COOPERATIVE BREEDING IN MAMMALS

Edited by

NANCY G. SOLOMON
Miami University, Oxford, Ohio

JEFFREY A. FRENCH
University of Nebraska at Omaha

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge CB2 1RP, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge CB2 2RU, United Kingdom
40 West 20th Street, New York, NY 10011–4211, USA
10 Stamford Road, Oakleigh, Melbourne 3166, Australia

First published 1997

Printed in the United States of America

Typeset in Times

Library of Congress Cataloging-in-Publication Data
Cooperative breeding in mammals / edited by Nancy G. Solomon, Jeffrey
A. French
p. cm.
Includes index.
ISBN 0–521–45491–3 (hc)
1. Mammals – Behavior. 2. Cooperative breeding in animals.
I. Solomon, Nancy G. II. French, Jeffrey A.
QL739.3.C665 1996
599.056–dc20

CAMBRIDGE
UNIVERSITY PRESS

96–17982
CIP

A catalog record for this book is available from the British Library.

ISBN 0 521 45491 3 hardback

7

Dynamic Optimization and Cooperative Breeding: An Evaluation of Future Fitness Effects

JEFFREY R. LUCAS, SCOTT R. CREEL, and PETER M. WASER

7.1 Introduction

Why do some reproductively mature animals stay at home, delay breeding, and help to rear the offspring of others? Over the past 25 years, this question has been addressed by authors studying a wide variety of animals, from insects (Alexander, Noonan, & Crespi 1991) to mammals (Brown 1987; Emlen 1991). On one level, the answer is simple: An individual should stay at home and help when its inclusive fitness is higher than it would be if it dispersed and attempted to breed (Hamilton 1964; Brown 1987; note: we will refer to alloparental behavior as "help"). Unfortunately, for several reasons, quantifying the inclusive fitness consequences of these alternatives is not a simple matter. For example, the sequence of behavioral decisions that lead to helping may differ among species, as we discuss later. Also, there are four components of inclusive fitness that need to be measured (Brown 1987): current direct fitness, current indirect fitness, future direct fitness, and future indirect fitness. The calculation of some of these components is quite complicated.

To quantify the fitness payoffs to individuals that make these decisions, we first need to understand clearly what decisions they are making. As Brown (1987) has suggested, cooperative breeding often involves three distinct decisions: to remain in the natal territory (as opposed to dispersing), to delay breeding, and to help. In empirical studies, these decisions are often simplified to a dichotomy: philopatry/help versus disperse/breed. For example, in black-backed and golden jackals, virtually all individuals that delay breeding and help do so on their natal territory, and conversely, virtually all dispersal events are associated with breeding attempts (Moehlman 1983).

In other cooperative breeders, however, the three decisions can be more independent. In dwarf mongooses (Creel & Waser 1994) and wild dogs (Malcolm & Marten 1982), dispersers often enter nonnatal groups as helpers.

Thus, in these species, the decision to help is decoupled from the decision to disperse. Similarly, decisions to help may be decoupled from decisions to attempt or to delay breeding. Reproductive suppression of subordinates is found in the majority of mammalian (and avian) cooperative breeders (Creel & Macdonald 1995; French this volume; Moehlman & Hofer this volume; Solomon & Getz this volume), but it is often incomplete, and occasional reproduction by subordinates can make a substantial contribution to fitness (e.g., dwarf mongooses: Keane et al. 1994).

Our approach here is to examine the consequences of what we view as a critical decision virtually all cooperative breeders make: whether to disperse instead of remaining at home. The consequences of the dispersal decision may dictate (or at least impact) the degree of alloparental care offered by an individual, and may also influence potential delays in breeding.

Species differ markedly in the ability of individuals to gather information about dispersal options. In many avian cooperative breeders, philopatric animals can remain in their natal groups and vie for breeding opportunities that arise from the deaths of dominant animals in nearby territories as well as in their own (Wiley & Rabenold 1984; Woolfenden & Fitzpatrick 1984; Zack & Stutchbury 1992). In dwarf mongooses, naked mole-rats (Lacey & Sherman this volume), and probably most mammalian cooperative breeders, animals vying for breeding opportunities cannot simultaneously assess options in more than one group. Subordinate animals may queue for a dominant position in their natal group or in a nonnatal group, but not both. The fundamental question is thus: Where to queue? The animal's subsequent decisions as to when to help and when to attempt breeding should depend on the breeding opportunities inherent in the queue it has joined. Our task is to calculate the four components of inclusive fitness associated with joining a natal or a nonnatal queue.

The direct components of fitness have been measured in several ways. The simplest estimate of a breeder's current direct fitness is the number of surviving young it produces during the present breeding season. Unfortunately, this method double counts offspring, because young produced due to the action of helpers will be attributed to both the breeder and to the helper (Grafen 1982). A common solution to the problem (which appears to follow from a verbal description of direct fitness in Hamilton 1964) has been to equate current direct fitness with the number of offspring the breeder would have in the absence of help (e.g., Grafen 1984). In short, this method strips the number of young produced as a result of aid by helpers from each breeder's reproductive success. Creel (1990a) has shown that this estimate also is incorrect, as becomes clear if one thinks of species like dwarf mongooses or African wild dogs in which unaided breeders raise no offspring. Following the traditional verbal definition of direct fitness, these breeders have no fitness at all. In fact, an extension of Hamilton's algebra shows that the direct component of fitness is the number of offspring produced by a breeder, decreased by "the average effect of one individual on others' reproductive success" (Creel 1990a, p. 220). Thus, breeders' reproductive success should be decremented by the increase in reproductive success attributable to the average individual in the population, including all helpers and nonhelpers. The calculation of direct fitness is discussed further when we outline our model.

Estimation of the current direct fitness of subordinates is also more complex than it might appear. The recent discovery in cooperative breeders of subordinate parentage (detected by DNA fingerprinting in bicolored and stripebacked wrens: Rabenold et al. 1990; Haydock et al. in review; and in dwarf mongooses: Keane et al. 1994; see also Mumme et al. 1985; Brooker et al. 1990; Faaborg et al. 1995) shows that the most common method used to estimate direct fitness effects – behavioral observations of mating and dominance – is imperfect. Some of the current direct fitness traditionally attributed to breeders in fact belongs to helpers.

The current indirect component of fitness is typically taken to be the contribution to the production of offspring from the marginal helper, devalued by the genetic relatedness between the helper and those offspring. (The contribution of the marginal helper would be the net effect on group reproductive success of the removal of a single helper.) Creel (1990a) has shown that a full accounting of the inclusive fitness accrued by helpers requires that this number, like the direct fitness of breeders, be devalued by the mean effect of an individual on others' reproductive success. When helpers are not completely suppressed, the breeders also may accrue indirect fitness. We resolve the resulting terminological morass by considering breeding and helping to be two roles that both dominant and subordinate mongooses can play; subordinates are helpers for most, but not all, of a group's offspring.

Some authors have estimated the inclusive fitness of reproductive alternatives based on the payoffs summed over a single year (e.g., Emlen & Wrege 1991; Creel & Waser 1994), but there is evidence that the future consequences of reproductive decisions can be substantial (Reyer 1984; Wiley & Rabenold 1984; Mumme, Koenig, & Ratnieks 1989; Creel 1990b; Emlen & Wrege 1994). Methods used to calculate future inclusive fitness consider the effect of helping on the survivorship and fecundity of the helper (e.g., a reduction in survivorship may represent one cost of helping) and the breeder (e.g., an increase in survivorship may increase future reproductive success and increase indirect fitness for the helper). In some cases, a helper's future inclusive fitness may also be enhanced by offspring that result from its assistance (Creel 1990b; Solomon 1994).

The dispersal decision can influence future inclusive fitness through several mechanisms. One possibility is that dispersal can shorten the queue occupied by an individual, in which case the disperser will breed earlier than will individuals that remain philopatric (Rood 1990; Creel & Waser 1994). In some species, experience can affect reproductive success; experience gained as a helper may increase the reproductive output of that individual when it finally breeds (Brown 1987). The same may be true for a breeder: Breeders may experience low reproductive success in their first year but may have enhanced success in future years as a result of this experience (Creel & Waser 1991). In both cases, these delayed effects can contribute to the fitness payoffs associated with dispersal decisions.

Delayed direct benefits of helping also include the possibility that the helper will ascend into the breeding position of the territory in which it helps (Woolfenden & Fitzpatrick 1984). The benefits are compounded through reciprocity if the offspring that the helper provides care for themselves assist the helper when it ascends (Wiley & Rabenold 1984). There can be several future indirect fitness effects, including an increase in the probability that a breeder will survive subsequent seasons and an increase in future production of offspring that arise as a result of help given by offspring the helper is currently aiding (Mumme et al. 1989; Creel 1990b). We assume that the act of helping increases the immediate reproductive output of breeders, or that it may increase survivorship of breeders. Solomon (1994) has recently shown that helpers also may increase the future reproductive success of young that they care for. This will be particularly important in species in which juvenile growth correlates with adult size and fecundity.

