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Dynamics of the Caring Family

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ABSTRACT: When several individuals simultaneously provide for offspring, as in families, the effort of any one individual will depend on the efforts of the other family members. This conflict of interest among family members is made more complicated by their relatedness because relatives share genetic interest to some degree. The conflict resolution will also be influenced by the differences in reproductive value between breeders and helpers. Here, we calculate evolutionarily stable provisioning efforts in families with up to two helpers. We explicitly consider that the behavioral choices are made in a life-history context, and we also consider how group sizes change dynamically; this affects, for example, average relatedness among group members. We assume two different scenarios: intact families in which the breeder is 100% monogamous and stepfamilies in which the breeder shifts mate between breeding events. The average relatedness among family members is allowed to evolve in concert with changes in provisioning effort. Our model shows that an individual's provisioning effort is not easy to predict from either its relatedness to the offspring or its reproductive value. Instead, it is necessary to consider the inclusive fitness effect of provisioning, which is determined by a combination of relatedness, reproductive value, and the reproductive value of the offspring.

Keywords: cooperative breeding, provisioning efforts, load lightening, family dynamics, ESS, evolutionary conflict.

Cooperatively breeding animals tend to live in families. In nonhuman animals, these families consist of related individuals living together into adulthood and helping to rear nondescendant young (Brown and Brown 1981; Emlen 1995, 1996, 1997; Emlen et al. 1995; Cockburn 1998). However, such a simple definition belies the complexity of family dynamics. For example, depending on birth, death, and dispersal events, the number of individuals living within a family will vary enormously over time. In addition, death, divorce, and cuckoldry will alter the degree of kinship both between and within generations. So, families can be subdivided into "intact" families, in which both original parents are still present, or "replacement" families or stepfamilies, in which at least one of the breeders is unrelated to at least some of the offspring in the group (sensu Emlen 1995). Finally, the environmental conditions experienced by members of a genetic lineage occupying the same territory will change from year to year. In concert, these three factors can influence the costs and benefits to individuals of living within a family and hence their contributions to caring for the offspring of the group.

Although group size, kinship, and environmental conditions will influence the amount an individual invests in helping behavior, when studying the evolution of families, one should not focus on an individual in isolation. By their very nature, families are the result of dynamic interactions among a number of individuals. To understand family dynamics, it is crucial to consider that whenever several individuals simultaneously provide care to offspring, the optimal effort of any one individual depends on the effort of the other individuals (Chase 1980; Crick 1992; Hatchwell 1999; Kokko et al. 2002). An optimal level of effort is determined by a trade-off between the benefit for the offspring and the cost in terms of future survival and reproduction. So, if a helper provides a lot of care, this enables the parents to decrease their effort and increase their survival chances while the survival probability of the young is maintained or even improved (Komdeur 1994). This effect of helping is known as the "load-lightening" hypothesis (Crick 1992). However, helping may decrease the helper's own chances of survival and reproduction (e.g., Heinsohn and Cockburn 1994). So, because all family members generally want the others to provide a greater share of the care, conflicts are built into the relationships among care providers. This game of conflict over provi-

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sioning has been thoroughly studied for parents but less well for cooperatively breeding species (Chase 1980; Houston and Davies 1985; Lazarus and Inglis 1986; Winkler 1987; Lazarus 1990; Motro 1994; Lessels 1998; Hatchwell 1999; Wright and Dingemanse 1999; Cant and Field 2001; Khan and Walters 2002). However, although parents are usually unrelated to each other, family members are usually relatives and share genetic interest in one another. This will affect the degree of conflict among members because the inclusive fitness of all parties now depends on the fitness of the associated individuals as well. This differentiation between the interparental conflict and intrafamily conflicts makes the general prediction of conflict more complex in cooperatively breeding groups.

Here, we present a theoretical model of the conflict game over caring in family groups and its resolution. The model allows us to examine the inclusive fitness and reproductive values of family members in intact families as well as stepfamilies. We treat individuals as having different states, defined as their position within the family. Any gene in any individual may change state in the future (e.g., from a helper to a breeder). These transitions occur with different rates that depend on the mortality and reproduction rates of family members. We calculate the inclusive fitness of all states on the basis of these differential rates of gene transition and find an evolutionarily stable provisioning effort for all individuals. The model automatically gives us the effort compensation rule followed by family members when the families increase in size. We compare the pattern in stepfamilies with the pattern in intact families and examine the variation in reproductive value among family members.

Simultaneously, we introduce a novel version of the method of evolutionary analysis where optimal behavior is automatically linked to the life history it generates (Taylor 1990; Houston and McNamara 1999). Although traditional life-history-based models use a discrete-time format, we will use an approach where births and deaths occur continuously over time. Particularly in applications to social behavior, the continuous-time approach allows a significant computational simplification because we do not have to consider the probability that several births and/or deaths occur between two computational stages.

In our model, fitness as well as relatedness values are determined through the dynamics of the population. So, instead of making direct assumptions at the start of the analysis about how helping behavior translates into individual fitness costs and benefits, we let the behavior create the fitness expression via its effect on life history and relatedness structure. This leads to a fitness expression that correctly balances fitness benefits and costs of helping behavior given the effects of helping on survival and productivity (Houston and McNamara 1999).

The Caring Game

Individual States and Decisions

We model a population of a cooperatively breeding species. The population is structured into floater individuals that do not breed and individuals that belong to breeding groups. We focus on "simple families" only (Emlen 1995), in which a breeding group has only one breeding individual and some breeding groups also contain one or two helpers that do not reproduce. Helpers are assumed to be offspring that stay at the parental territory instead of dispersing to breed independently.

We limit group sizes to a maximum of two helpers by assuming that families with two helpers produce only dispersing floaters. In principle, the model can be extended for any number of helpers, but this quickly leads to an exponentially increasing and intractable number of states to be followed. To limit the complexity of the model, we therefore restrict our attention to cases where both helpers benefit from staying, and we assume that group-size regulating factors exist to make additional offspring benefit from becoming floaters and thereby leaving voluntarily. Such factors might be territorial resource limitations (Brown and Balda 1977; Woolfenden and Fitzpatrick 1984; Balshine et al. 2001) or small prospects of territory inheritance (Kokko and Johnstone 1999; Ragsdale 1999; Kokko and Ekman 2002).

With our choice of group sizes, an individual may thus be in one of seven states: B_1, breeder without helpers; B_2, breeder with one helper; B_3, breeder with two helpers; H, helper in a group of two; HD, dominant helper in group of three; HS, subordinate helper in group of three; or F, floater. The individuals choose a level of caring effort in every state except the floater state. This effort, x, is assumed to increase reproductive success of the breeding group equally independent of the identity of the individual that makes the effort. The caring effort also increases the individuals' mortality rate $\mu(x)$. We assume that $\mu(0)$ has a small positive value corresponding to the mortality rate without any provisioning effort. Our variable x should thus be thought of as any costly parental or alloparental effort that does not include any direct costs of reproduction, such as egg production. Food provisioning for young is a clear example of such help effort, and we will use "provisioning effort" and "caring effort" interchangeably to denote this variable.

To indicate state-specific provisioning effort, we will use subscripts corresponding to the state (i.e., x_1, x_2, x_3, x_{H}, x_{HD}, x_{HS}). To shorten expressions, we will also use subscripts to indicate the mortality rate of different states (i.e., $\mu_1 = \mu(x_1)$, $\mu_2 = \mu(x_2)$, etc.). We will use $\mu(x) = 0.1 + kx^2$ as a specific cost function in all our examples and for all states. Although costs of helping may differ among

Table 1: Notation used in this article

	Abbreviation/variable
Breeder without helpers	B_1
Breeder with one helper	B_2
Breeder with two helpers	B_3
Helper in family of two	H
Dominant helper in family of three	HD
Subordinate helper in family of three	HS
Floater	F
State-specific provisioning efforts	x_1, x_2, x_3, x_{H}, x_{HD}, x_{HS}
Summed family effort	x_{T}
Mortality rate as a function of effort	$\mu(x) = 0.1 + kx^2$
Mortality acceleration with effort	k
Reproduction rate of single breeder, and with one or two helpers	g_1, g_2, g_3
State-specific reproductive values	v_1, v_2, v_3, v_{H}, v_{HD}, v_{HS}
Rate matrix for the gene transitions between states	$\mathbf{Q}$
Helper-parent relatedness in family of two	r_1
Relatedness between parent and dominant helper	r_2
Relatedness between dominant and subordinate helper	r_3

states (Heinsohn and Legge 1999), our primary interest here is to examine effects of relatedness and group composition, not those of variation in helping costs. The parameter k measures how fast mortality rate accelerates with increases in effort. Table 1 provides a summary of the notation we have used.

