whereas individual fitness does not depend on dispersal by the other sex (eqn 2), the female best-response curve is a negative function of male dispersal, and *vice versa*. This interdependence stems from kin interactions: a low male dispersal increases r, which promotes female dispersal as a kin competition avoidance mechanism. As will now be

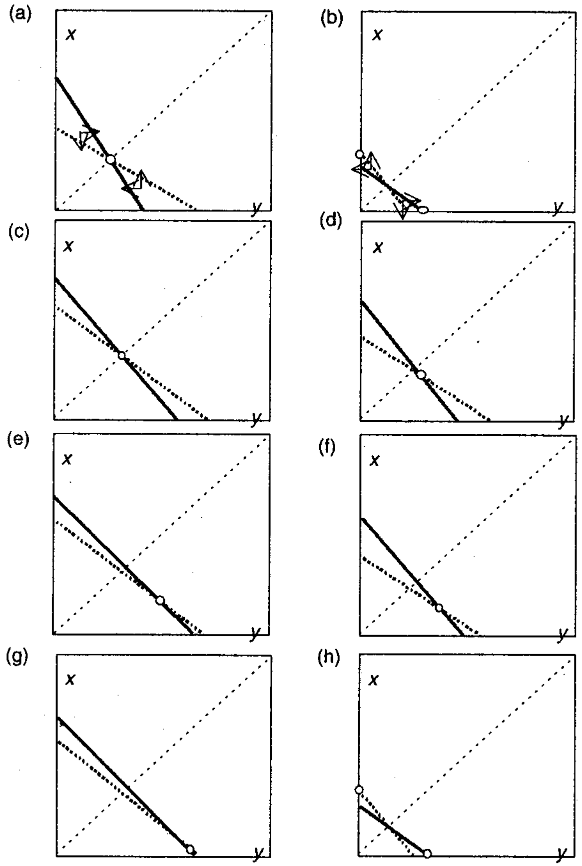

Figure 9.2. Evolutionarily stable dispersal patterns as functions of female (x) and male (y) dispersal. Plain lines plot male best response to female dispersal, and dashed lines plot female best response to male dispersal. Selection favours lower male dispersal to the right of plain lines, and higher dispersal to their left. Similarly, selection favours lower female dispersal above dashed lines, and higher dispersal below dashed lines (examples plotted on 2a and 2b). When male best response crosses the female one from above (e.g. 2a), the balanced equilibrium is a CSS (open circle). When it crosses it from below (e.g. 2b), the balanced equilibrium is unstable, and two border equilibria become CSSs. Parameter values were set to $N = 10$ and $c = 0.1$ in all simulations. (a) If kin competition is symmetrical and in the absence of genetic load, the balanced equilibrium is on the diagonal (open circle). (b) If inbreeding depression is the only selective pressure for dispersal ($\gamma = 1$) the balanced equilibrium is unstable. Two border CSSs coexist (open circles). (c) Combining kin competition and inbreeding depression destabilizes the inner equilibrium: the curves cross with a more acute angle than in (a). (d) A slight asymmetry in the benefits of philopatry (Greenwood's hypothesis; here $a_y = 1$, $a_x = 0.99$) induces a slight male bias in dispersal. (e) The male bias is much larger in the presence of genetic load ($\gamma = 1$), but other parameter values are as in (d). (f) A slight asymmetry in the benefits of kin cooperation (here $a_y = 1.0$ and $a_x = 0.98 + 0.02x$) induces a male-biased dispersal. (g) The male bias is much larger in the presence of inbreeding depression ($\gamma = 1$), but other parameter values are as in (f). (h) If both sexes benefit from kin cooperation, the balanced equilibrium may become unstable (here $\gamma = 1$, $a_x = 0.8 + 0.2x$ and $a_y = 0.8 + 0.2y$).

apparent appear, the sensitivity to dispersal by the other sex is one of the main points affected by inbreeding.

Inbreeding without competition

Inbreeding depression is unlikely to be the only selective pressure for dispersal, because inbreeding needs kin structures to arise, which, as soon as resources become limiting, create conditions for the evolution of kin competition avoidance. However, as inbreeding effects on dispersal are best understood when considered in isolation, we will assume for now unlimited breeding resources. This condition may be temporarily approximated under non-equilibrium dynamics, whereby extinction–colonization events generate important founder effects.