Complete accounting of future fitness effects has resisted treatment in part because of the number and complexity of the possible fitness components (e.g., Emlen & Wrege 1994). But in addition, there is a knotty problem that cannot be addressed by traditional methods of fitness accounting. This is that the fitness consequences of dispersal decisions to be made in the future feed back into current dispersal decisions.

Many of the papers published on helping behavior assume that a decision (e.g., to disperse or stay) is made only once in the animal's lifetime (Creel & Waser 1991; Emlen & Wrege 1991; Walters, Doerr, & Carter 1992), or if the current decision is to help, that the animal disperses the next year (e.g., Zack

& Stutchbury 1992). However, if there are delayed fitness effects or probabilistic changes in future reproductive options (e.g., the death of the breeder in the natal territory caused by some chance event), the consequences of current reproductive decisions will be influenced by decisions potentially made in the future. For example, if a subordinate is likely to ascend to dominance status in the near future, its best option might be to remain in its natal territory in order to capitalize on this possible event. On the other hand, if there is a chance that conditions will change such that the animal would do better to disperse the next year, it might be better to disperse immediately if experience gained in the nonnatal group in the current year increases reproductive success in the subsequent years. In particular, if the disperser found a breeding position, its reproductive success might be low in its first year in that position, but reproductive success in subsequent years might increase because of experience gained in that initial year. Thus, to calculate the payoff to current decisions, we need to estimate what future decisions the animal will make and how they will be impacted by current decisions.

The idea that future decisions should impact current decisions is well founded in the foraging literature (Houston & McNamara 1982; Lucas 1983) and has recently been used in the study of some aspects of life-history theory (Clark 1993; Lucas, Howard, & Palmer 1996). The best tool available to incorporate future fitness effects into the analysis of current reproductive decisions is dynamic programming (Mangel & Clark 1988).

Dynamic programming has not yet been applied to the analysis of cooperative breeding; our primary goal here is to show how it can be used to evaluate the inclusive fitness consequences, including future fitness components, for an animal faced with joining a natal versus a nonnatal queue. The rationale is as follows: Inclusive fitness payoffs to the subordinate will depend on relatedness to the breeders in the group. In the natal territory, stochastic mortality events will cause relatedness to be a random variable. For example, subordinates of the same age in different groups may vary in their relatedness to the dominants in their group as a result of random differences in dominants' mortality. We show later that dynamic programming can be used to address this problem. The model specifically deals with dwarf mongooses, although it can be generalized to other cooperative breeders. The motivation for the model is twofold. First, Creel and Waser (1991, 1994) have modeled helping and dispersal decisions in dwarf mongooses, considering only benefits that accrue over the course of a single breeding season. However, subordinates derive future fitness benefits from ascending into the breeding position in their territory, and the probability of ascending is higher in nonnatal territories (Creel &

Waser 1994). Also, breeding success increases with experience. These delayed effects could potentially influence dispersal tactics. We ask here whether the magnitude of delayed effects is sufficient to alter predictions about dispersal derived from Creel and Waser's analysis. Second, Creel and Waser (1994) found that there was individual variation among same-aged individuals in dispersal decisions (i.e., not all individuals of any given age dispersed), yet their fitness calculations considered only age-dependent effects. Dynamic programming allows dispersal decisions to be analyzed with more than one conditionality (e.g., age, group size, relatedness). Here we ask whether differences among subordinates in the genetic relatedness to dominants can account for some of the age-independent individual variation in dispersal observed in mongooses. Dynamic programming offers an evolutionary perspective of this problem by providing a means of calculating the lifetime inclusive fitness consequences of dispersal decisions.

We address one additional issue: How important are indirect fitness effects in the expression of dispersal decisions? This issue can be addressed by partitioning indirect and direct fitness effects derived from the model.

7.2 The Animals

Parameter values for the model come from demographic data recorded between 1974 and 1990 from 12 to 20 dwarf mongoose packs in the vicinity of the Serengeti Wildlife Research Institute, Tanzania (Rood 1990; Creel & Waser 1994). Mongooses were marked individually and censused at the beginning of each breeding season. Additional data came from behavioral observations during most breeding seasons and DNA fingerprinting of the members of 10 central packs from 1987 to 1990 (Keane et al. 1994; Creel & Waser, this volume).

7.3 The Model

The model focuses on dispersal decisions made by subordinate dwarf mongooses on their natal territory. These individuals are assumed to have two available alternatives: to remain in the natal queue or to disperse and enter the breeding queue in another territory. We assume that an individual will choose the alternative that maximizes its lifetime inclusive fitness. The lifetime reproductive success of either alternative includes inclusive fitness accrued as a subordinate in the current reproductive year and future reproductive fitness. Future reproductive fitness includes fitness accrued as a dominant weighted by the probability that dominant status will be attained, as well as fitness accrued as a subordinate weighted by the probability that dominant status will not be attained, each option devalued by its own mortality risk. Because both subordinates and dominants can contribute offspring to the litter (Keane et al. 1994), we estimate direct and indirect fitness for both classes of individuals each year they live. Males and females are treated separately because their survival and fecundity schedules differ, and age-related differences in fecundity and survival are explicitly considered.

We characterize each individual on the basis of three states: age, dominance status, and, if the dominance status is natal subordinate (i.e., subordinate individual in the territory in which it was born), relatedness to the dominants. Dominance status is divided into four categories: natal subordinate, natal dominant, nonnatal subordinate, and nonnatal dominant. Once individuals ascend to dominant status, we assume that they remain dominants on that territory until they die. Dominance is tightly related to age in dwarf mongooses, and the oldest dominant male and female are the parents of most offspring (Creel & Waser 1991).

At any given age, subordinates aid in the rearing of the dominant's offspring by guarding them from predators, carrying them, feeding them, grooming them, and, for some females, by nursing them (Rood 1978; Creel et al. 1991). By the same mechanisms, dominants increase the survival of those few young whose parents are subordinates. The probability that any given subordinate ascends to dominant status in its current group depends on the joint probability that the same-sex dominant dies, that there is an ascension from within the group, and that the subordinate is the oldest subordinate in its group (i.e., is first in the queue) (Creel & Waser 1994).

In our model, the genetic relationship between a subordinate and any one dominant falls into one of three categories: first-order relatives (dominant is the father or mother of the subordinate), second-order relatives (dominant is a group member that ascended to dominant status), and nonrelatives (dominant is an individual not born in the group). The coefficient of relatedness between subordinates and individuals in these three categories are 0.54, 0.26, and 0.0, respectively. These values are approximations derived from pedigree analyses (Creel & Waser 1991; and unpubl. data).

Our model does not include the effect of group size on mongoose dispersal decisions. In dwarf mongooses, mortality rates are higher in smaller groups, and the length of the queue is shorter (Rood 1990). However, the effect of a subordinate on group reproductive success is independent of group size (Creel & Waser 1991). Furthermore, group size is not temporally autocorrelated (Creel & Waser 1994), so if a subordinate is in a large group in any given year, this does not necessarily mean that it will breed in a large group if it ascends to the dominant breeding position. For simplicity and because relatedness between the subordinate and the dominant has historically been the condition most discussed in the cooperative breeding literature, we model the system assuming that subordinate–breeder relatedness is the most relevant state variable determining the expression of dispersal decisions.

7.3.1 The Dynamic Program

We use the standard dynamic programming algorithm (Mangel & Clark 1988) to calculate lifetime inclusive fitness of individuals occupying each of the four categories of breeding status. That is, we start at the maximum possible age (here operationally defined as 10 years – we assume that no animals live past this age; Waser et al. 1995) and work backward in time to age 1. For each breeding status, we calculate current inclusive fitness and expected future fitness. All individuals in the pack, both dominant and subordinate, derive inclusive fitness benefits directly from descendent offspring and indirectly from helping the offspring of others. However, since dominants produce more offspring than do subordinates, the weighting of these different avenues of fitness differs with status.

For dominant mongooses, production of offspring can increase with experience (i.e., with the number of years the individual has bred). For dominants in their natal territory, inclusive fitness (see Tables 7.1, 7.2, and 7.3 for definitions of terms and parameter values) is as follows:

$$\begin{aligned} I_{DN}[\mathit{age}, \mathit{experience}] &= (r_{breed} \times (\beta_{0\mathrm{N}} + \beta_{1\mathrm{N}} \times \mathit{experience}) \times (1 - P_{subrep})) \\ &\quad + (r_{DS} \times \Delta_{help} \times P_{subrep}) - e^{\circ} \\ &\quad + (P_{surv,D} \times I_{DN}[\mathit{age} + 1, \mathit{experience} + 1]) \end{aligned} \tag{7.1}$$

(Throughout, square brackets in these equations denote terms that are functions of the bracketed variables.) There are four parts to this relationship. The first is the current direct fitness, which is the number of offspring produced by the pack ($\beta_{0\mathrm{N}} + \beta_{1\mathrm{N}} \times \mathit{experience}$), multiplied by the fraction of these that are attributable to the dominant mongoose ($1 - P_{subrep}$), devalued by the relatedness between the dominant and its offspring (r_{breed}). The second is the indirect fitness derived from helping the offspring of subordinates ($\Delta_{help} \times P_{subrep}$), devalued by the relatedness between the dominant and the subordinates' offspring (r_{DS}). The third part is Hamilton's (1964) social factor (e°). The last part accounts for all future fitness effects ($I_{DN}[\mathit{age} + 1, \mathit{experience} + 1]$), discounted by the probability of survival ($P_{surv,D}$).