Any relation between the total effort of all family members (x_{T}) and breeder reproduction rate ($g_i(x_{\mathrm{T}})$, with i = group size) can be used in the model, but we will examine only two different cases. In the first case, the reproductive rate increases linearly with total effort x_{T}, so g is the sum of all members' efforts. For a single breeder, the reproductive rate is $g_1 = x_1$; for a breeder with two helpers, $g_2 = x_2 + x_{\mathrm{H}}$; and for a breeder with two helpers, $g_3 = x_3 + x_{\mathrm{HD}} + x_{\mathrm{HS}}$. This situation may occur when food is difficult to find, and offspring regularly starve to death.

In the second case, the marginal increase in breeder productivity decreases with total family effort. In other words, the function g increases steeply at low total efforts but saturates for high total efforts. The specific function we use is $g(x_{\mathrm{T}}) = 1 - \exp(-x_{\mathrm{T}})$. With this form, g first increases with the same slope as in the earlier linear case but gradually flattens out and reaches a stable level equal to 1 at high total efforts. This may occur when offspring starvation rate is low and food is easy to find, so carers are able to satisfy the chicks' metabolic needs. Next, we model how the provisioning efforts determine the rates of transition between states.

Gene Flow between States

Important aspects of a social system with many different states are that individuals may change state with time or their genes may in the future be found in individuals of another state. A breeder without helpers may produce one offspring that, according to our assumptions, stays as a helper. The breeder thus moves from state B_1 to B_2. Likewise, an individual in state B_2 moves to state B_3, which has two helpers, if it produces an additional offspring that stays as a helper. A helper (state H) becomes a dominant helper (HD) if its breeding group increases in size to three individuals. A helper becomes a breeder without helpers if the old breeder dies. An HD individual moves to state H if the subordinate helper (HS) dies or to state B_2 if the breeder in the group dies. An HS individual becomes a helper if either of the two other individuals in the group dies. Consequently, a randomly chosen gene in any individual may find itself in another state in the future. These transitions are results of deaths or reproduction and are therefore influenced by the reproductive choices made by all individuals.

The diagram in figure 1 shows all possible transitions between different states. The transition rates given in the figure are for a randomly chosen autosomal gene and assume sexual reproduction. We thus take a gene's-eye view in the formulation of the model. This is necessary because the dynamics involve both changes in state of the same individual and production of new individuals when genes are transferred via Mendelian inheritance. The rate of gene

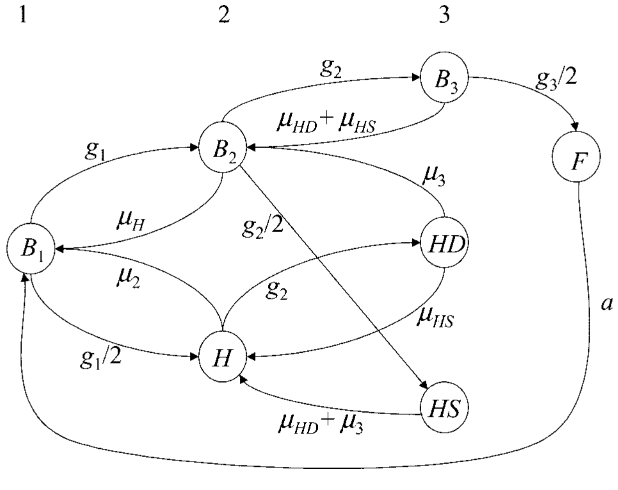

Figure 1: Diagram depicting the directions of gene flow in the social system. A focal gene in an individual in any of the states flows along an arrow to a different state with the rate indicated by the symbol beside the arrow. The states are grouped in columns by the breeding group size to which they belong. The numbers at the top of the graph indicate the breeding group size. For explanation, see table 1 and the text.

transition from state B_1 (breeder without helper) to H is $g_1/2$ because a randomly chosen gene in the parent breeder is present in the offspring helper with probability 0.5. The transition rate from B_2 to HS is $g_2/2$ because this happens when a breeder with one helper produces and retains one additional offspring. The rate of gene transition from B_3 to floater (F) is, for the same reasons, $g_3/2$. The rate of gene transition from floater to B_1 is the same as territory acquisition rate of floaters, a. When the population size is stable, floaters occupy new vacancies at the same rate as the rate of formation of vacancies (app. A).

Reproductive Values

Focusing on any individual, in any state, we may pick a gene at random and calculate the expected number of direct descendants of this gene at a time far into the future (Houston and McNamara 1999). This measure is called the direct reproductive value of this state. In doing this, we will make two assumptions. The first is that breeding occurs continuously over time. Most state-based game-theoretical models describe state dynamics in discrete time (e.g., Frank 1998; Houston and McNamara 1999). We have chosen a continuous-time approach partly because the model becomes mathematically more tractable when we measure the transitions with their time-constant rates rather than their probability. This is because we do not have to calculate the probability that several transitions occur between two computational stages, or "observations" of the system. From a biological standpoint, continuous time is also a good assumption because many cooperatively breeding birds are found in the tropics and subtropics, where breeding can occur almost all year round (Arnold and Owens 1998). The difference between continuous and discrete time is described in more detail in appendix A.

The second assumption is that density dependence acts to stabilize the population at an equilibrium size. At population equilibrium, the distribution of individuals in different states will be stable. The flow of genes between the different states can then be described by a linear system.

Let $\boldsymbol{v}$ denote a vector of reproductive values $[v_1, v_2, v_3, v_{\mathrm{H}}, v_{\mathrm{HD}}, v_{\mathrm{HS}}, v_{\mathrm{F}}]$ of different states. The dynamic system $d\boldsymbol{v}/dt = \boldsymbol{v}\mathbf{Q}$ is a system of differential equations that couples the reproductive values, where $\mathbf{Q}$ is a matrix that holds the instantaneous rates by which a gene in one state flows to a different state. The rate matrix $\mathbf{Q}$ is written out in appendix A. This system allows us to express the reproductive values in terms of the rates by which genes flow between states. If we know the transition rates in figure 1, we may calculate the resultant reproductive values at the equilibrium state where the reproductive values are constant over time (so $d\boldsymbol{v}/dt = 0$). This gives us the reproductive values traced through all possible state transitions and their rates (see app. A). To calculate the inclusive fitness of family members, we must also find the genetic relatedness among them. These relatedness coefficients are also derived from the family dynamics, as explained below.

Relatedness in Stepfamilies versus Intact Families

A helper will not always have relatedness 0.5 to the current breeder even if helpers are always retained offspring. For example, consider the case where two helpers are produced, but the breeder mated with different fathers to produce them. The helpers are thus half-sibs. If the breeder then dies and one of the helpers now accedes to dominant status, the relatedness between the new breeder and the remaining helper is 0.25. The expected value of the relatedness between the breeder and helper in a family of two must therefore be the weighted average of possible relatednesses weighted by the probability that the two-individual system arose in the various ways: from a group of size one by reproduction, from a group of size three by death of breeder, from a group of size three by death of dominant helper, or from a group of size three by death of subordinate helper. These probabilities are all directly affected by the dynamics of state changes. It follows that if we know the intensities of transition between states, we can deduce the relatedness among family members (Griffin and West 2002).

In appendix B, we solve for the stable levels of relatednesses that result from the dynamics associated with a given set of provisioning efforts $\{x_1, x_2, x_3, x_{\mathrm{H}}, x_{\mathrm{HD}}, x_{\mathrm{HS}}\}$. We do this for two scenarios termed "intact families" and "stepfamilies." In intact families, the breeder is 100% monogamous and never shifts breeding partner, so all its offspring have the same parents. We may, for example, imagine an insect female that mates only once and stores sperm for future use. In stepfamilies, the breeder always divorces its partner after every breeding event or has a high rate of extrapair paternity, so all its offspring are half-sibs. These two cases may be seen as extremes of intact families and stepfamilies. Although extremes will be biologically unrealistic in many cases, they will reveal the general impact of reduced relatedness in stepfamilies.

Intact families also introduce a kind of asymmetry between breeders and helpers in the evaluation of each other's fitness. From the helpers' viewpoint, offspring of the breeder may often be full sibs and thus be genetically equivalent to the helpers' own offspring (Reeve and Keller 1996; Reeve et al. 1998). Conversely, the breeder will never be related by more than 0.25 to offspring of the helper. In stepfamilies, the helper can never be full sib to the breeder's offspring, and there is thus no asymmetry. This difference between family types must be taken into account when calculating the evolutionarily stable provisioning strategy (see app. C). This strategy is a combination of efforts such that if the population uses it, it does not pay for any individual to switch to a different effort level in any state. A game-theoretical analysis gives us this solution.