Let the fecundity of a pair be a negative function of co-ancestry among partners (Fig. 9.1). Female fecundity will be b_p if she mates with a male from another group, and b_g if her mate stems from the same patch. In absence of competition her total fitness is thus:

$$W_x = x_{ij}sb_p + (1 - x_{ij})(k_y b_g + (1 - k_y)b_p) \tag{6a}$$

while that of males is:

$$W_y = y_{ij}sb_p + (1 - y_{ij})(k_x b_g + (1 - k_x)b_p) \tag{6b}$$

The selective pressures on female and male dispersal are given by substituting equation (6) into (3). Setting these pressures to zero, while equating $x_{ij} = x_j = x$ and $y_{ij} = y_j = y$ provides the evolutionarily stable dispersal for females:

$$c = Ik_y + rI(1 - k_x)k_{y_x} \tag{7a}$$

and for males:

$$c = Ik_x + rI(1 - k_y)k_{x_y} \tag{7b}$$

where $I = (b_p - b_g)/b_p$ is the cost of inbreeding (Fig. 9.1), $k_{y_x} \equiv (1 - y_j)/(1 - x_j + xs)$ is the number of local males per breeding female, and $k_{x_y} \equiv (1 - x_j)/(1 - y_j + ys)$ the number of local females per breeding male. Equation (7) receives the intuitive interpretation that, at inner equilibrium, the marginal costs of dispersal match the marginal benefits, which are of two sorts. The first one (Ik_y for females) expresses the direct cost of an inbred mating (weighted by its probability), while the second ($rI(1 - k_x)k_{y_x}$) quantifies the fact that a dispersing female decreases the risk of inbreeding for relative males (which adds to her own inclusive fitness).

For an explicit solution to equation (7), one needs to express I as a function of co-ancestry. For the purpose of illustration, we may assume a linear relationship, which has the merits of both simplicity and empirical support (e.g. Fig. 10.2 in Lynch and Walsh 1998): $I = \gamma F_{gp}$, where $\gamma = (\mathrm{d}b/\mathrm{d}H)(H_p/b_p)$ measures genetic load (Fig. 9.1). Figure 9.2b plots female best response to male dispersal for $\gamma = 1$. Compared with Fig. 9.2a, the slope is much steeper, stemming from the fact that female inbreeding costs depend primarily on male behaviour (eqn 7a). If all males stay home ($y = 0$) then even low inbreeding costs may exceed dispersal costs. By contrast, if (all males disperse), even huge inbreeding costs will have no effect. Thus, contrasting with kin competition mechanisms, the optimal decision of a female depends mostly on dispersal by the other sex. (Here, dispersal is a means to avoid interactions with relatives of the opposite sex.)

Note, however, that there is a slight dependence on the behaviour of other females, mediated by their effect on co-ancestry: the more females disperse, the lower the average co-ancestry within groups, thus the lower the inbreeding costs. This dependence on relatives of the same sex makes possible inner equilibria (i.e. for some male dispersal values, female best response is intermediate between 0 and 1).

As equations (7a) and (7b) are symmetrical, both curves cross on the diagonal. However, because of the strong dependence on the other sex, they cross now in the opposite way (Fig. 9.2b). The male response curve crosses the female one from below. This implies that the balanced equilibrium at the crossing of the curves is not convergence stable. Any drift of one sex away from this equilibrium will select for a further drift apart of the other sex in the opposite direction, so that the whole system will move towards one of the two border CSSs. Border solutions mean that one sex will remain entirely philopatric. Which sex disperses eventually is purely random, and may depend on evolutionary history as well as genetic drift. This obviously leaves a significant role for phylogenetic inertia in deciding which sex disperses (details and further discussion in Perrin and Mazalov 1999). Note that, at equilibrium, fitness in the dispersing sex does not depend on dispersal decision (which is not true in the philopatric sex).

The main conclusion of this part is that inbreeding depression, were it allowed to act in isolation, would select for some dispersal, but by one sex only. The fact that dispersal usually occurs in both sexes, even when it is sex biased, adds empirical argument to the above *a priori* comment that inbreeding depression is unlikely to be the only reason for dispersal.

Combining kin competition and inbreeding depression

Under the combined effects of competition and inbreeding depression, female fitness becomes:

$$W_x = x_{ij}s\frac{Nb_p}{Nb(1-x+sx)} + (1-x_{ij})\frac{N(k_y b_g + (1-k_y)b_p)}{Nb(1-x_j+sx)} \tag{8a}$$

while male fitness is given by:

$$W_y = y_{ij}s\frac{Nb_p}{Nb(1-y+sy)} + (1-y_{ij})\frac{N(k_x b_g + (1-k_x)b_p)}{Nb(1-y_j+sy)} \tag{8b}$$

Substituting equation (8) into (3) provides:

$$\frac{dw_\xi}{d\xi} = \frac{sb_p}{b(1-x+xs)} - \frac{k_y b_g + (1-k_y)b_p}{b(1-x_j+xs)} + r\left(k_x\frac{k_y b_g + (1-k_y)b_p}{b(1-x_j+xs)} + (1-k_x)\frac{k_y(b_p-b_g)}{b(1-x_j+xs)}\right) \tag{9}$$

from which are calculated female evolutionarily stable dispersal:

$$c = rk_x(1-Ik_y) + Ik_y(1+r(1-k_x)) \tag{10a}$$

and male evolutionarily stable dispersal:

$$c = rk_y(1-Ik_x) + Ik_x(1+r(1-k_y)) \tag{10b}$$

Or, in words, for a balanced equilibrium, marginal dispersal costs must match the sum of marginal benefits. A first benefit ($rk_x(1-Ik_y)$ for females) can be attributed to kin competition avoidance (although it interacts partially with inbreeding), and the second ($Ik_y(1+r(1-k_x))$) to inbreeding (although it interacts partially with kinship).