Table 7.1. *Age-independent parameter values used in the dwarf mongoose dynamic program*

Parameter	Female	Male	Definition
β_{0N}	1.78	2.00	Intercept of function relating offspring production and age of natal dominant
β_{1N}	0.73	0.00	Slope of function relating offspring production and age of natal dominant
β_{0O}	1.55	2.52	Intercept of function relating offspring production and age of nonnatal dominant
β_{1O}	0.28	0.00	Slope of function relating offspring production and age of nonnatal dominant
r_{breed}	0.5	0.50	Relatedness between dominant breeder and its offspring
r_{DS}	0.33	0.33	Genetic relatedness between the dominant and offspring produced by the subordinates
P_{subrep}	0.15	0.24	Proportion of young for which subordinates are actual parents
Δ_{help}	0.21	0.25	Number of additional offspring each helper contributes to group reproduction
$P_{surv,D}$	0.70	0.69	Probability that breeder survives 1 year
RS_{sub}	0.10	0.16	Direct fitness (number of offspring produced) of average subordinate
P_{inpack}	0.77	0.68	Probability that a dead breeder is replaced from within the group

Sources: Creel & Waser 1991, 1994; Waser et al. 1994.

As discussed in the introduction, Hamilton's social factor is the mean effect of nonbreeders on breeders' reproductive output. Following Creel (1990a), e° is subtracted from all individuals in the population. In essence, subtracting e° balances the indirect fitness added to helper fitness therefore eliminating double accounting. For the dwarf mongooses, Hamilton's social factor is calculated as follows:

$$\begin{aligned} e^{\circ} = {} & (\Delta_{help} \times \rho_{dom} \times P_{subrep}) \\ & + (\Delta_{help} \times \rho_{sub} \times (1 - P_{subrep} + \frac{\mathrm{GS} - 2}{\mathrm{GS} - 1} \times P_{subrep})) \end{aligned} \tag{7.2}$$

This represents the mean contribution of help given by dominants ($\Delta_{help} \times \rho_{dom} \times P_{subrep}$), plus the mean contribution of help given by subordinates to dominants ($\Delta_{help} \times \rho_{sub} \times (1 - P_{subrep})$), plus the mean contribution of help given by subordinates to other subordinates in the group ($\Delta_{help} \times \rho_{sub} \times (GS - 2)/(GS - 1) \times P_{subrep}$), where $GS = (1 - \rho_{sub})^{-1}$. Note that our defini-

Table 7.2. *Age-dependent parameter values used in dwarf mongoose dynamic program*[a]

Parameter	Sex	AGE									
		1	2	3	4	5	6	7	8	9	10
r_{SO}	Female	0.46	0.26	0.14	0.05	0	0	0	0	0	0
	Male	0.22	0.15	0.10	0.08	0.05	0.03	0.01	0	0	0
$P_{surv,SO}$	Male[b]	0.60	0.77	0.77	0.63	0.63	0.63	0.63	0.63	0.63	0.63
	Male[b]	0.73	0.90	0.90	0.67	0.67	0.67	0.67	0.67	0.67	0.67
	Female[b]	0.74	0.74	0.74	0.74	0.74	0.74	0.74	0.74	0.74	0.74
	Female[b]	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80
$P_{surv,SN}$	Male[b]	0.62	0.79	0.79	0.63	0.63	0.63	0.63	0.63	0.63	0.63
	Male[b]	0.73	0.90	0.90	0.67	0.67	0.67	0.67	0.67	0.67	0.67
	Female[b]	0.74	0.74	0.74	0.74	0.74	0.74	0.74	0.74	0.74	0.74
	Female[b]	0.77	0.77	0.77	0.77	0.77	0.77	0.77	0.77	0.77	0.77
$P_{surv,disp}$	Male[b]	0.56	0.67	0.67	0.55	0.55	0.55	0.55	0.55	0.55	0.55
	Male[b]	0.40	0.48	0.48	0.40	0.40	0.40	0.40	0.40	0.40	0.40
	Female[b]	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
	Female[b]	0.28	0.28	0.28	0.28	0.28	0.28	0.28	0.28	0.28	0.28
P_{breed}	Male	0	0.28	0.28	0.43	0.43	0.43	0.43	0.43	0.43	0.43
	Female	0.23	0.46	0.46	0.46	0.46	0.46	0.46	0.46	0.46	0.46
$P_{maxage,O}$	Male	0.14	0.28	0.51	0.77	1	1	1	1	1	1
	Female	0.50	0.50	0.62	1	1	1	1	1	1	1
$P_{maxage,N}$	Male	0.09	0.14	0.38	0.83	1	1	1	1	1	1
	Female	0.09	0.12	0.24	0.38	0.60	0.67	0.80	1	1	1

Sources: Creel & Waser 1991, 1994; Waser et al. 1994.

[a] Discontinuities are caused by the combining of age classes where sample sizes were low (see Creel & Waser 1994).

[b] Two sets of parameter values represent the upper and lower bounds of our estimates of these mortality risks.

Table 7.3. *Definitions of terms not defined in Table 7.1*

Term	Definition
age	Chronological age of the dominant breeder (measured in years).
experience	Number of years the dominant breeder has been reproducing.
e°	Hamilton's social factor, which is the mean effect of an individual on breeder reproductive output.
GS	Number of same-sex individuals in a group.
$P_{surv,SO}[age]$	Age-dependent survivorship of the nonnatal subordinate.
$P_{surv,SN}[age]$	Age-dependent survivorship of the natal subordinate.
$P_{maxage}[age]$	Age-dependent probability that the helper is the oldest in the group and therefore takes over the breeding position.
$P_{surv,disp}[age]$	Probability that the dispersing mongoose survives until it finds a territory (this is assumed to take about 1 month).
$P_{dom}[age]$	Probability that the individual will enter the new group as a dominant.
$P_{ascend,O}[age]$	Probability that the nonnatal subordinate will ascend to the dominant breeding position in the next year.
$\pi_{PS}[parent\ state]$	Transition probabilities from the current breeder status (*parent state*) to the breeder status next year (*PS*).
$r_{SO}[age]$	Relatedness between a nonnatal helper and the offspring it helps to rear.
ρ_{sub}	Percentage of subordinates in the population (estimated from forward iteration).
ρ_{dom}	Percentage of dominants in the population (estimated from forward iteration).

tion of group size, $GS = (1 - \rho_{sub})^{-1}$, can be thought of as the number of individuals per each dominant individual in the group. The contribution of subordinates to other subordinates' reproduction assumes that the number of subordinates of a given sex is $GS - 1$, and that the number of subordinates a given subordinate will help is $(GS - 1) - 1$. We estimate ρ_{sub} and ρ_{dom} by using forward iteration, which is discussed later.

The inclusive fitness of dominants in nonnatal territories is similar to that of dominants in their natal territories (only offspring production, $\beta_{00} + \beta_{10}$, and future fitness, I_{DO} [*age* + 1, *experience* + 1], are different):

$$\begin{aligned} I_{DO}[age, experience] &= (r_{breed} \times (\beta_{00} + \beta_{10} \times experience) \times (1 - P_{subrep})) \\ &+ (r_{DS} \times \Delta_{help} \times P_{subrep}) - e^{\circ} \\ &+ (P_{surv,D} \times I_{DO}[age + 1, experience + 1]) \end{aligned} \quad (7.3)$$

We assume that in any given year nonnatal subordinates remain in the subordinate position that year. They then either ascend to breed the next year if the dominant dies and if they are first in the queue, or they continue as subordinates for at least one more year:

$$\begin{aligned}I_{SO}[age] &= (RS_{sub} \times r_{breed}) \\ &+ (r_{SO}[age] \times \Delta_{help} \times (1 - P_{subrep}) + r_{SO}[age] \times 0.26) \\ &\times \Delta_{help} \times \frac{\mathrm{GS} - 2}{\mathrm{GS} - 1} \times P_{subrep}) \\ &- e^{\circ} + (P_{surv,SO}[age] \times ((P_{ascend,O}[age] \\ &\times I_{DO}[age + 1, experience = 0]) \\ &+ ((1 - P_{ascend,O}\,[age]) \times I_{SO}\,[age + 1]))) \end{aligned} \tag{7.4}$$