Calculation of Fitness

A provisioning strategy specifies for each state the effort that should be used in that state and can be represented by a vector $\boldsymbol{x}$ that contains the provisioning efforts in all states. A requirement for an effort to be the best is that no other effort will increase the inclusive fitness of that individual. To understand this, we may imagine that separate genes determine the effort in every state and that almost all individuals have identical genes and thus use the same "resident" strategy $\boldsymbol{x}$. We also assume that the frequencies of individuals in different states do not change over time. For a strategy to be stable, it should be impossible for any alternative "mutant" strategy to invade the resident strategy. To provide an example, we focus on a breeder without helpers (state B_1) that uses an alternative strategy. The difference from the resident strategy is caused by a mutant allele that codes for the effort x_1' instead of the residents' effort x_1 when the individual is in state B_1. To investigate that fate of the mutant allele, we look at the change in inclusive fitness (IF) corresponding to the change in behavior. Inclusive fitness is the personal fitness of the actor plus the sum of the personal fitness of all relatives of the actor weighted with the corresponding relatednesses. The mutant allele can invade if the mutant behavior results in higher IF (app. C). A discrete-time model measures the amount of extra IF after some fixed time unit (Taylor 1990). Because we instead work with continuous time, fitness is measured at every instant in time, and we therefore look at the rate of change in IF over time, dW_1/dt.

The provisioning effort x_1' of the breeder influences only the rate $g_1(x_1')$ at which a helper is produced to join the group and the rate $\mu(x_1')$ at which the breeder dies. Both of these events are associated with changes in inclusive fitness.

If the mutant breeder dies, the mutant allele loses its reproductive value ($\bar{v}_1$). The reproductive value measures the average number of future offspring and is calculated from the resident strategy and not the mutant. This will always correctly predict the direction of selection, which is what is important for our purposes (for further explanation, see Taylor and Frank 1996; Frank 1998; Houston and McNamara 1999). Thus, the mutant loses personal fitness at the rate $\mu(x_1')\bar{v}_1$.

The effect of reproduction on the fitness of the mutant gene can be divided into two parts. First, reproduction results in a new individual with reproductive value $\bar{v}_H$. This is equivalent to $0.5\bar{v}_H$ of the breeder's own reproductive value, where 0.5 is the breeder's relatedness to the new helper. Keeping the gene's-eye view, we can also say that 0.5 is the probability that the mutant is present in the helper, and if so, mutant fitness is $\bar{v}_H$. Second, reproductive value of the breeder changes with $\bar{v}_2 - \bar{v}_1$ when a helper is produced, which leads to a personal fitness increase rate of $g_1(x_1')(\bar{v}_2 - \bar{v}_1)$ over time. The net rate of change in the mutant's IF W_1 over time is thus

$$\frac{dW_1}{dt}(x_1', \boldsymbol{x}) = g_1(x_1')(\bar{v}_2 - \bar{v}_1) - \mu(x_1')\bar{v}_1 + 0.5g_1(x_1')\bar{v}_H. \quad (1)$$

In general, the net rate of change in mutant allele IF over time can be calculated by first taking the sum of all changes in fitness directly affected by the gene (i.e., $\bar{v}_2 - \bar{v}_1$ and $-\bar{v}_1$) weighted with the instantaneous rates at which they occur over time ($g_1(x_1')$, $\mu(x_1')$; app. C). Add to this the changes in the personal fitness of all associated individuals ($\bar{v}_H$; Taylor 1996; Taylor and Frank 1996; Frank 1998) similarly weighted with the instantaneous rates at which they occur and also weighted with the relatedness between the focal individual and the associated individuals (app. C). The relatedness coefficients to use in this weighting are those derived from the dynamics of the state transitions (app. B). Although we assume that, in its decision about provisioning effort, a breeder weights offspring reproductive value with 0.5, the actual genetic relatedness to offspring, we assume that the breeder does not recognize its own offspring among the adult helpers (app. C). Offspring recognition among eggs or chicks does not imply recognition at other life stages (Komdeur and Hatchwell 1999). A breeder that has one adult helper therefore weights helper reproductive value according to the statistical average relatedness to helpers, which is calculated in appendix B.

An evolutionarily stable strategy (ESS) $\boldsymbol{x}^*$ is a combination of provisioning efforts such that no individual is able to increase its IF by an effort alteration. We used a numerical best response dynamic procedure (Hofbauer and Sigmund 1998; Houston and McNamara 1999; app. C) to find the ESS. The best response strategy maximizes mutant fitness when all other individuals follow the population strategy. Iteratively replacing elements of $\boldsymbol{x}$ by the vector of best replies $\boldsymbol{x}^{\circ}$ eventually leads to the equilibrium (see app. C).

The Decision to Stay

We have assumed that the upper limit to group size is three individuals. Group size in cooperative breeders is likely to be influenced by availability of resources (Brown and Balda 1977; Reyer 1984; Komdeur et al. 1995; Balshine et al. 2001). Also, helpers of low rank have small chances of eventually attaining breeder status, which further decreases the incitement to stay for additional helpers (Kokko and Johnstone 1999; Ragsdale 1999; Kokko and Ekman 2002). Although we have not explicitly included any effects of resource limitation, we assume that a combination of such effects would make staying unprofitable for a potential third helper, so groups do not exceed the size of three. There is no significance in the specific choice of maximum group size; the model and its results apply to groups of any size.

Given that helpers should be free to leave the breeding group if they wish, we must make sure that helper IF at the equilibrium is higher than that of floaters lest the helpers leave the group voluntarily (East and Hofer 1991, 2001; Komdeur et al. 1995; Kokko and Sutherland 1998; Kokko et al. 2001; Kokko and Ekman 2002). In appendix D, we show how to check this. If a helper leaves the group, the reproductive values of the remaining individuals will change. The helper is related to the remaining individuals, so this affects inclusive fitness of the helper. So, by comparing a helper's total IF before and after leaving the group, we can get a measure of the benefit gained by becoming a floater. In our examples, we restrict our attention to cases where this is costly, that is, where leaving would result in a negative inclusive fitness effect for the first and second helper (app. D). The assumption that both helpers stay is therefore consistent.

Results and Discussion

To understand the variation in optimal provisioning effort among family members, we must consider a large number of factors. As more individuals participate in providing care for the offspring, each individual can afford to increase its survival by decreasing its own effort, without seriously compromising the survival of offspring. This aspect of the conflict of interest among family members (Chase 1980) is the basic reason for an "expected" decrease in parental and alloparental effort in larger families (e.g., fig. 2*c*, 2*d*; fig. 3*c*, 3*d*). However, this expected pattern may be altered by complex interactions between the caring behavior and its effects on relatedness and reproductive values. Furthermore, the mate infidelity shown by the breeder in a stepfamily is reflected in the evolutionarily stable provisioning efforts of all family members, as we will see by comparing stepfamilies with the monogamy of intact family breeders.

Consider, for example, the case in figure 2*a*, which shows the stable efforts in a stepfamily where productivity is a linear function of total effort. Why does a breeder with one helper spend about as much effort as one without a helper? This is not intuitively easy to understand, especially when the breeder decreases its effort once a second helper joins the group (fig. 2*a*). The answer lies in comparing the effects of producing a subordinate helper on breeder and helper IF. The relatedness between a breeder and a subordinate helper is always 0.5, so the breeder receives an IF benefit of $0.5\bar{v}_{\mathrm{HS}}$ when another, subordinate, helper is produced. In comparison, the helper will not increase its inclusive fitness much if a subordinate helper is produced since stepfamily helpers have different fathers. The resulting decrease in relatedness is automatically taken into account by our calculation of relatedness from the transition dynamics (app. B). In this particular example, a dominant helper is related to the subordinate helper on average by only 0.19. In comparison, a helper in a group of two individuals will not benefit much by producing a subdominant helper and therefore invests much less than does the breeder (fig. 2*a*). If the family consists of three individuals, floaters are produced with a reproductive value of one unit. This is much lower than any reproductive value of the family members in figure 2*a* (they reach between 12.7 and 4.2 units of reproductive value). Although the breeder is related by 0.5 to floaters, the floaters' low reproductive value means that breeder IF is not increased much by producing them. This helps to explain why breeder effort is lower with two helpers than it is with one helper. When the breeder decreases its effort, the helpers respond by increasing their effort, so the total effort is still higher when three individuals contribute help (fig. 2*a*).

We can contrast this with the situation where productivity reaches a maximum at high levels of effort. In other words, the marginal increase in productivity decreases at high efforts (fig. 2*c*, 2*d*). Because of the lower marginal increase, breeder IF does not increase as much for a given level of effort compared with the linear case. The optimum effort for a breeder with one helper is therefore lower, and this is partly compensated for only by the increased effort of the helper (fig. 2*c*).