Interactions are not symmetrical. The selective pressure stemming from kin competition avoidance is devalued by the effect of inbreeding, because dispersal then brings fewer benefits (the share of reproduction left behind for relatives is smaller). By contrast, inbreeding avoidance is strengthened by the inclusive fitness component, as already discussed.

This kin inbreeding–avoidance argument was first put forward by Bengtsson (1978). Starting from a situation in which all female offspring are philopatric, and all male offspring disperse, Bengtsson searched the conditions for a rare philopatric mutant male to succeed. As groups were assumed to consist of a single breeding female ($N = 1$), philopatric males would mate and reproduce with sisters. The model showed that male philopatry would not evolve unless

$$c > \frac{3I}{2} \tag{11}$$

a condition to which equation (10b) reduces under Bengtsson's assumptions of complete female philopatry ($k_x = 1$), complete male dispersal ($k_y = 0$) and a patch size reduced to $N = 1$ (so that offspring are full sibs and $r = 0.5$). This result has a straightforward interpretation: the higher the relatedness among patch mates, the lower the inbreeding costs needed to favour dispersal, because inbreeding depression affects both the male's own reproduction and that of his sisters.

Using an explicit genetic approach for an haploid organism in small patches ($N = 1$), Motro (1991, 1994) showed that, depending on the intensity of inbreeding depression, the male curve may cross the female one either from above or from below, resulting in either a stable or an unstable balanced ESS. In Fig. 9.2c, the balanced ESS is stable and, compared with Fig. 9.2a, shows only a slightly increased dispersal. (Effects are not simply additive, since dispersal rates induced by kin competition avoidance prevent inbreeding, and *vice versa*.) But the slopes of the best-response curves are steeper, because individual decisions are now more sensitive to behavioural decisions of patch mates from the other sex. Thus, even when inbreeding depression is not strong enough to make the inner ESS unstable, it contributes to destabilizing it, in the sense of making the response curves cross with a more acute angle (Fig. 9.2c). This matters in the case of sex asymmetry in costs or benefits, because it then induces much larger sex biases in dispersal, as will become apparent when the effects of mating systems and social structures are taken into account.

Mating systems

Greenwood (1980, 1983) suggested that interactions between inbreeding and dispersal were affected by mating systems. He first noticed that dispersal was often sex biased.

the bias itself being assumed to stem from inbreeding avoidance: if one sex disperses, the other does not need to. Second, he observed that the identity of the dispersing sex was dependent on mating systems. Here, the amount of paternal investment is a central issue. At one end of the range lie polygynous or promiscuous species in which females invest (almost) all the time and energy necessary for reproduction, the male contribution being restricted to a few sperm cells and a few seconds of copulation time. Mammalian breeding systems often resemble this, owing to the physiological burden of pregnancy and lactation imposed on females. At the other end of the range lies the monogamous system of many bird species, in which nest feeding enlarges the scope for males to increase their fitness through paternal care. Males may then adopt a resource-defence strategy (as opposed to the female-defence strategy found in many mammals), and play a significant role in territory acquisition and defence. As a result of their restricted paternal investment, the males of polygynous or promiscuous species also enjoy a much larger potential reproductive rate than females, as opposed to monogamous species in which sex differences in potential reproductive rates may vanish.

Polygyny itself has an effect on dispersal. The fact that a few males are able to monopolize reproduction within breeding groups enhances gene correlations within these groups, which affects relatedness r as well as inbreeding depression I. This both increases dispersal and contributes to destabilization of the inner equilibrium, but it does not, *per se*, induce a bias (Perrin and Mazalov 1999). By contrast, the several correlates of mating systems delineated above have the potential to induce such sex biases.

The resource-competition hypothesis

Greenwood (1980, 1983) noticed that the philopatric sex is usually female in mammals and male in birds, which in both cases corresponds to the sex that benefits most from acquaintance with territory (i.e. the sex most involved in territory acquisition). A few exceptions in mammals and birds are linked to atypical mating systems (resource-defence systems in male mammals, or female defence in male birds), and thus corroborate the theory (e.g. Pusey 1987; Clarke *et al.* 1997; Wolff and Plissner 1998). Other exceptions seem best explained by inbreeding avoidance as well. Some cases of female-biased dispersal in mammals correspond to situations in which males are able to monopolize reproduction over a breeding group for a period longer than the maturation time of their daughters (Clutton-Brock 1989).