Equation (7.4) sums the current direct ($\mathrm{RS}_{sub} \times r_{breed}$) and indirect fitness accrued by the nonnatal subordinate, devalued by Hamilton's social factor (e°). There are two components to the indirect fitness: that derived from caring for the dominant's young ($r_{SO}[age] \times \Delta_{help} \times (1 - P_{subrep})$) and that derived from caring for the young of other subordinates ($(r_{SO}[age] \times 0.26) \times \Delta_{help} \times ((GS - 2)/(GS - 1)) \times P_{subrep}$). We assume that the mean relatedness of a subordinate to another breeding subordinate is its relatedness to the dominant multiplied by an approximation (0.26) of the relatedness of dominants to breeding subordinates, $r_{SO}[age] \times 0.26$. The increase in litter size, Δ_{help}, is attributed to the presence of a subordinate. Some fraction of this increase (P_{subrep}) is caused by subordinate reproduction, and a fraction of this fraction ($(GS - 2)/(GS - 1)$) is attributable to subordinates other than the focal individual being modeled. All future effects are weighted by the probability that the subordinate will survive at least one more year ($P_{surv,SO}[age]$). The future fitness of a nonnatal subordinate is the fitness of a dominant ($I_{DO}[age + 1, experience = 0]$) if it ascends (with probability $P_{ascend,O}[age]$), or the fitness of a subordinate ($I_{SO}[age + 1]$) if it does not ascend (with probability $(1 - P_{ascend,O}[age])$). The probability that a subordinate will ascend in a nonnatal group is as follows:

$$P_{ascend,O}[age] = (1 - P_{surv,D}) \times P_{inpack} \times P_{maxage,N}[age] \tag{7.5}$$

Thus the probability of ascending is the probability that the dominant will die ($1 - P_{surv,D}$) times the probability that the dominant will be replaced from within the pack (P_{inpack}) times the probability that the subordinate will be first in the queue ($P_{maxage,N}[age]$).

Subordinates on their natal territories have two alternatives: They can remain there at least one more year or disperse and attempt to join another group. The inclusive fitness of an individual choosing the dispersal option is as follows:

$$\begin{aligned}
I_{disp}[age] &= P_{surv,disp}[age] \\
&\times (P_{dom}[age] \times ((r_{breed} \times \beta_{OO} \times (1 - P_{subrep})) + (r_{DS} \times \Delta_{help} \times P_{subrep}) \\
&+ (P_{surv,D}[age]^{11/12} \times I_{DO}[age + 1, experience = 1]) \\
&+ (1 - P_{dom}[age]) \times ((r_{SO}[age] \times \Delta_{help} \times (1 - P_{subrep}) \\
&+ (r_{SO}[age] \times 0.26) \times \Delta_{help} \times \frac{\mathrm{GS} - 2}{\mathrm{Gs} - 1} \times P_{subrep}) + (RS_{sub} \times r_{breed}) \\
&+ P_{surv,SO}[age]^{11/12} \times ((P_{ascend,O}[age] \times I_{DO}[age + 1, experience = 0]) \\
&+ ((1 - P_{ascend,O}[age]) \times I_{SO}[age + 1])))) - e^{\circ}
\end{aligned} \tag{7.6}$$

Here we assume that the disperser suffers some mortality risk ($P_{surv,disp}[age]$ is the probability that it survives) during the dispersal event that we assume to take about 1 month. If it survives, it enters a nonnatal pack. If it enters as a dominant (with probability $P_{dom}[age]$), its expected current fitness is $(r_{breed} \times \beta_{OO} \times (1 - P_{subrep}) + (r_{DS} \times \Delta_{help} \times P_{subrep})$. If it survives the following 11 months (with probability $P_{surv,D}[age]^{11/12}$), then its future fitness is $I_{DO}[age + 1, experience = 1]$. Finally, if the mongoose enters as a subordinate (with probability $(1 - P_{dom}[age])$), then its current fitness will be $(r_{SO}[age] \times \Delta_{help} \times (1 - P_{subrep}) + (r_{SO}[age] \times 0.26) \times \Delta_{help} \times ((GS - 2)/(GS - 1)) \times P_{subrep}) + (RS_{sub} \times r_{breed})$. If it survives the following 11 months (with probability $P_{surv,SO}[age]^{11/12}$), it will ascend the next year with probability $P_{ascend,O}[age]$, in which case its future fitness is $I_{DO}[age + 1, experience = 0]$, or it will fail to ascend the next year with probability $(1 - P_{ascend,O}[age])$, in which case its future fitness is $I_{SO}[age + 1]$.

The inclusive fitness of the individual that remains as a subordinate in its natal pack is dependent, in part, on its relatedness to the current dominants and on the expected change in relatedness in the future. We define *parent state* as the current relationship between a single dominant (i.e., either the male or female) and a subordinate. There are three different levels of *parent state*, first-order, second-order, and nonrelative, and the level will change in any year that at least one of the dominants dies. The following transition matrix was used to estimate the transition probabilities, $\pi_{PS}[parent\ state]$, from the current degree of relatedness (*parent state*) to the relatedness for the next year (*PS*):

Parent State	PS = First Order	PS = Second Order	PS = Nonrelative
First order	$P_{surv,D}$	$(1 - P_{surv,D}) \times P_{inpack}$	$(1 - P_{surv,D}) \times (1 - P_{inpack})$
Second order	0	$(1 - P_{surv,D}) \times P_{inpack} + P_{surv,D}$	$(1 - P_{surv,D}) \times (1 - P_{inpack})$
Nonrelative	0	$(1 - P_{surv,D}) \times P_{inpack}$	$(1 - P_{surv,D}) \times (1 - P_{inpack}) + P_{surv,D}$

These transition probabilities are used to calculate the inclusive fitness of the mongoose that remains as a subordinate on its natal territory, as follows:

$$
\begin{aligned}
&I_{SN}[age, parent\ state] = \\
&(r_{SN}[parent\ state] \times \Delta_{help} \times (1 - P_{subrep}) \\
&\quad + (0.26 \times \Delta_{help} \times \frac{GS-2}{GS-1} \times P_{subrep}) \\
&\quad + (RS_{sub} \times r_{breed}) - e^{o} \\
&\quad + P_{surv,SN}[age] \times (P_{ascend,N}[age] \times I_{DN}[age + 1, experience = 0] \\
&\quad + (1 - P_{ascend,N}[age]) \times \sum_{PS=1}^{9} (\pi_{PS}[parent\ state] \times I_{SN}[age + 1, PS])) \qquad (7.7)
\end{aligned}
$$

Here current indirect ($r_{SN}[parent\ state] \times \Delta_{help} \times (1 - P_{subrep}) + (0.26 \times \Delta_{help} \times ((GS - 2)/(GS - 1)) \times P_{subrep})$) and direct ($RS_{sub} \times r_{breed}$) inclusive fitness are devalued by Hamilton's social factor (e^{o}). Future fitness is accrued as a dominant ($I_{DN}[age + 1, experience = 0]$) if the subordinate survives (with probability $P_{surv,SN}[age]$) and ascends (with probability $P_{ascend,N}[age]$), and future fitness is accrued as a subordinate ($\sum_{PS=1}^{9} (\pi_{PS}[parent\ state] \times I_{SN}[age + 1, PS])$) in the next year if it survives but fails to ascend then (with probability $(1 - P_{ascend,N}[age])$).

If $I_{Sn}[age,parent\ state] \geq I_{disp}[age]$ (i.e., if the fitness from philopatry exceeds the fitness from dispersal), we assume that the individual will remain on its natal territory, and that otherwise it will disperse.

7.4 Forward Iteration

The dynamic program will generate the optimal age-specific dispersal decisions for natal subordinates. We can use these age-specific dispersal decisions in a population simulation (i.e., a forward iteration). The forward iteration can be used to estimate several demographic characteristics of the population, including the expected age structure of the population, the expected proportion of the population that are subordinates, and the mean genetic relationship between dominants and subordinates. The forward iteration starts with a population of juveniles that are resident on their natal territories. Given the survivorship values for parents and offspring, the state-specific dispersal decisions and the transition equations from the dynamic program (see previous section), we can then trace the expected fate of these juveniles.

Forward iteration, as we have used it here, is a standard approach to solving a second type of problem: Predicted decisions may depend on certain variables that in turn are affected by decisions made by the animals (e.g., Green 1980; Houston & McNamara 1987). For example, in game theory models the payoff on any given decision is affected by the frequencies with which alternative decisions are expressed by individuals of the population, but these frequencies are in turn affected by the payoff matrix (e.g., Maynard Smith 1982).

In our model the proportion of individuals in the population that are subordinates will covary with the state-dependent decisions made by those subordinates. This is because Hamilton's social factor (e°) is a function of the proportion of subordinates in the population (see Eq. 7.2) and will affect the fitness consequences of the dispersal decision. But the proportion of subordinates in the population will vary with the dispersal decisions made by the mongooses. Thus e° will affect the dispersal decisions, but its value is dependent in part on the dispersal decisions.

There are two alternatives for incorporating this feedback into the model. One is essentially to ignore it by fixing the proportion of subordinates at the level observed in our mongoose populations and estimating the dispersal decisions based on this fixed number. The other is to use a forward iteration process to estimate both the decision matrix and the proportion of subordinates. We have taken the latter approach: We start with an estimate of the proportion of subordinates, then use dynamic programming to determine the optimal decision matrix, and then use forward iteration to estimate the expected proportion of subordinates that would result from this decision matrix. We then rerun the dynamic program with this new estimate of the proportion of subordinates. This process is repeated until the proportion of subordinates generated from the forward iteration is the same as the proportion of subordinates used in the dynamic program.