All else being equal, helpers make higher provisioning efforts in intact families (fig. 3) than they do in stepfamilies. Breeders respond to the increased helper effort by decreasing their own effort and therefore suffer lower mortality in intact families. The total care received by offspring in intact families is at the same time higher than it is in stepfamilies (fig. 3; the load-lightening hypothesis: Brown 1978; Crick 1992). The basic reason for this differentiation between family types is the higher relatedness among intact family members caused by mate fidelity (app. B). Although breeders should benefit more from the intact family situation, this might not be an important selection pressure for mate fidelity. For example, helpers may not lower their

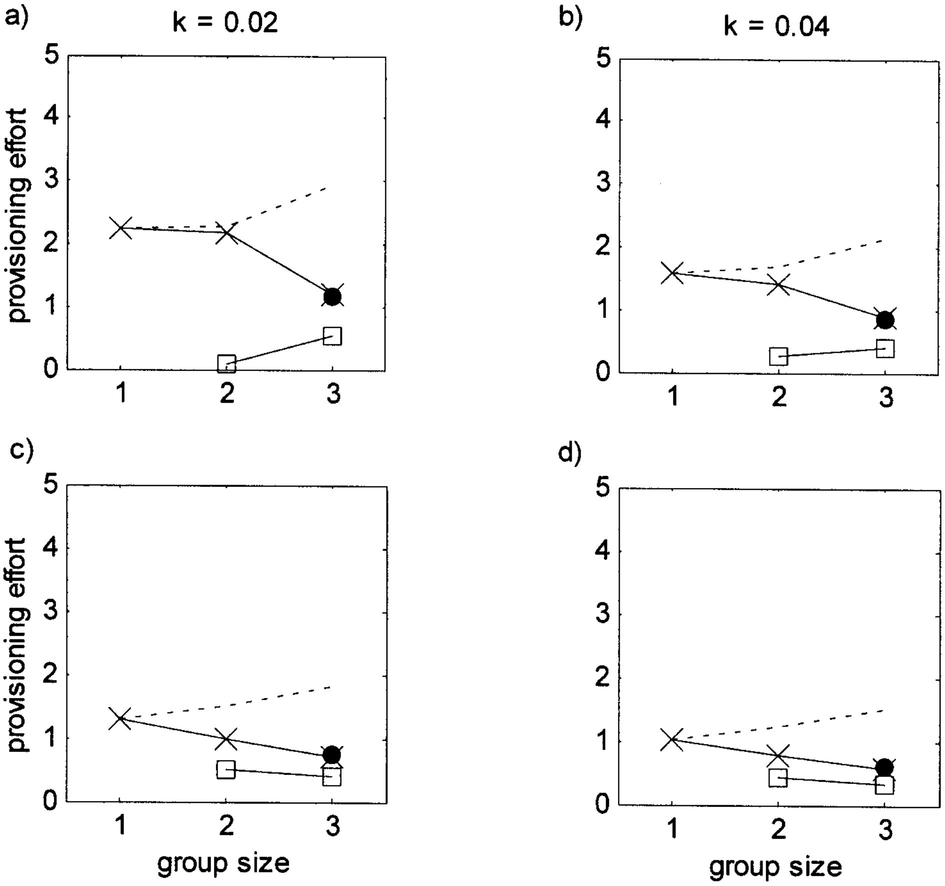

Figure 2: Evolutionarily stable provisioning efforts in stepfamilies, where the dynamics are governed by equations (C1). Efforts are shown for all family members. Mortality rate is given by $\mu(x)$ (table 1). In *a* and *c*, the mortality acceleration value (k) equals 0.02, and in *b* and *d*, $k = 0.04$. Panels *a* and *b* show the case where $g(x_T) = x_T$ (table 1), and in *c* and *d*, $g(x_T) = 1 - \exp(-x_T)$, so productivity asymptotically reaches a maximum. Breeder effort is indicated by a cross, helper and dominant helper effort is indicated by a square, and the black dot shows the effort of the subordinate helper. The dashed line is the summed family effort.

effort facultatively in response to unfaithfulness of a breeder. Then if infidelity has an initial advantage, this behavior will spread in the population, and the smaller load lightening by helpers might evolve later only once the whole population of female breeders starts behaving in this way.

Although relatedness may explain the generally higher efforts in intact families, an individual's provisioning effort is partially explained only by its relatedness to the produced offspring. For example, in stepfamilies, helpers make less effort than do breeders, whereas in intact families, helper effort often exceeds breeder effort (fig. 3). Helpers are, however, always on average less related to the breeders' offspring than is the breeder. In contrast, the breeder is equally related to offspring in both stepfamilies and intact families. The reason for the big efforts of helpers in an intact family is that helpers have lower reproductive value than does the breeder, an effect of the low probability that the helpers eventually become breeders. Consequently, death and loss of all prospects of future personal reproduction is more costly for the breeder than it is for the helper. Within family types, the relatedness coefficients do not vary much with k, the mortality acceleration rate. However, the different environmental conditions reflected by the variation in k may result in quite different levels of effort (fig. 4).

It is paradoxical that when we consider the effect of relatedness within family types, helper effort may even decrease when relatedness increases (fig. 4), although relatedness does not vary much. This is because of the two effects of k, the costs of caring, on relatedness and effort. A decrease in k decreases the mortality rate of all individuals, but the strongest effect is in this example on the mortality rate of dominant helpers. This means that help-

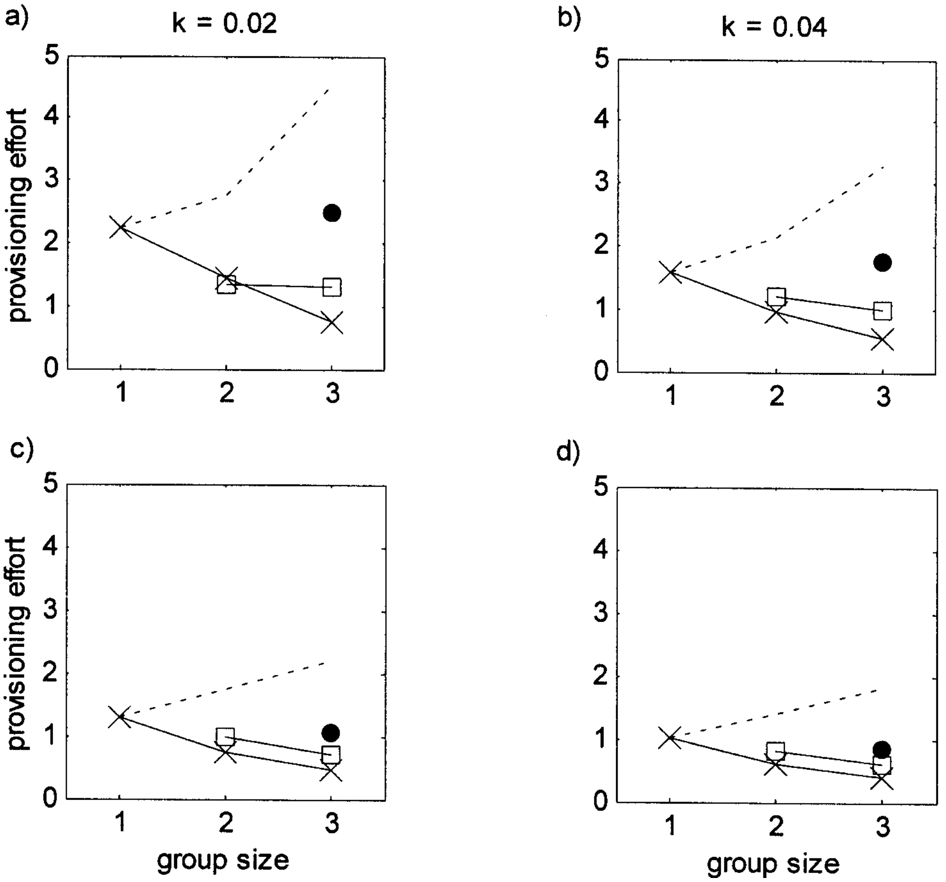

Figure 3: Evolutionarily stable provisioning efforts in intact families, where the dynamics are governed by equations (C1a)–(C1c) and (C8). Efforts are shown for all family members. Mortality rate is given by $m(x)$ (table 1), and mortality acceleration value (k) is 0.02 in *a* and *c* and 0.04 in *b* and *d* to make the figure comparable with figure 2. In *a* and *b*, $g(x_T) = x_T$ (table 1), and in *c* and *d*, $g(x_T) = 1 - \exp(-x_T)$, so productivity asymptotically reaches a maximum. Breeder effort is indicated by a cross, helper and dominant helper effort is indicated by a square, and the black dot shows the effort of the subordinate helper. The dashed line is the summed family effort.

ers tend to outlive the breeder, so family units of one breeder and one helper are formed more often because of the death of the breeder in a group of three individuals. The surviving individuals will often be sibs, and the end result is therefore that average breeder-helper relatedness is lowered. A second effect of lowering k is of course to increase effort levels in general. Together, these effects may produce a negative correlation between relatedness and effort (fig. 4).

In families with two helpers, the subordinate helper makes a larger effort than does the dominant helper (figs. 2, 3). One reason for this is that dominant helpers have higher reproductive value than do subordinate helpers because a dominant helper has a higher chance of inheriting breeder status. With higher reproductive value, dominant helpers of high reproductive value potentially lose more fitness by helping (Cant and Field 2001). A second reason why subordinate helpers provide more care is that they are on average more related to the breeder and its offspring than is the dominant helper. This is because the youngest, subordinate, helper will often be an offspring of the present breeder, while the mother of the dominant helper will often have already died (Reeve and Ratnieks 1993; Reeve et al. 1998). Our approach automatically takes this effect into account because we calculate the relatedness coefficients from the group dynamics instead of assuming fixed relatedness values.