The benefits from philopatry assumed by Greenwood (acquaintance with natal territory) may arise in two ways: philopatric individuals may either make better use of local resources (which translates into higher fecundity) or have a greater chance of obtaining a breeding opportunity (territory or mate). As these alternatives are mathematically equivalent, we develop the second one only, assuming immigrants to suffer from a lower competitive ability. This may be expressed through a coefficient a_z that measures the relative weight of an immigrant of sex z when competing for a breeding opportunity. Female fitness may be written:

$$W_x = x_{ij}s\frac{a_x N b_p}{Nb(1 - x + a_x sx)} + (1 - x_{ij})\frac{N(K_y b_g + (1 - K_y)b_p)}{Nb(1 - x_j + a_x sx)} \tag{12a}$$

while male fitness is:

$$W_y = y_{ij}s\frac{a_y N b_p}{Nb(1 - y + a_y sy)} + (1 - y_{ij})\frac{N(K_x b_g + (1 - K_x)b_p)}{Nb(1 - y_j + a_y sy)} \tag{12b}$$

where $K_y \equiv (1 - y_j)/(1 - y_j + a_y sy)$ is the proportion of breeding males that are of local origin and $K_x \equiv (1 - x_j)/(1 - x_j + a_x sx)$ the proportion of breeding females that are of local origin. Searching for ESSs as above provides the following best response for females:

$$C_x = rK_x(1 - IK_y) + IK_y(1 + r(1 - K_x)) \tag{13a}$$

and for males:

$$C_y = rK_y(1 - IK_x) + IK_x(1 + r(1 - K_y)) \tag{13b}$$

where $C_z = 1 - a_z s$ acts as a compound, sex-specific cost to dispersal, that affects the territorial sex more markedly.

Equations (13a) and (13b) become asymmetrical as soon as a_x and a_y differ, which induces a sex bias in dispersal. Figure 9.2d and 9.2e illustrates the case of a slight asymmetry in the benefits of philopatry for a female-defence system (i.e. $a_x < a_y$). Dispersal decreases in females and increases in males, but the effect is much stronger with inbreeding depression (Fig. 9.2e compared with 9.2d), first because co-ancestry induced by female philopatry promotes male dispersal through its effect on I (in addition to its effect on r), and second because the sensitivity to the other sex induced by inbreeding makes the response curves much steeper, thereby rendering the joint equilibrium much more sensitive to asymmetry (this illustrates the destabilizing effect of inbreeding depression discussed above).

Thus, Greenwood's argument indeed predicts a male-biased dispersal in female-defence systems, and a female-biased one in resource-defence systems. Synergistic interactions arise between inbreeding and resource competition, because inbreeding depression enhances the bias introduced by the weighting coefficient a_z. However, there is an important difference to note between this model and Greenwood's verbal argument. If, as in the latter, inbreeding (rather than kin competition) was the only ultimate reason for dispersal, then (13) would reduce to a system similar to that in equation (7), which would bring instability to the inner equilibrium and induce border CSSs. Asymmetry in the benefits of philopatry would result not in a lower dispersal rate by the territorial sex, but in a higher probability that the territorial sex would be the philopatric one (Perrin and Mazalov 1999).

Local mate versus local resource competition

The link between male-biased dispersal and female-defence strategy may also arise from different causes. In our formulation of the Hamilton–May model, the balanced CSSs were on the diagonal because both sexes were assumed to suffer identically from local competition. This might be true for a strictly monogamous species in which males and females would play an equivalent role in resource acquisition. But, in the female-defence systems of many mammals, sexes do not compete for the same items: females compete for resources (breeding sites) and thus display local resource competition (Clarke 1978), while males compete for females and thus suffer from local mate competition (Hamilton 1967). Furthermore, because of sex differences in potential reproductive rates, these items may not be equally limiting. As copulation normally takes only a few seconds, male fitness is likely always to be limited by female availability. By contrast, the process of transforming resources into nurturing of offspring is time consuming, so that female fitness may often be limited by her rate of processing resources, rather than resources themselves. As a result, local mate competition between males may often exceed local resource competition between females.

Perrin and Mazalov (2000) contrasted a situation like the one envisioned above (equal competition among males and females; eqns 8a and 8b) with a situation in which only males suffer from local mate competition (combination of equations 6a and 8b), corresponding to a female-defence system in an unsaturated environment. Female evolutionarily stable dispersal becomes:

$$c = k_y(I - r + rI) \tag{14}$$

whereas that for males remains identical to equation (11b). Kin competition thus provides a strong incentive for males to disperse (avoidance of local mate competition) which is not counterbalanced by local resource competition among females. This situation induces a strong sex bias in evolutionarily stable dispersal rates. In the precise situation investigated by Perrin and Mazalov, female philopatry was actually complete, partly because the bias was further amplified by inbreeding depression, and partly because resources were assumed to be not at all limiting. (Partially limiting resources are expected to have the potential to induce a balanced equilibrium, a point that deserves further investigation.) This analysis points to the balance between local resource and local mate competition as a central factor in deciding which sex disperses. Similar arguments were developed in the context of sex ratio theory, according to which kin competition is avoided by producing less of the sex that suffers more from local competition (Taylor and Bulmer 1980; Taylor 1981; Bulmer 1986).