This iteration process solves for the equilibrium set of state- and age-dependent behaviors, which will in turn determine the equilibrium proportion of subordinates in the population (i.e., group size). Again, the calculations are necessary because behavior affects group size and group size affects behav-

Table 7.4. *Equilibrium proportion of helpers predicted by the dynamic program*

Model	Sex	$P_{surv,disp}[age]$[a]	Proportion helpers
Current fitness only	Female	low	0.869
		high	0.748
	Male	low	0.836
		high	0.807
Lifetime fitness	Female	low	0.872
		high	0.765
	Male	low	0.836
		high	0.807
Breeder reprod. only	Female	low	0.872
		high	0.765
	Male	low	0.849
		high	0.807

[a]See Table 7.1 for low and high parameter values.

ior. If group size were fixed, the model would not be internally consistent, because the predicted behavior matrix for a given group size may generate a population characterized by a different group size. Table 7.4 shows that the equilibrium proportion of helpers determined by forward iteration using a wide range of parameter values ranges from 0.748 to 0.872, in close agreement with the true proportion of helpers in mongoose groups.

Note that although the iteration procedure is similar to the algorithm typically used to solve dynamic games (see Houston & McNamara 1987), this is not a dynamic game because none of the payoffs are assumed to be frequency dependent. Also, with some dynamic games the iteration process never reaches a steady state (e.g., Houston & McNamara 1987; Lucas et al. 1996); however the results reported here always reached a steady state within three iterations.

7.5 Decisions Based on Immediate Payoffs

To determine the importance of future fitness effects for reproductive decisions by subordinate mongooses, we ran our dynamic program both by using equations (7.1) to (7.7) and by using them minus all the future fitness terms. The results of the latter procedure should resemble those obtained by alternative models based solely on current fitness. Creel and Waser (1991, 1994) developed two different sets of equations estimating age-specific current fitness for philopatric and dispersing mongooses. In Creel and Waser (1991), the subordinate mongoose was assumed to remain subordinate on its natal territory if it chose to stay. Alternatively, it could enter a new group as either a subordinate or as a dominant if it chose to disperse, and if it survived the dispersal event. This is an oversimplification because approximately 30 percent of dominants turn over every year, and some of this turnover occurs during the breeding season. Thus, there is some (relatively low) probability that a subordinate will ascend during the current breeding season.

Creel and Waser (1994) allowed for the additional possibility that the natal subordinate may ascend on its territory during the current year by assuming that all turnover occurs before the breeding season starts. Unfortunately, this latter formulation overestimates the probability that a subordinate will ascend into dominant breeder status. Implicitly, it assumes that all dominants that die do so before breeding begins, so that all the direct fitness they would have acquired that year goes to the ascending subordinate.

The better of the two estimates of inclusive fitness comes from Creel and Waser (1991), and we use this estimate. In essence, we assume that the year begins at the beginning of the breeding season and that dominants that die do so after the year's breeding is complete.

7.6 Lifetime Inclusive Fitness, Fitness Gradients, and Parameter Estimates

The results of our model were calculated as the net fitness consequences associated with choosing to stay (i.e., inclusive fitness of a philopatric subordinate minus the inclusive fitness of a dispersing subordinate), taken as a fraction of the expected lifetime inclusive fitness (essentially its reproductive value v_x; Fisher 1958). This ratio is the fitness gradient; it gives the net consequences to lifetime fitness for each of the options available to the natal subordinate (see McNamara & Houston 1986 for a somewhat different approach). The consequences of all decisions are given as a function of two variables: the subordinate's age and its genetic relatedness to the current dominants.

We have direct estimates from field observations of all parameter values except mortality rates (see Tables 7.1, 7.2). We estimated reasonable bounds on mortality rates that were based on known disappearance rates, immigration rates, and mortality rates of individuals unlikely to disperse (i.e., dominants). The technique is described in detail in Waser, Creel, and Lucas (1994). In short, from annual census data, we know how many individuals of any given age and sex survive in a group and how many immigrate into a group. From these data, we can estimate an average mortality risk in the population, but we do not know the circumstances of these deaths. More specifically, some unknown fraction occur during dispersal, some unknown fraction occur in the natal group, and some unknown fraction occur after a subordinate immigrates into a nonnatal group. We can place absolute bounds on the three sources of mortality because they must sum to the overall mortality rate in the population. We have narrowed these bounds by assuming that mortality risks are the same in the natal and nonnatal groups and by assuming that the mortality risk experienced during dispersal is no less than the risk experienced in the group. One result of our method of estimating mortality risk is that there is a negative correlation between dispersal mortality risk and the mortality risk experienced by philopatric individuals. As a result, maximum estimates of dispersal risk are used with minimum estimates of mortality risk on the territory.

7.7 Results

Our results strongly suggest that future fitness effects cannot be ignored in modeling the evolution of cooperative breeding. Moreover, they indicate that differences among individuals in relatedness to the dominants can result in individual differences in dispersal tactics, even after accounting for the effects of age (which covaries strongly with relatedness). Finally, they suggest that predicted dispersal tendencies are strongly influenced by assumptions about mortality risk. This last finding points up a critical need for better data from field studies, because dispersal mortality has been notoriously difficult to measure with accuracy.

7.8 Future Effects

Creel and Waser (1994) showed that dispersal in female mongooses occurs primarily at 2 years of age; females that fail to emigrate at this age tend to remain on their natal territories. In contrast, males disperse at all ages, although most leave before they are 4 years old. The version of our model in which dispersal decisions are based solely on consequences in the current year correctly predicts a more extensive dispersal in males than in females but does not correctly predict the age distribution of dispersers, especially in females. The model generally predicts that dispersal decisions should be approximately age independent for all individuals older than 1 year of age (Figure 7.1); the prediction holds for females irrespective of dispersal mortality, and it holds for males if dispersal mortality is low. If the dispersal mortality is high for males, then all dispersal is predicted to occur before individuals are 4 years old. Neither of these patterns was observed. The discrepancy between the model results and the observed dispersal patterns suggests that

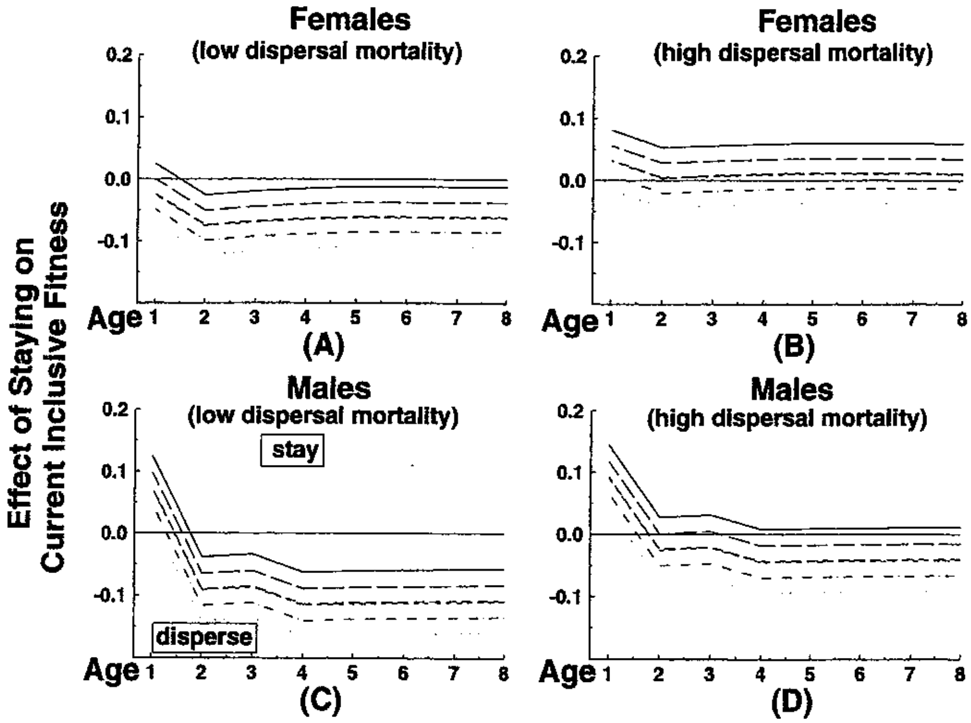

Figure 7.1. Net effect of nondispersal on current inclusive fitness as a function of age for subordinate mongooses on their natal territory. The net effect of nondispersal is the inclusive fitness accrued in the current year by staying minus the inclusive fitness accrued in the current year by dispersing females (A, B) and males (C, D). Figures 7.1A and B assume low dispersal mortality and high mortality on the territory; B and D assume high dispersal mortality and low mortality on the territory. Different lines represent different levels of relatedness to dominant breeders: solid line: $r = 0.54$, long dash: $r = 0.40$, medium dash: $r = 0.27$, short dash: $r = 0.26$, dot dash: $r = 0.13$, dots: $r = 0.00$. Parameter values are given in Tables 7.1 and 7.2. For values >0, the mongoose should remain on the territory; for values <0, the mongoose should disperse.

dispersal decisions are governed by more than just immediate fitness consequences.