Another difference between family types is that the reproductive values are higher for all family members in intact families (fig. 5). This may seem counterintuitive since intact family helpers should have lower probability of reproducing in the future when they invest more and suffer higher mortality. Although this is true, the higher productivity of intact families more than compensates for

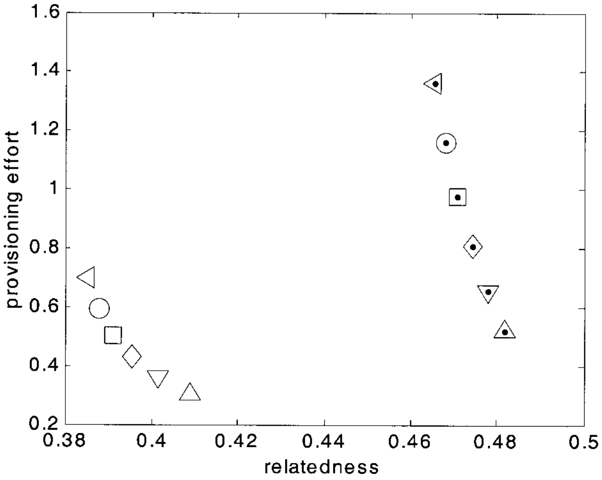

Figure 4: Provisioning effort versus relatedness to offspring for a helper in a group of two individuals. The open symbols show relatedness and effort of the helper in a stepfamily, where the dynamics are governed by equations (C1). The symbols containing dots show the same for an intact family, where dynamics are governed by equations (C1a)–(C1c) and (C8). The different symbols denote solutions with the same mortality acceleration value (k; table 1). Starting with the uppermost symbol, the sequence triangle left, circle, square, diamond, triangle down, and triangle up denotes k values of 0.005, 0.01, 0.02, 0.04, 0.08, and 0.16. For all lines, productivity is an increasing concave function of total family effort (i.e., $g(x_T) = 1 - \exp[-x_T]$).

this, so an intact family helper can count on a much higher reward once it attains breeder status, compared with a stepfamily helper.

The reproductive value of a breeder may decrease or increase as the family increases in size (fig. 6). Decreasing breeder reproductive value may seem paradoxical because this at first sight seems to indicate that breeders in large families could increase their expected value of future offspring by expelling current helpers. However, this reasoning considers only effects on personal reproduction, and the paradox is resolved once we investigate the full inclusive fitness expression.

Inclusive fitness is the reproductive value of the individual in the focal state plus the reproductive values of the other individuals in the same breeding group weighted by the relatedness among the individual in the focal state and the other individuals in the group. So, for example, the inclusive fitness of a breeder with two helpers is $\bar{v}_3 + r_2\bar{v}_{HD} + 0.5\bar{v}_{HS}$, given that it is always related by 0.5 to the second helper. (This does not introduce any "double accounting" of offspring because the behaviors we analyze are state specific [Queller 1996] and because reproductive values measure personal reproduction only.) In all our calculations, breeders in larger families have higher inclusive fitness (fig. 6). Similarly, a helper in a group of two gets higher inclusive fitness if another offspring is produced, so it attains the status of dominant helper. Provisioning for offspring in order to increase family size can therefore be favored even when reproductive values of individual group members may decrease in larger families.

We have introduced a theoretical method for analyzing evolution in social systems, where we allow the life-history consequences of the analyzed trait to balance the cost and benefits in the fitness expression (Houston and McNamara 1999). This is in contrast to a traditional method of investigating optimality or game-theoretic equilibria in evolutionary analysis. There, one makes a qualified guess at the start as to how the effects of a specified behavior, or other trait, translate into inclusive fitness benefits and costs. The optimum is then found by balancing these fitness effects. The problem with that approach is that the common currency for fitness benefits and costs is the reproductive value of the individual, and this depends on the behavior in question and its effects on the organism's life history (Taylor 1990; McNamara 1991). When analyzing the behavior of social animals, we must also take into account the relatedness among individuals, which may also depend on the specified behavior (Griffin and West 2002). So, we cannot specify benefits or costs without knowing the stable solution to the game.

The way to deal with these ties is to consider the life-history and population dynamic consequences of the behavior (see also Webb et al. 1999). We can then specify the fitness of a mutant individual with behavior different

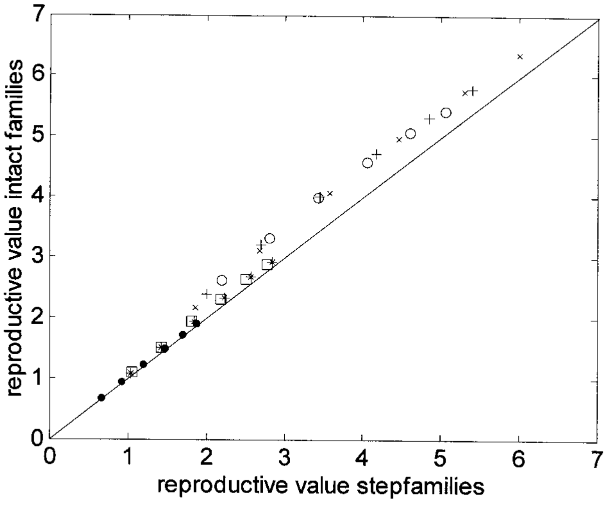

Figure 5: Each point shows the reproductive value of one state in an intact family and a stepfamily, given that the dynamics are as in figure 4. The diagonal line is the line of equal reproductive value. The different symbols correspond to different states: *cross*, B_1; *plus*, B_2; *circle*, B_3; *asterisk*, H; *open square*, HD; and *dot*, HS.

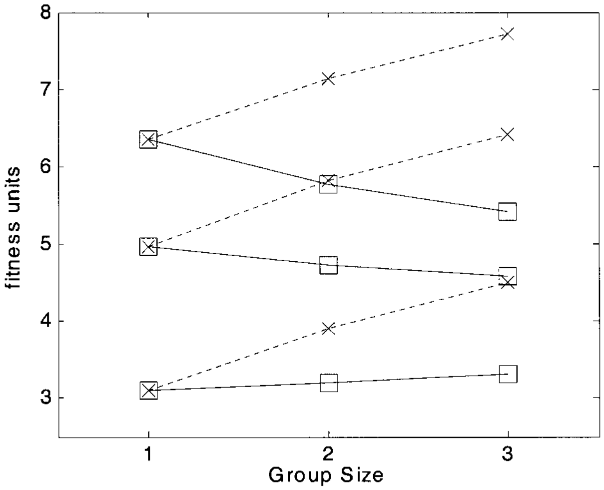

Figure 6: Examples of the relation between breeder inclusive fitness (*crosses*, *dashed line*) and breeder reproductive value (*squares*, *solid line*) in different group sizes. The case shown is for an intact family where productivity is an increasing concave function of total family effort, $g(x_T) = 1 - \exp(-x_T)$. Three different values of mortality acceleration are shown, from upper to lower pairs of lines: $k = 0.005$, $k = 0.02$, and $k = 0.08$. When the group size $= 1$, breeder fitness has no indirect components, so breeder direct reproductive value and breeder inclusive fitness are identical.

from the population norm. This leads to an evolutionarily stable strategy where the reproductive values, and thus the fitness benefits and costs, are consistent with the assumed life history of the species, which is unlikely to be the case if they are assumed beforehand (Taylor 1990; McNamara 1993; Houston and McNamara 1999).

We have assumed that transitions from floating to breeding status are limited by the rate at which vacancies occur in the population. This stabilizes a population in which territoriality limits the number of breeding opportunities (Pen and Weissing 2000). A territoriality-limited population equilibrium is an appropriate context for an analysis of cooperative breeder behavior because lack of breeding territory or other constraining factors that limit the opportunities for independent breeding are often the reasons why offspring stay as helpers (Stacey and Ligon 1987, 1991; Komdeur 1992; Emlen 1997; Arnold and Owens 1998; Hatchwell and Komdeur 2000). Because this makes our solutions consistent with the assumption of a population equilibrium density, we are confident that mutants would not be able to invade a natural population following the ESS rule.

Although our model provides a framework for understanding family conflicts in a proper, dynamical setting, it does not take into account the possibility that a particular family member exploits the behavioral rules of the others. Theoretically, if one family member is aware of the provisioning rules of its partners, it can take advantage of them by adjusting its effort (McNamara et al. 1999). For example, the parent may increase its fitness by decreasing its effort and thereby force the helpers to increase their effort. Then, the stability analysis we have used cannot be expected to lead to a correct result. We have assumed that the decision process makes such exploitation impossible, for example, if individuals are unaware of the effort of their partners within the group or if the provisioning effort in each state is genetically determined. In other words, although in our model the behavior of all family members is adjusted to what the partners are doing, this adjustment is based on an expectation of the average behavior of the partners and not on their individual behavior.