Conclusions from this model rejoin those of the preceding paragraph in that, while inbreeding depression is not required to induce a sex bias in dispersal, it will enhance it. They also meet empirical patterns, as reviewed in mammals by Dobson (1982): while polygynous and promiscuous species display a male-biased dispersal, no such bias occurs in monogamous species. From his review, Dobson concluded that competition for mates was more likely to be responsible for the general mammalian dispersal pattern than either competition for resources or inbreeding, the latter acting mostly through synergistic interactions.

Asymmetry in inbreeding costs

The difference among sexes in potential reproductive rate also has the consequence that sexes may differ with respect to inbreeding costs. The argument was first made by Parker (1979, 1983) that inbreeding is most costly for the sex that contributes more to the parental investment. In polygynous or promiscuous systems, because of their low levels of paternal investment, males do not forfeit other mating opportunities by siring a relative's offspring. They therefore benefit directly from an inbred mating, which simply

adds offspring to those stemming from other matings rather than replacing them. In females, by contrast, an inbred mating entirely forfeits one breeding opportunity, so that inbreeding depression bears large direct costs that will not be matched by inclusive fitness benefits (enhancement of related males' reproductive output). Inbreeding is therefore less costly for males in a female-defence system.

Building on this argument, Waser *et al.* (1986) suggested that females should be the dispersing sex in polygynous systems, because their threshold for accepting inbreeding is lower. Since this opposes what has been observed (the male is usually the dispersing sex in such systems), Waser *et al.* (1986) concluded that inbreeding plays only a marginal role (if any) in dispersal. However, as noted by Perrin and Mazalov (1999) this argument may actually be reversed if females have the ability to choose their partner according to his dispersal status (kin recognition).

Mate choice and sexual selection on dispersal

Indeed, because of their large commitment to reproductive effort, females should evolve choosiness. In particular, they should refuse copulation with relatives and prefer immigrant males. Female preference might be formalized by attributing a larger weight to immigrant males than to local males in their competition for local females. Setting $a_y > 1$ in equations (12b) and (13b) would obviously constitute a further incentive for males to disperse, and thereby induce a stronger male bias in the dispersal of polygynous or promiscuous species.

Interestingly, if males also evolve some form of choosiness in female-defence systems (which may arise if one mating at least partly forfeits other mating opportunities), then they should prefer philopatric females under Greenwood's resource competition hypothesis, at least in the case where females benefit from philopatry through a better use of resources. Indeed, philopatric females in this case have a higher fecundity, so that males have more to gain from mating with them. Thus, sexual selection should in any case reinforce the trend predicted under Greenwood's resource competition hypothesis, and enhance the link between male dispersal and female-defence systems.

Social structures

The two components of kin selection considered up to now (kin competition avoidance and kin inbreeding avoidance) favour dispersal. A third, potentially important, effect lies in the benefits of cooperation and reciprocal altruism, which, opposing the two other components, may provide strong benefits to philopatry. Social structures based on kin interactions are widespread among birds and mammals. How do they interact with the selective forces for dispersal investigated here?

In their simplest form, benefits may arise simply because territory owners are less aggressive towards related neighbours (e.g. Watson *et al.* 1994; Koprowski 1996). Local settlement is made easier because of acquaintance, not with territory, but with kin. Owners may even share part of their territory, if the inclusive benefits of allowing relatives to reproduce exceed the costs of sharing. More evolved forms of cooperation appear in social groups, such as helping at the nest (e.g. Emlen and Wrege 1991; Powell and Fried 1992; Komdeur 1996; Dickinson and Akre 1998), or cooperation among related adults (e.g. Mappes *et al.* 1995; Lambin and Yoccoz 1998). Kin cooperation may help in acquiring not only a territory, but possibly also social status or direct access to reproduction, as observed in the females of several monkey species, and in the males of hamadryas baboons or chimpanzees (Packer 1979; Pusey 1980). Kin cooperation has been shown to enhance fitness: 'there is evidence from various species that philopatric females have higher reproductive success than females that have left their natal area or Group' (Pusey 1987, p. 298).