The predictions differ in several respects when future reproductive success is added to the model (Figure 7.2). First, the mongooses should be more philopatric if future effects are considered. These effects are primarily a result of the low contribution of current reproductive success to lifetime fitness. Current inclusive fitness payoffs are only about 10 percent of the total lifetime fitness of young individuals (Figure 7.3). Because future fitness effects represent a majority of the lifetime fitness of subordinates, mongooses should be more sensitive to mortality risk if they base dispersal decisions on total lifetime reproductive success as opposed to basing their decision on just the payoff accrued during the current year. A longer time horizon to the dispersal

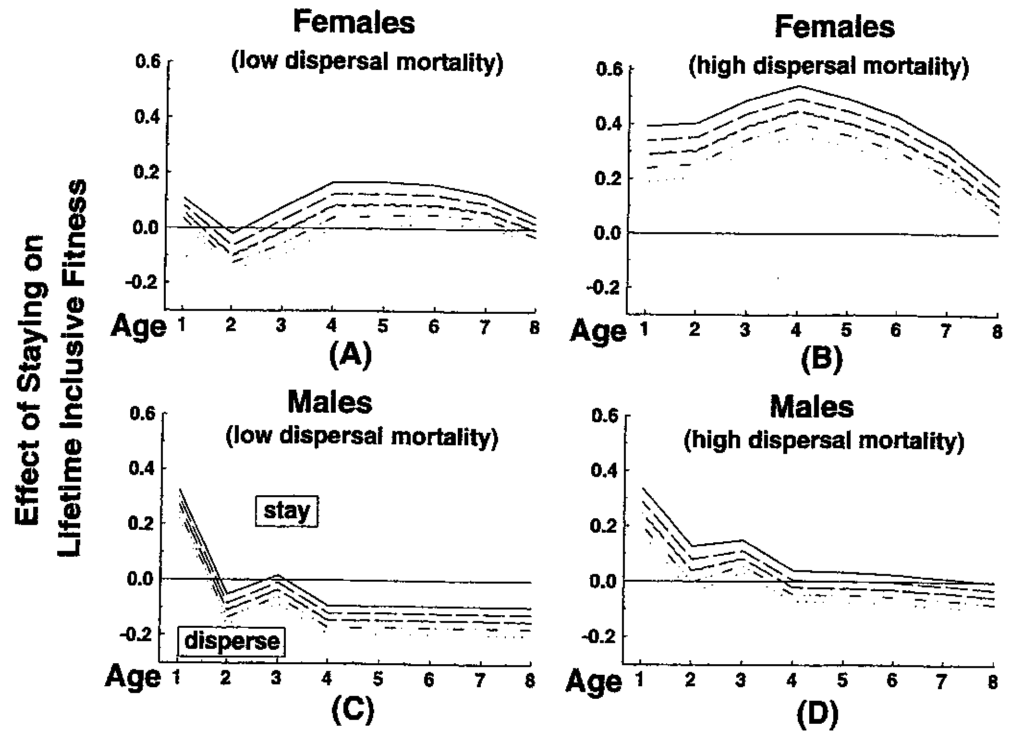

Figure 7.2. Net effect of staying on lifetime inclusive fitness, as a function of age, for subordinate mongooses on their natal territory. These results consider current and future and both indirect and direct fitness effects. See Figure 7.1 for details.

decision should favor philopatry, because the mortality risk during dispersal is relatively high (see Tables 7.1 and 7.2).

Second, female dispersal decisions are potentially more strongly age dependent than those of males (see Figure 7.2). Assuming that mortality rates during dispersal are near our lower estimated rates, the patterns predicted by the model incorporating lifetime consequences of dispersal decisions are consistent with the observed dispersal behavior: Some females leave at age 2, but those that stay should remain in the natal territory for their lifetime. The high cost of leaving for older females is not seen in males (see Figure 7.2).

However, a major caveat to these conclusions is that the results are strongly affected by the assumptions made concerning mortality rates. If the dispersal mortality rates are high, then no dispersal is predicted, except by older males. In addition, if the dispersal mortality rates are high, the fitness consequences of dispersal are quite severe for females; they would lose more than 50 percent of their age-specific lifetime inclusive fitness (i.e., current plus future fitness) if they dispersed at any age. Thus, if the dispersal mortality rates were high, there would be very strong selection against dispersal. Given that about 20 percent of 2-year-old females disperse (Creel & Waser 1994), these results

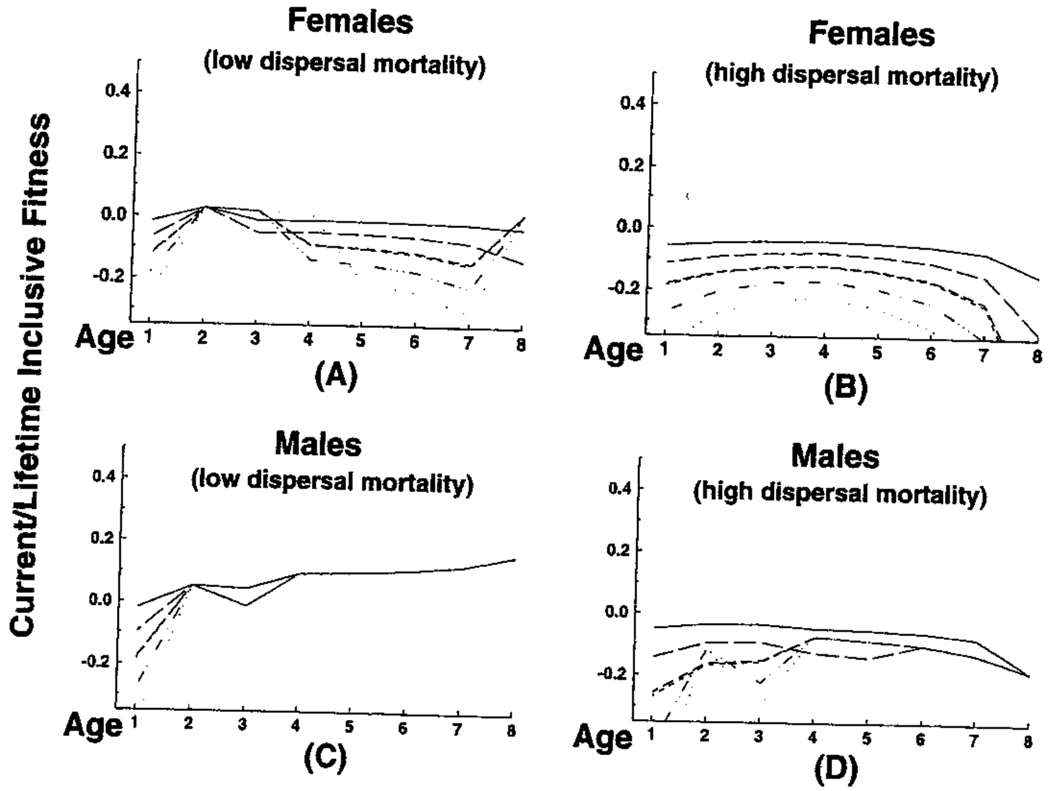

Figure 7.3. Ratio of current to lifetime inclusive fitness for subordinate mongooses on their natal territory, as a function of age. Results assume that dispersal decisions are based on lifetime inclusive fitness, considering both indirect and direct effects: (A,B) females, (C,D) males. Figures 7.3A and B assume low dispersal mortality and high mortality on the territory; B and D assume high dispersal mortality and low mortality on the territory.

indicate that the true dispersal risk faced by female mongooses is closer to our lower estimate. At this point, nothing more can be said about this conclusion, except that it is a testable hypothesis.

7.9 Indirect Effects

We can evaluate the relative impact of indirect fitness effects on dispersal decisions by assuming that the dispersal decisions are based solely on dispersal's current and future consequences for mortality and production of offspring. If indirect fitness effects are important determinants of dispersal decisions in dwarf mongooses, then the predicted decisions should change when indirect effects are dropped from the model.