We also assume that there is no innate kin recognition, in that the individuals respond to the average relatedness among family members and take only their own state into account. This may be so if an individual knows the position it has within the family and what family it belongs to (e.g., via associative learning [Komdeur and Hatchwell 1999; Hatchwell et al. 2001]) but does not know exactly how the members are related or its exact relatedness to any family member (Wright et al. 1999). However, our modeling method could easily be extended to investigate cases in which there is innate kin recognition (e.g., through phenotype matching [Komdeur and Hatchwell 1999; see also Hatchwell and Russell 1996; Painter et al. 2000; Russell and Hatchwell 2001]). In this case, the number of states in the model simply increases to account for the different kinds of families: for example, a family with two half-siblings is treated as different from a family with two full siblings, and transition rates are calculated for each one separately.

Conclusions

We calculate evolutionarily stable provisioning efforts in simple families (Emlen 1995) with one breeder and a number of nonreproducing helpers, who all simultaneously provide for offspring. First, the more members there are in the family, the less effort each member will make (figs. 2, 3). Second, the breeding system has an influence through its effect on relatedness among family members. Alloparental efforts are higher if the breeder is monogamous because helpers are then more related to the breeder's offspring than if the breeder shifts mate regularly. The breeder, in contrast, adjusts its effort to the effort of the helpers, and breeder effort is therefore lower with monogamy. An individual's relatedness to the offspring that are produced is, however, in itself a poor predictor of that individual's effort. Other important factors to consider are the reproductive value of the offspring that are produced and the individual's own reproductive value. If the offspring have low reproductive value, as when they are destined to become floaters, the breeders and helpers will make low efforts. An individual will also make a low provisioning effort if its own future prospects of reproduction are good, so the potential cost of helping is high.

Life-history parameters may interact with the dynamics of family size and relatedness to produce counterintuitive patterns. For example, because we include the family dynamics in the model, caring effort and relatedness to offspring may be negatively correlated. With decreasing mortality cost of caring, the stable caring effort increases. Simultaneously, the average relatedness between breeders and helpers decreases because of increased longevity of helpers. When helpers tend to outlive their parents, breeding groups are more frequently composed of siblings that are less related to one another than parents are to offspring.

Helpers enable the breeder to decrease its effort and thereby increase its survival, an effect known as load lightening (Brown 1978; Crick 1992). In our model, breeders decrease their investment as the family grows, but this is not only due to the help received but also due to changes in offspring reproductive values. Helpers may appear to lighten the parental load, although the main reason for the decreasing breeder effort may be the lower reproductive value of offspring that become low-ranked helpers, or floaters. Finally, we also show that the reproductive value of a breeder may be maximized when breeding without helpers. This apparent suboptimality of breeding with helpers is explained away when we look at the full inclusive fitness of the breeder, which is higher in larger families.

Acknowledgments

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APPENDIX A

Let the vector $\boldsymbol{v}$ hold the reproductive values $v_1, v_2, \ldots, v_F$ of the different states. We can find the stable reproductive values from a model of the life history of the organism (e.g., Caswell 2001), but although most published evolutionary models of this kind use a discrete-time format (see, e.g., Frank 1998; Houston and McNamara 1999), we will use a continuous-time approach. Here, we will outline how to make the move from discrete time to continuous time. In discrete time, let $\mathbf{A}$ denote a fitness matrix where a_{ij} is the average number of i-class offspring per class-j individual after one unit of time t. We choose a time unit that is the same as the time between generations. At equilibrium, the class frequencies and reproductive values are stable, which means that we can solve the equation $\boldsymbol{v}(t+1) = \boldsymbol{v}(t)\mathbf{A}$ for the reproductive values. We thus assume that the reproductive value of an individual in any class is constant in all generations.

Let us now decide that we "look" at the system with time intervals of length dt instead of every full time unit. We can then rewrite the system as $\boldsymbol{v}(t+dt) = \boldsymbol{v}(t)\mathbf{A}$, where the elements a_{ij} of $\mathbf{A}$ are now functions of dt because their value depends on how often we look at the system $a_{ij} = a_{ij}(dt)$. When we observe the system more often (dt small), $\mathbf{A}$ will be closer to $\mathbf{I}$, the identity matrix. We therefore rewrite the model as $\boldsymbol{v}(t+dt) = \boldsymbol{v}(t)(\mathbf{I} + \mathbf{Q}(dt)dt)$, where the elements $q_{ij}(dt)$ of $\mathbf{Q}(dt)$ hold the changes per time unit. This is the same as $\boldsymbol{v}(t+dt) - \boldsymbol{v}(t) = \boldsymbol{v}(t)\mathbf{Q}(dt)dt$. Dividing both sides by dt and letting dt approach 0 gives us the equation $d\boldsymbol{v}/dt = \boldsymbol{v}\mathbf{Q}$, where $\mathbf{Q}$ is $\mathbf{Q}(0)$, the limit as dt approaches 0.

Explicitly, the rate matrix $\mathbf{Q}$ is

$$\mathbf{Q} = \begin{bmatrix} -\mu_1 - g_1 & \mu_H & 0 & \mu_2 & 0 & 0 & a \\ g_1 & -\mu_2 - \mu_H - g_2 & \mu_{HS} + \mu_{HD} & 0 & \mu_3 & 0 & 0 \\ 0 & g_2 & -\mu_3 - \mu_{HS} - \mu_{HD} & 0 & 0 & 0 & 0 \\ g_1/2 & 0 & 0 & -\mu_H - \mu_2 - g_2 & \mu_{HS} & \mu_3 + \mu_{HD} & 0 \\ 0 & 0 & 0 & g_2 & -\mu_{HD} - \mu_3 - \mu_{HS} & 0 & 0 \\ 0 & g_2/2 & 0 & 0 & 0 & -\mu_{HS} - \mu_3 - \mu_{HD} & 0 \\ 0 & 0 & g_3/2 & 0 & 0 & 0 & -\mu_F - a \end{bmatrix}, \tag{A1}$$

where symbols are explained in the text and table 1. We assume that the population strategy is $\boldsymbol{x} = [x_1, x_2, x_3, x_H, x_{HD}, x_{HS}]$, which defines the values that go into the matrix. Floaters are assumed to attain breeder status at the per capita rate a, and at the equilibrium, $an_F = n_1\mu_1$. This assumption means that floaters gain territories at the same rate as new vacancies become available via death of single breeders. As explained, the differential equation system $d\boldsymbol{v}/dt = \boldsymbol{v}\mathbf{Q}$ holds for the reproductive values. To normalize the reproductive values, we choose $v_F = 1$. This in no way limits the options we consider for floater future prospects but merely allows us to compare reproductive values of different states. At population equilibrium, the reproductive values are stable over time ($d\boldsymbol{v}/dt = 0$). By solving the system $\boldsymbol{v}\mathbf{Q} = 0$, we obtain the equilibrium reproductive values $\bar{v}_0$, $\bar{v}_1$, $\bar{v}_2$, $\bar{v}_H$, $\bar{v}_{HD}$, and $\bar{v}_{HS}$.

APPENDIX B

Calculation of Relatedness

Four different relatedness coefficients need to be considered. Let $r_1 =$ the relatedness between the breeder and helper in a family of two individuals. In a family of three individuals, the relatedness between the breeder and the dominant helper is called r_2. The relatedness between the dominant and subordinate helper is called r_3. In addition, we might want to consider the relatedness between breeder and subordinate helper, but in our simple families, this is always 0.5 because subordinate helpers come to exist only because of breeder reproduction, and breeders are related to their own offspring by 0.5.

All provisioning effort strategies $\boldsymbol{x}$ produce stable frequencies of the three family types: single breeder (frequency p_1), family of two individuals (p_2), and family containing three individuals (p_3). We let $p_4 =$ frequency of floaters. The frequencies are easily found from the system $\mathbf{M}\boldsymbol{p} = 0$, where the elements m_{ij} of $\mathbf{M}$ represent the rate by which a family of type j turns into a family of type i.