On the one hand, kin cooperation thus constitutes an important selective pressure for philopatry. On the other hand, inbreeding depression opposes this pressure. Could inbreeding be sufficiently detrimental to impede the evolution of social structures? Not necessarily, as a sex-biased dispersal may suffice to prevent inbreeding, and meanwhile allow significant kin structures to arise (Chesser and Ryman 1986; Chesser 1991a,b). A male-biased dispersal, often associated in mammals with polygyny, allows the building of fairly high relatedness values ($r > 0.3$) without any noticeable inbreeding (i.e. $F_{ip} = 0$), as shown for instance in black-tailed prairie dogs (Chesser *et al.* 1993; Sugg *et al.* 1996; Dobson *et al.* 1997). It is worth noting in this context that 'particularly striking examples of sex differences in natal dispersal occur in species which live in permanent social groups' (Pusey 1987, p. 295). Why should this be so?

The difference between selective pressure in Greenwood's resource competition hypothesis and that stemming from kin cooperation lies in the fact that, in the latter, the benefits of philopatry are not constant, but depend on the proportion of local individuals among other settlers. This induces a positive feedback cycle in philopatry: the more local settlers among patch mates, the higher the benefits from settling locally. This can be formalized by making the coefficient a_x weighting immigrants in equation (12a) an increasing function of x_j, rather than a constant. Thus, when x_j is very small (i.e. most locally born stay), immigrants have a relatively low probability of settling successfully (because their local competitors help one another), while as x_j tends to unity (all locally born disperse), immigrants have the same weight in competition as any locally born. Applying the direct fitness approach (eqn 3) to equations (12a) and (12b), while considering a_x a function of x_j rather than a constant, provides the best-response curves for females:

$$C_x = r\beta_x K_x(1 - IK_y) + IK_y(1 + r(1 - \beta_x K_x)) \quad (15a)$$

and for males:

$$C_y = r\beta_y K_y(1 - IK_x) + IK_x(1 + r(1 - \beta_y K_y)) \quad (15b)$$

which are identical to equations (13a) and (13b), except that patch mates *of the same sex* (K_z) are now weighted by a coefficient $\beta_z = 1 - sz(da_z/dz)$ (N. Perrin and C.R. Lehmann, unpublished manuscript).

As this coefficient is smaller than unity (and all the smaller given that a_z increases strongly with z), it weakens markedly the dispersal pressure stemming from kin competition avoidance (because it affects the whole kin competition term), and enhances slightly the dispersal pressure from inbreeding avoidance (only its kin-selected component is affected). The net effect is a dispersal pressure that is both of lower intensity and more dependent on the other sex's strategy. Together with inbreeding depression, kin cooperation has the potential strongly to destabilize the balanced equilibrium.

The effect of inbreeding depression, in the case of a weak benefit from kin cooperation among females, can be seen by comparing Fig. 9.2f with Fig. 9.2g. A strong sex bias is observed in Fig. 9.2g, even though kin cooperation advantages to the philopatric sex are very low. The destabilizing effect of within-sex cooperation also appears when both sexes benefit from it. Added to inbreeding depression, it can make the inner ESS unstable, as plotted in Fig. 9.2h. Two border CSSs coexist, implying that one sex remains entirely philopatric, while the other disperses, even though both sexes benefit equally from cooperation.

In the example plotted in Fig. 9.2h, the 26% equilibrium dispersal by one sex results in about 10% co-ancestry and 20% relatedness within breeding groups, corresponding in our model to a 10% inbreeding depression. This last value may actually be much larger, provided kin cooperation brings enough benefits. Assuming, for example $a_x = x_j$ and $a_y = y_j$, the 8% equilibrium dispersal by one sex boosts relatedness within breeding groups to 77%, corresponding in our model to a very significant inbreeding cost of 62%. This extreme value shows that strong inbreeding does not stem necessarily from high mortality costs of dispersal (fixed to 10% in our simulations): the benefits of kin cooperation may induce individuals to withstand extreme inbreeding costs. This also means that selective pressure stemming from inbreeding avoidance may exceed that from kin competition avoidance and become the most relevant force driving dispersal in social species, constituting a very significant incentive for those few individuals that disperse (even though actual dispersal rates remain limited). It is worth noting that all studies on non-human primates reviewed by Johnson and Gaines (1990) offer inbreeding avoidance as an explanation for the evolution of dispersal.

Social species studied also often evolved kin recognition mechanisms (e.g. Hoogland 1982; Harvey and Ralls 1986; Keane 1990; Potts *et al.* 1991), which may allow behavioural incest avoidance (i.e. mate choice based on co-ancestry). If breeding groups are so small that incest cannot be avoided through mate choice, then even a moderate and occasional dispersal might suffice to lower inbreeding significantly, provided it is condition dependent (i.e. dependent on co-ancestry with local potential mates). This is usually the case in troop transfer among social mammals (e.g. Packer 1979; Clutton-Brock 1989; review in Hoogland 1995). The way in which kin recognition may co-evolve with dispersal deserves further theoretical formalization.