When we compare model predictions with and without indirect fitness effects, the results suggest a reason why controversy over this topic has been so persistent. On the one hand, the general pattern of age-dependence in the

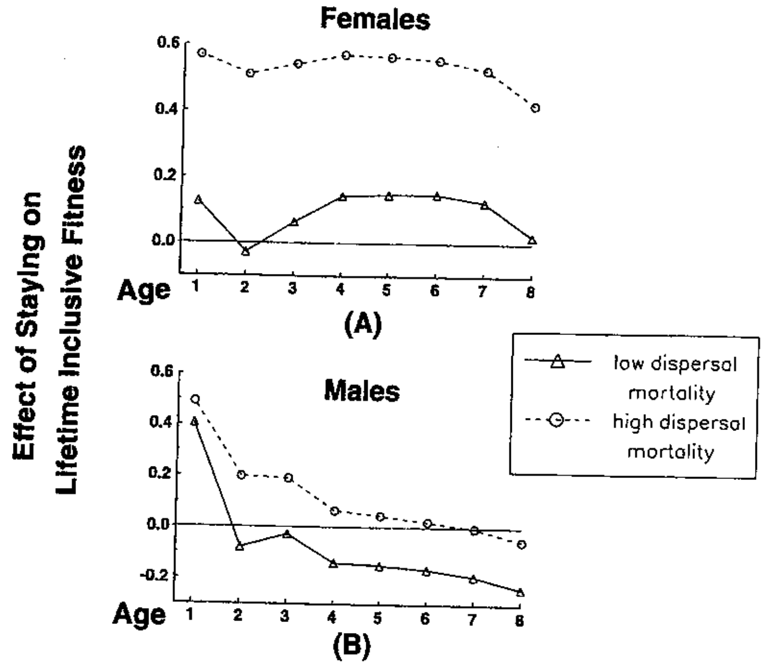

Figure 7.4. Effect of staying on lifetime direct fitness, as a function of age, for subordinate mongooses on their natal territory. These results measure only the effects of the dispersal decision on mortality and production of young; indirect effects are not considered.

fitness gradient is similar with or without indirect fitness included (compare Figure 7.2 and 7.4). On the other hand, Figure 7.2 demonstrates that indirect fitness effects can tip the balance in favor of staying in the natal group. Higher relatedness between subordinates and dominants substantially shifts the fitness gradient toward philopatry. Indirect effects have a particularly marked effect on the dispersal decision if dispersal mortality is low (see Fig. 7.2).

The results of the model reflect the impact of a number of age-related tradeoffs that potentially affect mongoose dispersal decisions. The genetic relatedness between subordinate and dominant declines with subordinate age. The decrease is greater for males than for females and occurs on both natal and nonnatal territories (Creel & Waser 1994). The decline in relatedness on the natal territory is caused by mortality of the subordinate's parents and by the potential ascension of less closely related dominants. The high relatedness in young nonnatal subordinates is primarily a result of group dispersal of related individuals into a territory and to the ascension of co-dispersing kin into the breeding position (Creel & Waser 1994). As these kin die, relatedness declines (see Table 7.2). One result of the decrease in mean relatedness between helper and breeder is a decrease with age in the expected contribution of indirect fitness to total lifetime inclusive fitness. This also means that indirect fitness consequences will have greater effects on decisions of young animals.

An important factor that causes inclusive fitness to be low for subordinates is the relatively high value of $e°$, Hamilton's social factor. This is subtracted from the inclusive fitness of all individuals in the population. Subordinates accrue some direct fitness benefits, but these are not very large (fewer than 0.2 offspring/subordinate/year; see Table 7.1). The number of offspring equivalents added by each subordinate as a result of its aid of pack mates is somewhat larger (see Table 7.1). However, both types of fitness are generally less than Hamilton's social factor for nondispersing subordinates, so the inclusive fitness of this class of individual tends to be negative (see Figure 7.3). The primary reason is the high proportion of subordinates in the population. Hamilton's social factor is the mean amount of assistance each individual in the population gives to its neighbors. To simplify the discussion, we consider a system in which there is a perfect dichotomy between helpers and breeders. In such a system, $e°$ is equivalent to the effect on breeder reproductive success of the helper multiplied by the proportion of helpers in the population. Indirect fitness is the effect on breeder reproductive success of a helper, devalued by its relatedness to the breeder. Thus, if the proportion of helpers is greater than the relatedness between helper and breeder, helpers will realize a negative inclusive fitness. Because both subordinates and dominants help, the calculations are somewhat more complicated for mongooses, but the general problem still holds.

Given the negative inclusive fitness values, the decision made by older female natal subordinates to stay in their natal territories (see Figure 7.2) is more a reflection of expected future breeding opportunities than of the indirect fitness derived from helping the dominants rear offspring. In this respect, a number of factors favor philopatry in females compared to males: (1) breeder survivorship is lower in females and therefore the dominant position is more likely to open up (see Table 7.1); (2) given that a dominant position has become vacant, females from within the pack (as opposed to immigrants) are more likely than are resident subordinate males to ascend into the dominant position (see Table 7.1); and (3) the mortality risk of dispersal appears to be higher for females than for males (see Table 7.2).

7.10 Discussion

The relative importance of indirect inclusive fitness on the evolution of helping behavior is controversial. Some authors feel that indirect effects are likely to be relatively unimportant (Zahavi 1974; Ligon 1981; Walters et al. 1992), whereas others argue that indirect effects cannot be overlooked (Mumme et al. 1989; Emlen & Wrege 1991; Creel & Waser 1994). Our results from the dwarf mongooses add an additional complication to this controversy. Indirect effects may account for a small fraction of the total lifetime inclusive fitness on average, yet they potentially have a major impact on dispersal decisions in cases where the fitness consequences of dispersal are similar to the fitness consequences of philopatry. We have shown that this condition is met when the mortality risk associated with dispersal is low. Thus, for mongooses of some age–sex classes, indirect fitness can be critical to dispersal decisions.

This raises a second complication: The predicted behavior is sensitive to assumptions about mortality risks. Unfortunately, mortality risks are exceedingly difficult to measure directly (e.g., Lima & Dill 1990). We show elsewhere that certain types of demographic data can be used to estimate bounds on mortality risks (Waser et al. 1994), and we have employed this method here. Our bounds are based on >1,600 mongoose years of demographic data, yet they are still too wide to allow unequivocal predictions from the model! Perhaps the strongest comment we can make is that the lack of good data on dispersal mortality may be a major cause of the persistence of controversy over the "causes" of cooperative breeding. Perhaps part of the effort currently devoted to obtaining more precise estimates of parentage would be better spent using telemetry to get better estimates of dispersal mortality.

An additional point is worth mentioning about the magnitude of indirect fitness effects. In species where virtually all individuals are either helpers or breeders, and in particular where the proportion of helpers in the population is large, the inclusive fitness to helpers may be negative for all helpers in the population. This follows from the formulation of Hamilton's social factor derived by Creel (1990a), who showed that Hamilton's social factor was the mean amount of help given by the average individual in a population (or alternatively, the mean amount of help received). If the fraction of helpers in a population is large (as is the case in dwarf mongooses) and each contributes a substantial amount of help in rearing young, then Hamilton's social factor could be a relatively large number. Creel (1990a) also showed that this number should be subtracted from each individual in the population. Thus, when the indirect fitness accrued by helpers is less than Hamilton's social factor, then the current inclusive fitness derived by helpers will be negative.

Creel (1990a; also see Creel & Waser 1994) suggested that the magnitude of e° should not affect behavioral decisions because it is a constant subtracted equally from all individuals in the population. The implication is that relative payoff of different dispersal tactics can be correctly evaluated even if we miscalculate e°. This is important because e° has rarely been calculated correctly.

However, when future effects are considered, the magnitude of e° can alter the predictions about dispersal behavior if the mortality risks associated with the alternative behaviors differ. To show this, we consider a simple example. Assume that dispersing subordinates always die in the current year and that nondispersing subordinates survive the current year but always die the following year. The net impact of e° on dispersers will be $1 \times e^\circ$, and on nondispersers it will be $2 \times e^\circ$. In this case, the magnitude of e° could be quite important in the net benefit of dispersal. Given that mortality risks of behavioral alternatives will generally differ, an accurate evaluation of e° seems warranted.

Dwarf mongooses exhibit a great deal of individual variation in their dispersal behavior. For example, some individuals can remain as natal subordinates after 9 years of age, whereas others leave at age 1 (Rood 1987). A full understanding of the evolution of dispersal requires that we refine our analyses by identifying variables that account for a significant amount of variation among individuals. Much of the individual variation in the mongooses can be accounted for by variables that change with age. These include mortality risks and the probability of ascending into the dominant breeding position. These age-related effects were the basis of our previous modeling efforts (Creel & Waser 1991, 1994). However, there are additional variables that can potentially account for some of this variation that is not age-related per se. We have shown here that variation in the relatedness between subordinate and dominants can account for some of the variation in dispersal tendencies in same-aged individuals; helpers closely related to the current dominants should be more likely to stay than subordinates that are only distantly related.

7.11 Conclusions

Models of the inclusive fitness of helping have been developed in an incremental fashion. Early models (e.g., Grafen 1984) considered only the immediate effects of helping on inclusive fitness. Future effects were added by a number of authors, including Brown (1987), Mumme et al. (1989), and Creel (1990b). Hamilton's e°, the social factor that should be stripped from breeders' and helpers' fitness, has only recently been rigorously defined (Creel 1990a). Our models contribute to this iterative process by showing how dispersal can be modeled as a series of dynamic decisions (Houston, Clark, & Mangel 1988; Mangel & Clark 1988), in which both state (here relatedness) and the effect of future decisions are considered in the evaluation of a behavioral trait. Our model by necessity leaves out some additional states. Perhaps the most important is group size. Our original models (Creel & Waser 1991,

1994) ignored group size as a factor affecting dispersal decisions, and we have done so here as well. Several factors that influence the inclusive fitness of subordinates are independent of group size. These include the contribution each subordinate makes to group reproductive output (Creel & Waser 1991) and the temporal autocorrelation in group size (Creel & Waser 1994). However, survival rates can increase with group size, at least for breeders (Rood 1990). Two other factors that we have ignored are individual differences in size or nutrition and in the opportunity for dispersal. These additional factors may account for some variation between individuals in dispersal decisions, in addition to the differences in relatedness considered in our model.