Although frequencies are stable, individuals continue to change states at the dynamic equilibrium. The rate of losses of two families equals the production rate of new such families. Every loss of one r_1 value is thus "replaced" by a new relatedness value, and we may write down a differential equation for this process by taking the rate by which new families are formed minus the rate by which they are lost through deaths or family growth and weighting the rates with the corresponding relatednesses. For example, families with one helper are lost at the rate $p_2(\mu_2 + \mu_{\mathrm{H}} + g_2)$. This is exactly balanced by an "inflow" at the rate $p_1 g_1 + p_3(\mu_2 + \mu_{\mathrm{HD}} + \mu_{\mathrm{HS}})$. The weighted expression for the dynamics is $p_1 g_1 0.5 + p_3 \mu_3 r_3 + p_3 \mu_{\mathrm{HD}} 0.5 + p_3 \mu_{\mathrm{HS}} r_2 - p_2(\mu_2 + \mu_{\mathrm{H}} + g_2) r_1$. We consider two cases. In stepfamilies, each offspring has a different father, and the dynamics for the relatednesses are

$$\frac{dr_1}{dt} = g_1 p_1 0.5 + \mu_3 p_3 r_3 + \mu_{\mathrm{HD}} p_3 0.5 + \mu_{\mathrm{HS}} p_3 r_2 - p_2(\mu_2 + \mu_{\mathrm{H}} + g_2) r_1, \tag{B1a}$$

$$\frac{dr_2}{dt} = g_2 p_2 r_1 - p_3(\mu_3 + \mu_{\mathrm{HD}} + \mu_{\mathrm{HS}}) r_2, \tag{B1b}$$

$$\frac{dr_3}{dt} = g_2 p_2 0.5 r_2 - p_3(\mu_3 + \mu_{\mathrm{HD}} + \mu_{\mathrm{HS}}) r_3. \tag{B1c}$$

In the inflow expression of equation (B1c), $0.5r_2$ is the product of a subordinate helper's relatedness to its mother and the mother's relatedness to the dominant breeder. The solution is easy to find by solving $dr/dt = 0$. It is

$$r_1 = r_2 = \frac{g_1 p_1 + \mu_{\mathrm{HD}} p_3}{2g_1 p_1 + \mu_3 p_3 + 2\mu_{\mathrm{HD}} p_3},$$

$$r_3 = \frac{0.5(g_1 p_1 + \mu_{\mathrm{HD}} p_3)}{2g_1 p_1 + \mu_3 p_3 + 2\mu_{\mathrm{HD}} p_3}. \tag{B2}$$

To find the solutions in equation (B2), we have made use of the fact that the rate of flow "in" is equal to the flow "out," which allows substitution of one expression for the other. In intact families, the breeder mates once and saves sperm, so all its offspring get the same father. The inflow expression of dr_3/dt is then changed to $(0.5 + 0.5F) r_2$, where F is the probability that the subordinate helper has the same father as the dominant helper. This is the same as the probability that the helper in a group of two is an offspring of the breeder in that group. This is calculated as

$$F = 1 - \frac{\mu_3 p_3}{g_1 p_1 + \mu_3 p_3 + \mu_{\mathrm{HD}} p_3 + \mu_{\mathrm{HS}} p_3}, \tag{B3}$$

because it is true unless the group is formed because the breeder in a group of three died. These two limiting cases of intact families versus stepfamilies are the only ones we will use in this model. The solution is now

$$r_1 = r_2 = \frac{g_1 p_1 + \mu_{\mathrm{HD}} p_3}{2g_1 p_1 + \mu_3 p_3 - \mu_3 p_3 F + 2\mu_{\mathrm{HD}} p_3},$$

$$r_3 = \frac{1}{2}\left(\frac{g_1 p_1 + \mu_{\mathrm{HD}} p_3 + g_1 p_1 F + \mu_{\mathrm{HD}} p_3 F}{2g_1 p_1 + \mu_3 p_3 - \mu_3 p_3 F + 2\mu_{\mathrm{HD}} p_3}\right). \tag{B4}$$

APPENDIX C

The rate by which net inclusive fitness of an individual changes over time = (the rate by which a change of state occurs) × (the change in inclusive fitness associated with this change of state), summed over all state transitions that the individual may experience. It will be necessary to consider stepfamilies and intact families separately because they lead to different relatedness structures.

Stepfamilies

A breeder with one helper may experience three state transitions. First, it dies with rate μ_2, and this leads to a change in inclusive fitness that equals $r_1\bar{v}_1 - \bar{v}_2 - r_1\bar{v}_{\mathrm{H}}$, where r_1, the relatedness to the helper, transforms the helper reproductive value to breeder reproductive value “equivalents.” Second, the helper may die (rate μ_{H}), and this leads to a change in breeder IF equal to $\bar{v}_1 - \bar{v}_2 - r_1\bar{v}_{\mathrm{H}}$. Third, an additional helper is produced with rate g_2, and the associated change in IF is $\bar{v}_3 + r_2\bar{v}_{\mathrm{HD}} + 0.5\bar{v}_{\mathrm{HS}} - \bar{v}_2 - r_1\bar{v}_{\mathrm{H}}$, where $0.5 =$ the relatedness between breeder and subordinate helper. When reproducing, breeders always weight offspring reproductive value by 0.5. This is because we assume that a breeder recognizes its own offspring at the egg or chick stage but is unable to distinguish its offspring from among adult helpers. The weighting must therefore be the average relatedness. The following is the rate of change in IF over time for each of the six states that provide for offspring:

$$\frac{dW_1}{dt}(x_1', \boldsymbol{x}) = -\mu(x_1')\bar{v}_1' + g_1(x_1')(\bar{v}_2 + 0.5\bar{v}_{\mathrm{H}} - \bar{v}_1), \tag{C1a}$$

$$\begin{aligned}\frac{dW_2}{dt}(x_2', \boldsymbol{x}) = {} & \mu(x_2')(r_1\bar{v}_1 - \bar{v}_2 - r_1\bar{v}_{\mathrm{H}}) + \mu_{\mathrm{H}}(\bar{v}_1 - \bar{v}_2 - r_1\bar{v}_{\mathrm{H}}) \\ & + g_2(x_2' + x_{\mathrm{H}})(\bar{v}_3 + r_2\bar{v}_{\mathrm{HD}} + 0.5\bar{v}_{\mathrm{HS}} - \bar{v}_2 - r_1\bar{v}_{\mathrm{H}}),\end{aligned} \tag{C1b}$$

$$\begin{aligned}\frac{dW_3}{dt}(x_3', \boldsymbol{x}) = {} & \mu(x_3')(r_2\bar{v}_2 + 0.5\bar{v}_{\mathrm{H}} - \bar{v}_3 - r_2\bar{v}_{\mathrm{HD}} - 0.5\bar{v}_{\mathrm{HS}}) + \mu_{\mathrm{HD}}(\bar{v}_2 + 0.5\bar{v}_{\mathrm{H}} - \bar{v}_3 - r_2\bar{v}_{\mathrm{HD}} - 0.5\bar{v}_{\mathrm{HS}}) \\ & + \mu_{\mathrm{HS}}(\bar{v}_2 + r_2\bar{v}_{\mathrm{H}} - \bar{v}_3 - r_2\bar{v}_{\mathrm{HD}} - 0.5\bar{v}_{\mathrm{HS}}) + g_3(x_3' + x_{\mathrm{HD}} + x_{\mathrm{HS}})0.5\bar{v}_{\mathrm{F}},\end{aligned} \tag{C1c}$$

$$\begin{aligned}\frac{dW_{\mathrm{H}}}{dt}(x_{\mathrm{H}}', \boldsymbol{x}) = {} & \mu(x_{\mathrm{H}}')(r_1\bar{v}_1 - r_1\bar{v}_2 - \bar{v}_{\mathrm{H}}) + \mu_2(\bar{v}_1 - \bar{v}_{\mathrm{H}} - r_1\bar{v}_2) \\ & + g_2(x_2 + x_{\mathrm{H}}')(\bar{v}_{\mathrm{HD}} + r_3\bar{v}_{\mathrm{HS}} + r_2\bar{v}_3 - \bar{v}_{\mathrm{H}} - r_1\bar{v}_2),\end{aligned} \tag{C1d}$$

$$\begin{aligned}\frac{dW_{\mathrm{HD}}}{dt}(x_{\mathrm{HD}}', \boldsymbol{x}) = {} & \mu(x_{\mathrm{HD}}')(r_2\bar{v}_2 + r_3\bar{v}_{\mathrm{H}} - \bar{v}_{\mathrm{HD}} - r_2\bar{v}_3 - r_3\bar{v}_{\mathrm{HS}}) + \mu_3(\bar{v}_2 + r_3\bar{v}_{\mathrm{H}} - \bar{v}_{\mathrm{HD}} - r_2\bar{v}_3 - r_3\bar{v}_{\mathrm{HS}}) \\ & + \mu_{\mathrm{HS}}(\bar{v}_{\mathrm{H}} + r_2\bar{v}_2 - \bar{v}_{\mathrm{HD}} - r_2\bar{v}_3 - r_3\bar{v}_{\mathrm{HS}}) + g_3(x_3 + x_{\mathrm{HD}}' + x_{\mathrm{HS}})0.5r_2\bar{v}_{\mathrm{F}},\end{aligned} \tag{C1e}$$

$$\begin{aligned}\frac{dW_{\mathrm{HS}}}{dt}(x_{\mathrm{HS}}', \boldsymbol{x}) = {} & \mu(x_{\mathrm{HS}}')(0.5\bar{v}_2 + r_3\bar{v}_{\mathrm{H}} - \bar{v}_{\mathrm{HS}} - 0.5\bar{v}_3 - r_3\bar{v}_{\mathrm{HD}}) + \mu_{\mathrm{HD}}(\bar{v}_{\mathrm{H}} + 0.5\bar{v}_2 - \bar{v}_{\mathrm{HS}} - 0.5\bar{v}_3 - r_3\bar{v}_{\mathrm{HD}}) \\ & + \mu_3(\bar{v}_{\mathrm{H}} + r_3\bar{v}_2 - \bar{v}_{\mathrm{HS}} - 0.5\bar{v}_3 - r_3\bar{v}_{\mathrm{HD}}) + g_3(x_3 + x_{\mathrm{HD}} + x_{\mathrm{HS}}')0.25\bar{v}_{\mathrm{F}}.\end{aligned} \tag{C1f}$$

We search for an uninvadable strategy of provisioning behavior, and therefore the fitness expressions above are given for mutant behavior, indicated by the prime (′).