Another point deserving investigation is the dynamics of genetic load. (Load was assumed to be constant in our simulations.) It is unlikely that inbreeding costs as high as 60% will remain for long in a breeding group: recurrent inbreeding will lead to the purging of deleterious mutations, resulting in the progressive reinforcement of philopatry. There are several examples of social mammals showing no sign of inbreeding avoidance or inbreeding depression (e.g. Reeve *et al.* 1990; Keane *et al.* 1996), which is best explained by a history of strong inbreeding and purging of deleterious mutations.

Conclusions and perspectives

The formalization presented here, like any other model, is an approximation of the exact processes involved. In addition to the simplifying assumptions made above, the point should be made that the approach is deterministic (which may be important when inbreeding occurs in small patches), and that some approximations were used (e.g. the dependence of b on dispersal and inbreeding patterns of the previous generation was not taken into account in eqn 8). Similarly, the shape of the relationship between inbreeding depression and co-ancestry matters. Some authors found that the balanced ESS might be unstable when both kin competition and inbreeding depression interact (Motro 1991; Gandon 1999, Gandon and Michalakis, chapter 11), which presumably stems from different assumptions. (Motro assumes inbreeding depression is independent of co-ancestry, and Gandon assumes an exponential negative function of co-ancestry.)

The usefulness of our model lies in the fact that it provides a unifying approach, allowing us to account simultaneously for inbreeding and kin competition in the evolution of dispersal, making explicit in particular the ways in which these two forces interact. It also sheds light on the ways in which mating systems and social structures interfere with these selective forces. Our main conclusions can be summarized as follows:

(1) Were inbreeding the only reason for dispersal, then a strong effect on dispersal would arise, but be restricted to one sex only (the balanced equilibrium is unstable). This situation is, however, unlikely for logical reasons (inbreeding implies kin structures, and thereby also kin competition as soon as resources are limiting) as well as empirical reasons (usually both sexes disperse, even when dispersal is biased). This implies that inbreeding cannot be the only ultimate cause of dispersal when both sexes disperse (even at very different rates), opposing implicit or explicit assumptions of many verbal models (e.g. Greenwood 1980, 1983).
(2) In absence of inbreeding depression, kin competition favours a balanced dispersal. The inner equilibrium is continuously stable because dispersal evolves in this case as a way to avoid patch mates of the same sex.
(3) Combining inbreeding depression and kin competition has little influence on dispersal rates. More importantly, the stability of the inner equilibrium is weakened, because dispersal now becomes a way of avoiding patch mates of the opposite sex.
(4) This destabilizing effect is apparent in the case of sex asymmetries in selective forces, as may arise within certain mating systems. Several arguments converge to predict a male-biased dispersal in female-defence systems, and a female-biased dispersal in resource-defence systems. This may stem from sex biases in (a) benefits of territory, (b) local competition, (c) inbreeding costs, and/or (d) sexual selection.
(5) Within-sex kin cooperation also has the potential to induce asymmetries in dispersal. Because of self-reinforcing benefits of philopatry, this pressure further destabilizes the balanced equilibrium, and should thus induce a lower, but more sex-biased, dispersal. Inbreeding avoidance might constitute the most important selective pressure for dispersal in social species.
(6) Inbreeding depression is thus not required to produce sex biases in dispersal, even though it may boost such biases. Similarly, negative (interspecific) correlations between male and female dispersal do not imply inbreeding avoidance either (Pusey 1987). A strong philopatry by one sex (induced, for example, by a lower local competition) enhances relatedness within groups, which then favours more dispersal in the other sex as a kin competition avoidance mechanism.

These conclusions are consistent with empirical patterns, since male-biased dispersal is associated with female-defence and polygynous mating systems, while female-biased dispersal occurs mainly in resource-defence and monogamous systems (Greenwood 1980, 1983; Dobson 1982; Clarke *et al.* 1997). Also, stronger sex biases appear in social species (Pusey 1987), and inbreeding avoidance seems to play a more significant role (Johnson and Gaines 1990), even though the average dispersal rate is lower. However, a general problem appearing recurrently throughout our approach is that the predictions arising from inbreeding depression-avoidance arguments differ only quantitatively (as opposed to qualitatively) from a null model of pure kin competition avoidance. This situation is bound to make extremely difficult any field test of the importance of inbreeding depression in moulding dispersal patterns.

Empirical investigations might try to focus on situations in which competition for resources vanishes, as may happen when prey populations are heavily controlled by predation, or when extinction–recolonization dynamics create strong founder effects. Unfortunately, these situations are also likely to impose other selective forces on dispersal (Ronce *et al.*, chapter 24; Weisser, chapter 12b). Further modelling work is necessary to delineate the interaction of these forces with inbreeding. Non-equilibrium dynamics offers a particularly interesting case. Founder effects create inbreeding and, reciprocally, inbreeding depression contributes to extinction rate and metapopulation dynamics (e.g. Saccheri *et al.* 1998). The dynamics of genetic load would have to be taken into account, as well as other selective forces stemming from extinction risk and the benefits of dispersing towards less crowded patches.