Acknowledgments

Computer time was provided by Purdue University. Recent field work and demographic analysis by S. R. Creel and P. M. Waser was supported by the National Geographic Society, the Frankfurt Zoological Society, and the National Science Foundation. Modeling by J. R. Lucas was supported by NSF grant IBN–9222313.

References

Alexander, R. D., Noonan, K. M., & Crespi, B. J. (1991). The evolution of eusociality. In *The biology of the naked mole-rat,* ed. P. W. Sherman, J. U. M. Jarvis, & R. D. Alexander, pp. 3–44. Princeton: Princeton University Press.

Brooker, M. G., Rowley, I., Adams, M., & Baverstock, P. R. (1990). Promiscuity: An inbreeding avoidance mechanism in a socially monogamous species? *Behav. Ecol. Sociobiol.* 26:191–200.

Brown, J. L. (1987). *Helping and communal breeding in birds.* Princeton: Princeton University Press.

Clark, C. W. (1993). Dynamic models of behavior: an extension of life history theory. *Trends Ecol. Evol.* 8:205–209.

Creel, S. (1990a). How to measure inclusive fitness. *Proc. Royal Soc. Lond.* B241:229–231.

Creel, S. (1990b). The future components of inclusive fitness: Accounting for interactions between members of overlapping generations. *Anim. Behav.* 40:127–134.

Creel, S. R., & Macdonald, D. W. (1995). Sociality, group size, and reproductive suppression in carnivores. *Adv. Study Behav.* 24:203–257.

Creel, S. R. & Waser, P. M. (1991). Failure of reproductive suppression in dwarf mongooses (*Helogale parvula*): Accident or adaptation? *Behav. Ecol.* 2:7–15.

Creel, S. R., & Waser, P. M. (1994). Inclusive fitness and reproductive strategies in dwarf mongooses. *Behav. Ecol.* 5:339–348.

Creel, S. R., Monfort, S. C., Wildt, D. E., & Waser, P. M. (1991). Spontaneous lactation is an adaptive result of pseudopregnancy. *Nature, Lond.* 351:660–662.

Emlen, S. T. (1991). Evolution of cooperative breeding in birds and mammals. In *Behavioural ecology: An evolutionary approach,* 3rd ed., ed. J. R. Krebs & N. B. Davies, pp. 301–335. Oxford, U.K.: Blackwell.

Emlen, S. T., & Wrege, P. H. (1991). Breeding biology of white-fronted bee-eaters at Nakuru: The influence of helpers on breeder fitness. *J. Anim. Ecol.* 60:309–326.

Emlen, S. T., & Wrege, P. H. (1994). Gender, status and family fortunes in the white-fronted bee-eater. *Nature, Lond.* 367:129–132.

Faaborg, J., Parker, P. G., Delay, L., deVries, T., Bednarz, J. C., Paz, S. M., Naranjo, J., & Waite, T. A. (1995). Confirmation of cooperative polyandry in the Galapagos Hawk (*Buteo galapagoensis*). *Behav. Ecol. Sociobiol.* 36:83–90.

Fisher, R. A. (1958). *The genetical theory of natural selection.* New York: Dover.

Grafen, A. (1982). How not to measure inclusive fitness. *Nature, Lond.* 298:425.

Grafen, A. (1984). Natural selection, kin selection and group selection. In *Behavioural ecology: An evolutionary approach,* 2nd ed., ed. J. R. Krebs & N. B. Davies, pp. 62–84. Oxford, U.K.: Blackwell.

Green, R. F. (1980). Bayesian birds: A simple example of Oaten's stochastic model of optimal foraging. *Theo. Pop. Biol.* 18:244–256.

Hamilton, W. D. (1964). The genetical evolution of social behaviour. *J. Theo. Biol.* 7:1–16.

Houston, A. I., & McNamara, J. M. (1982). A sequential approach to risk-taking. *Anim. Behav.* 30:1260–1261.

Houston, A. I., & McNamara, J. M. (1987). Singing to attract a mate: A stochastic dynamic game. *J. Theo. Biol.* 129:57–68.

Houston, A., Clark, C., McNamara, J., & Mangel, M. (1988). Dynamic models in behavioural and evolutionary ecology. *Nature, Lond.* 332:29–34.

Keane, B., Waser, P. M., Creel, S. R., Creel, N. M., Elliot, L. F., & Minchella, D. J. (1994). Subordinate reproduction in dwarf mongooses. *Anim. Behav.* 47:65–75.

Ligon, J. D. (1981). Demographic patterns and communal breeding in the green woodhoopoe, *Phoeniculus purpuratus.* In *Natural selection and social behavior: Recent research and new theory,* ed. R. D. Alexander & D. W. Tinkle, pp. 231–243. New York: Chiron Press.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68:619–640.

Lucas, J. R. (1983). The role of foraging time constraints and variable prey encounter in optimal diet choice. *Am. Nat.* 122:191–209.

Lucas, J. R., Howard, R. D., & Palmer, J. G. (1996). Callers and satellites: Chorus behaviour in anurans as a stochastic dynamic game. *Anim. Behav.* 51:501–518.

Malcolm, J. R., & Marten, K. (1982). Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). *Behav. Ecol. Sociobiol.* 10:1–13.

Mangel, M., & Clark, C. W. (1988). *Dynamic modeling in behavioral ecology.* Princeton: Princeton University Press.

Maynard Smith, J. (1982). *Evolution and the theory of games.* Cambridge: Cambridge University Press.

McNamara, J., & Houston, A. I. (1986). The common currency for behavioral decisions. *Am. Nat.* 127:358–378.

Moehlman, P. (1983). Socioecology of silverbacked and golden jackals, *Canis mesomelas* and *C. aureus.* In *Advances in the study of mammalian behavior,* ed. J. F. Eisenberg & D. L. Kleiman, pp. 423–453. Lawrence, Kans.: American Society of Mammalogists Special Publication #7.

Mumme, R. L., Koenig, W. D., & Ratnieks, F. L. W. (1989). Helping behaviour, reproductive value, and the future component of indirect fitness. *Anim. Behav.* 38:331–343.

Mumme, R. L., Koenig, W. D., Zink, R. M., & Martin, J. A. (1985). Genetic variation and parentage in a California population of acorn woodpeckers. *Auk* 102:305–312.

Rabenold, P. P., Rabenold, K. N., Piper, W. H., Haydock, J., & Zack, S. W. (1990). Shared paternity revealed by genetic analysis in cooperatively breeding tropical wrens. *Nature, Lond.* 348:538–540.

Reyer, H.-U. (1984) Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). *Anim. Behav.* 32:1163–1178.

Rood, J. P. (1978). Dwarf mongoose helpers at the den. *Z. Tierpsychol.* 48:277–287.

Rood, J. P. (1987). Dispersal and intergroup transfer in the dwarf mongoose. In *Mammalian dispersal patterns: The effects of social structure on population genetics,* ed. B. D. Chepko-Sade & Z. Halpin, pp. 85–102. Chicago: Chicago University Press.

Rood, J. P. (1990). Group size, survival, reproduction, and routes to breeding in dwarf mongooses. *Anim. Behav.* 39:566–572.

Solomon, N. G. (1994). Effect of the pre-weaning environment on subsequent reproduction in prairie voles, *Microtus ochrogaster. Anim. Behav.* 48:331–341.

Walters, J. R., Doerr, P. D., & Carter, J. H. III. (1992). Delayed dispersal and reproduction as a life-history tactic in cooperative breeders: Fitness calculations from red-cockaded woodpeckers. *Am. Nat.* 139:623–643.

Waser, P. M., Creel, S. R., & Lucas, J. R. (1994). Death and disappearance: estimating mortality risks associated with philopatry and dispersal. *Behav. Ecol.* 5:135–141.

Waser, P. M., Elliott, L. F., Creel, N. M., & Creel, S. R. (1995). Habitat variation and mongoose demography. In *Serengeti II: Dynamics, management, and conservation of an ecosystem,* ed. A. R. E. Sinclair & P. Arcese, pp. 421–450. Chicago: Chicago University Press.

Wiley, R. H., & Rabenold, K. N. (1984). The evolution of cooperative breeding by delayed reciprocity and queuing for favorable social positions. *Evolution* 38:609–621.

Woolfenden, G., & Fitzpatrick, J. (1984). *The Florida scrub jay: Demography of a cooperative-breeding bird.* Princeton: Princeton University Press.

Zack, S., & Stutchbury, B. J. (1992). Delayed breeding in avian social systems: The role of territory quality and "floater" tactics. *Behaviour* 123:194–219.

Zahavi, A. (1974). Communal nesting by the Arabian babbler. *Ibis* 116:84–87.