Chapter aims and structure

After introducing the evolution of the dispersal, this chapter explores the role of cooperation and interaction in the dispersion of organisms. It discusses how cooperation can enhance the success of dispersal, allowing individuals to work together to overcome environmental challenges. The chapter also examines the impact of interaction between individuals, highlighting how cooperation can be facilitated or hindered by various factors. Finally, it explores the implications of these findings for conservation and management strategies.
Some definitions and a few words about the context

Selection coefficients are used to measure the proportion of a population that is selected against. The selection coefficient, s, is defined as the difference between the fitness of the selected and the non-selected genotypes. A positive selection coefficient indicates a selection for the selected genotype, while a negative selection coefficient indicates a selection against the selected genotype.

The fixation index, F, is a measure of the degree of inbreeding in a population. It is calculated as the difference between the expected number of heterozygotes and the observed number of heterozygotes, divided by the expected number of heterozygotes.

Selection coefficients and fixation indices are important tools in population genetics, as they allow us to understand the mechanisms that are driving evolution in a population.
A modeling approach

By now, much of the question is not whether or not the interaction effects are present. Our work in modeling is devoted to characterizing processes that address not only the interactions but also the ways in which they operate across the system. We therefore have good reason to be skeptical of the importance of interactions in the context of robustness to change.
The competition model works in the following way. In any given ecosystem, the competition between species for resources (like food, water, and space) leads to a decrease in the population size of each species. This is because as the population of one species increases, the availability of resources decreases, leading to a decrease in the growth rate of that species. Conversely, the population of another species increases, leading to a decrease in the availability of resources for that species. This cycle continues, leading to a dynamic equilibrium between the species in the ecosystem.

The model can be represented by a set of differential equations, where the growth rate of each species is a function of its current population size and the population sizes of the other species in the ecosystem. The equations take into account the interactions between species, such as predation, competition for resources, and mutualistic relationships (like cooperation for resource sharing).

In the model, the population size of each species is represented by a variable, and the growth rate of each species is represented by a function of the current population size and the population sizes of the other species. The equations are solved numerically to simulate the dynamics of the ecosystem over time, allowing us to analyze the long-term behavior of the species and predict the outcomes of different scenarios, such as changes in environmental conditions or the introduction of new species into the ecosystem.
The page contains mathematical expressions and diagrams. The text is partially obscured, but it appears to be discussing mathematical concepts or theories, possibly related to physics or mathematics. The expressions and diagrams suggest a complex subject matter, potentially involving calculus, algebra, or other advanced mathematical topics. The page seems to be part of a textbook or a scientific publication, given the formal presentation of the content.
Inference, equivocation, and the evolution of mind and dispersal

(401) \( ((y-1)^2 + 1)^2) y + ((y-1)^2)^2 = c \)

From which are calculated female evolutionary stable dispersal

(6) \( \frac{(x + x - 1)q}{(q - q) r^2} \frac{((y-1)^2 + 1)}{((y-1)^2) r^2} + \frac{(x + x - 1)q}{(q - q) r^2} \frac{((y-1)^2 + 1)}{((y-1)^2) r^2} = \frac{2p}{\delta_0 p} \)

Substituting equation (5) into (6) provided:

(7) \( \frac{(x + x - 1)q}{(q - q) r^2} \frac{((y-1)^2 + 1)}{((y-1)^2) r^2} + \frac{(x + x - 1)q}{(q - q) r^2} \frac{((y-1)^2 + 1)}{((y-1)^2) r^2} = \frac{4}{\delta_0 p} \)

where male fitness is given by:

(8) \( \frac{(x + x - 1)q}{(q - q) r^2} \frac{((y-1)^2 + 1)}{((y-1)^2) r^2} + \frac{(x + x - 1)q}{(q - q) r^2} \frac{((y-1)^2 + 1)}{((y-1)^2) r^2} = \frac{4}{\delta_0 p} \)

Under the combined effect of competition and infraspecific dispersion female fitness

**Combining competition and infraspecific dispersion**

**Dissipation**

Above a certain common infraspecific dispersion is added to the main race of sex dispersal because competition augments only the male's.

Moreover, if sex is constant and is considered to be a constant in the population, the condition of the infraspecific dispersion was arrived at earlier in the population as a whole.

This condition of the main sex is where the infraspecific dispersion is added to the main race of sex dispersal. (Note that the infraspecific dispersion added to the main race of sex dispersal is added to the main race of sex dispersal because competition augments only the male's.

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The text in the image is in Chinese. Here is a plain text representation of the content:

The text in Chinese discusses the standard reduction of a quartic polynomial equation. It mentions the standard reduction formulas and provides examples of how to apply them. The text is focused on mathematical analysis and algebraic manipulations.

For instance, it shows how to standardize a quartic equation into a simplified form. The text also includes derivations and explanations of the reduction process, making it easier to understand the steps involved in solving such equations.

The text further elaborates on the importance of these reductions in simplifying complex mathematical problems, making them more accessible and understandable for students learning algebra.

The content is detailed and comprehensive, covering various aspects of quartic equations and their standard reductions. It is written in a clear and concise manner, suitable for those studying advanced algebra or mathematics.

Overall, the text provides a thorough explanation of the standard reduction of quartic polynomials, highlighting its significance in the field of mathematics.

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Note: The text is in Chinese and is not translated into English in the current format. The provided information is based on the visual content and the context of the mathematical topic discussed.
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. Fp = 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 fitness benefit from settling locally. This can be formalized by making the coefficient a, weighting immigrants in equation (12a) an increasing function of x, rather than a constant. Thus, when x 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 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, a function of x, rather than a constant, provides the best-response curves for females:

\[ C_f = r \beta_f K_f (1 - 1K_f) + K_f (1 + r(1 - \beta_f K_f)) \]  \hspace{1cm} (15a)

and for males:

\[ C_m = r \beta_m K_m (1 - 1K_m) + K_m (1 + r(1 - \beta_m K_m)) \]  \hspace{1cm} (15b)

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

As this coefficient is smaller than unity (and all the smaller given that \( \alpha_i \) 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 \( a_i = x_i \) and \( a_i = y_i \), 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 behavioral 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
Acknowledgments

Proper intellectual property and access to information is crucial to the development and advancement of any field of study. In the context of this document, the following points are highlighted:

(3) In the context of the cooperation and access to information, the emphasis on intellectual property and dissemination is critical.

(4) The intellectual property aspects in the area of data management are significant.

(5) Within the cooperation and access to information, the protection of intellectual property warrants further emphasis.

(6) Information dissemination is not only essential to the development of effective systems but also to fostering innovation and collaboration.

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Introduction

Keywords: cooperative breeding, pen, dispersal, relatedness, inclusive fitness

Abstract

M. Justin O'Hara and Shimon Brener

Wild populations of naked mole-rats
Introducing versus outbreeding in captivity and
Genetic marker

Appendix: List of parameters

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