Other potentially fruitful perspectives include the study of conditional dispersal. The dependence of dispersal on the presence of parents or relatives of each sex may bring useful information, since inbreeding avoidance fosters dispersal as a means to avoid opposite-sex relatives, while kin competition fosters dispersal in order to avoid relatives of the same sex. The importance of kin selection (relative to direct inbreeding costs) might be inferred from individual fitness differences between residents and dispersers. Dispersal distance may also differ among males and females, and this may tell something about the relative impact of inbreeding and kin competition, although this avenue would obviously require further formalization. The same is true of the ideas about sexual selection mentioned above. Female choosiness is likely to depend on the balance between inbreeding risk and the competitive disadvantage of immigrants, as well as on her own status as an immigrant or philopatric. Finally, the co-evolution of kin recognition and dispersal as alternative ways to avoid inbreeding, as well as their interaction, deserve proper treatment.

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Appendix: List of parameters

Genetic measures are taken among offspring before dispersal. Sex-specific parameters are listed for females only, but the same notation also applies to males, with relevant changes.

H_i, H_g, H_p	Observed heterozygosity and Hardy–Weinberg expectations at the group and population level, respectively.
F_{ip}, F_{gp}	Inbreeding and co-ancestry among patch mates.
$r \equiv 2F_{gp}/(1+F_{ip})$	Relatedness among patch mates.
b_g, b_p	Fecundity of pair, as a function of partner's genetic similarity. Without a subscript, b is the average fecundity within a patch.
$\gamma = (\mathrm{d}b/\mathrm{d}H)(H_p/b_p)$	Marginal increase in relative fecundity with relative heterozygosity, a measure of genetic load.
$I \equiv (b_p - b_g)/b_p = \gamma F_{gp}$	Cost of breeding with a patch mate, assumed to be proportional to co-ancestry.
N	Patch size (number of breeding females).
x_{ij}	Dispersal probability of female i in patch j. x_j is the average for the patch j and x is the average for the population.
W_x	Fitness of a female; a function of its dispersal probability.
W_ξ	Fitness of an allele coding for female dispersal; a function of its breeding value (expected phenotypic effect) ξ.
$c = 1 - s$	Mortality cost of dispersal.
a_x	Relative competitive weight of an immigrant female. $C_x = 1 - sa_x$ combines both the mortality and competitive cost of dispersal.
$K_x = (1 - x_j)/(1 - x_j + a_x sx)$	Probability that a female breeding in patch j is of local origin.

10

Inbreeding versus outbreeding in captive and wild populations of naked mole-rats

M. Justin O'Riain and Stanton Braude

Abstract

In this chapter we review the evidence for inbreeding versus outbreeding as the principal mating strategy in both captive and wild colonies of naked mole-rats. The naked mole-rat is a cooperatively breeding mammal occurring in large colonies with non-breeding individuals working on behalf of a fecund minority. Evidence from preliminary genetic studies and laboratory observations suggests that these rodents routinely inbreed, with new colonies forming through fission of the parent colony. While occasional inbreeding is especially deleterious in normally outbred species, constant ecological pressure selecting for inbreeding becomes progressively less costly. Theoretical predictions, however, suggest that close inbreeding cannot continue indefinitely since the accumulation of genes with mild deleterious effects and the loss of the ability to track changing environments ultimately selects for dispersal. Recent laboratory and field studies provide evidence in support of the above prediction with the finding that naked mole-rat colonies do in fact harbour potential dispersers and that outbreeding in the field is far more common than previously suspected. Low levels of genetic variation in previous molecular genetic studies may be explained in part by a recent common ancestor of the population, in conjunction with population viscosity, typical of fossorial rodents. Naked mole-rats illustrate the importance of understanding the different F statistics, their biological meanings, and the methodologies used to estimate them. The dispersers from naked mole-rat colonies provide a good example of phenotypic plasticity and are consistent with the theory that dispersal patterns have multiple causes and that dispersing individuals benefit from both increased access to unrelated mates and decreased intrasexual competition.

Keywords: cooperative breeding, inbreeding, dispersal morph

Introduction

Mole-rats within the family Bathyergidae exhibit a range in social organization from strictly solitary and aggressive to highly social, cooperatively breeding species (Jarvis *et al.* 1994). However, only the naked mole-rat (*Heterocephalus glaber*), the most social of these species, will engage in consanguineous matings in the laboratory following the death or removal of a dominant breeder. Close inbreeding (parent–offspring and sib–sib matings) have frequently been observed in captive colonies. Genetic studies (Reeve *et al.* 1990) of wild populations reported the highest known coefficient of inbreeding ($F =$ 0.62) yet recorded among free-living mammals. Early field data from Brett (1986, 1991)