In the case of the breeder with one helper, a mutant allele can invade if switching to mutant behavior x_2' instead of the predominant x_2 results in an increase in the rate of inclusive fitness gain. The parental effort x_2 of the breeder influences two state transition rates: the probability that another helper is produced to join the group and the probability that the breeder dies.

The difference in rate of IF change over time through production of a new offspring when switching from behavior x_2 to x_2' is

$$[g_2(x_2' + x_{\mathrm{H}}) - g_2(x_2 + x_{\mathrm{H}})](\bar{v}_3 + r_2\bar{v}_{\mathrm{HD}} + 0.5\,\bar{v}_{\mathrm{HS}} - \bar{v}_2 - r_1\bar{v}_{\mathrm{H}}). \tag{C2}$$

The difference in rate of IF change through dying is

$$[\mu(x_2') - \mu(x_2)](r_1\bar{v}_1 - \bar{v}_2 - r_1\bar{v}_{\mathrm{H}}). \tag{C3}$$

Thus, a mutant x_2' can invade if replacing x_2 by x_2' leads to a positive IF effect or net change in the rate of IF change over time, that is, if

$$[g_2(x_2' + x_\mathrm{H}) - g_2(x_2 + x_\mathrm{H})](\bar{v}_3 + r_2\bar{v}_\mathrm{HD} + 0.5\bar{v}_\mathrm{HS} - \bar{v}_2 - r_1\bar{v}_\mathrm{H}) + [(\mu(x_2') - \mu(x_2)](r_1\bar{v}_1 - \bar{v}_2 - r_1\bar{v}_\mathrm{H}) > 0. \tag{C4}$$

If we divide equation (C4) by $x_2' - x_2$ and take the limit as $x_2' - x_2$ decreases to 0, we find that

$$\frac{d}{dx_2'}\left[\frac{dW_2}{dt}(x_2', \boldsymbol{x})\right] > 0 \tag{C5}$$

is a condition for mutant invasion. Differentiating equations (C1) with respect to mutant behavior therefore gives the direction of fitness increase, and maximization of each of the six equations gives the best reply (Motro 1994) in one of the six dimensions. The requirement for a best reply $x^\circ{}_2$ is thus

$$\frac{dW_2}{dx_2'}(x^\circ{}_2, \boldsymbol{x}) = 0 \tag{C6}$$

and

$$\frac{d^2W_2}{d(x_2')^2}(x^\circ{}_2, \boldsymbol{x}) < 0 \tag{C7}$$

(Maynard Smith 1982; Motro 1994). Collect the best replies for all states in the vector $\boldsymbol{x}^\circ$. To find the ESS $\boldsymbol{x}^*$, we first make one initial guess of the resident provisioning strategy. We then proceed iteratively and exchange in each stage s the resident vector with the vector of best replies $\boldsymbol{x}^\circ$, using the formula $\boldsymbol{x}_{s+1} = p\boldsymbol{x}^\circ{}_s + (1 - p)\boldsymbol{x}_s$ (Hofbauer and Sigmund 1998; Houston and McNamara 1999), where p is a proportion. Eventually, the provisioning strategy converges to the evolutionarily stable provisioning strategy $\boldsymbol{x}^*$. Formally, the iterative procedure demonstrates that the stable point is a Nash equilibrium (Houston and McNamara 1999), but in our case, the best responses are unique at the equilibrium, so we can say that it is an ESS. It also demonstrates convergence of the best response adjustment dynamics (Hofbauer and Sigmund 1998), which can loosely be taken as a version of convergence stability, that is, that the ESS is attainable (Houston and McNamara 1999).

Intact Families

In our intact families, where females mate once and store sperm for all future offspring, the relatedness structure is different. Specifically, a breeder may produce full sibs to the helpers. The helpers will consider these sibs genetically equivalent to their own offspring. Then again, helper offspring can be related by only 0.25 to the breeder, so there is a built-in asymmetry in the evaluation of offspring. This makes it necessary to change the fitness expressions of the helpers and take into account that breeder offspring share more genetic material with the helpers. For example, in a family of two individuals, the breeder values the helper according to the relatedness (r_1) times the number of future offspring of the helper ($\bar{v}_\mathrm{H}$). The helper's evaluation of the breeder is relatedness via maternal gametes (r_1) times breeder reproductive value ($\bar{v}_2$) plus relatedness via paternal gametes (r_1) times breeder reproductive value (i.e., $2r_1$).

The three helper equations become

$$\frac{dW_{\mathrm{H}}}{dt}(x'_{\mathrm{H}}, \boldsymbol{x}) = \mu(x'_{\mathrm{H}})(2r_1\bar{v}_1 - \bar{v}_{\mathrm{H}} - 2r_1\bar{v}_2) + \mu_2(\bar{v}_1 - \bar{v}_{\mathrm{H}} - 2r_1\bar{v}_1)$$

$$+ g_2(x_2 + x'_{\mathrm{H}})(\bar{v}_{\mathrm{HD}} + r_3\bar{v}_{\mathrm{HS}} + 2r_2\bar{v}_3 - \bar{v}_{\mathrm{H}} - 2r_1\bar{v}_1), \tag{C8a}$$

$$\frac{dW_{\mathrm{HD}}}{dt}(x'_{\mathrm{HD}}, \boldsymbol{x}) = \mu(x'_{\mathrm{HD}})(2r_2\bar{v}_2 + r_3\bar{v}_{\mathrm{H}} - \bar{v}_{\mathrm{HD}} - 2r_2\bar{v}_3 - r_3\bar{v}_{\mathrm{HS}}) + \mu_3(\bar{v}_2 + r_3\bar{v}_{\mathrm{H}} - \bar{v}_{\mathrm{HD}} - 2r_2\bar{v}_3 - r_3\bar{v}_{\mathrm{HS}})$$

$$+ \mu_{\mathrm{HS}}(\bar{v}_{\mathrm{H}} + 2r_2\bar{v}_2 - \bar{v}_{\mathrm{HD}} - 2r_2\bar{v}_3 - r_3\bar{v}_{\mathrm{HS}}) + g_3(x_3 + x'_{\mathrm{HD}} + x_{\mathrm{HS}})r_2\bar{v}_{\mathrm{F}}, \tag{C8b}$$

$$\frac{dW_{\mathrm{HS}}}{dt}(x'_{\mathrm{HS}}, \boldsymbol{x}) = \mu(x'_{\mathrm{HS}})(\bar{v}_2 + r_3\bar{v}_{\mathrm{H}} - \bar{v}_{\mathrm{HS}} - \bar{v}_3 - r_3\bar{v}_{\mathrm{HD}}) + \mu_{\mathrm{HD}}(\bar{v}_{\mathrm{H}} + \bar{v}_2 - \bar{v}_{\mathrm{HS}} - \bar{v}_3 - r_3\bar{v}_{\mathrm{HD}})$$

$$+ \mu_3(\bar{v}_{\mathrm{H}} + r_3\bar{v}_2 - \bar{v}_{\mathrm{HS}} - \bar{v}_3 - r_3\bar{v}_{\mathrm{HD}}) + g_3(x_3 + x_{\mathrm{HD}} + x'_{\mathrm{HS}})0.5\bar{v}_{\mathrm{F}}. \tag{C8c}$$

It is not necessary to make any changes in the breeder equations. The evolutionarily stable strategy is then calculated with the same method as before.

APPENDIX D

The inclusive fitness effect of leaving the breeding group and becoming a floater is simply the difference between the inclusive fitness of an individual before and after leaving. We call this Δw_{L}. This measure must consider the differences between family types in relatedness (app. B) and the asymmetry in how breeder and helper evaluate each other's offspring (app. C). For helper, dominant helper, and subordinate helper, respectively, Δw_{L} is

$$\Delta w_{\mathrm{L,H}} = (1 + r_1\bar{v}_1 - r_1\bar{v}_2 - \bar{v}_{\mathrm{H}}), \tag{D1}$$

$$\Delta w_{\mathrm{L,HD}} = (1 + r_2\bar{v}_2 + r_3\bar{v}_{\mathrm{H}} - \bar{v}_{\mathrm{HD}} - r_2\bar{v}_3 - r_3\bar{v}_{\mathrm{HS}}), \tag{D2}$$

$$\Delta w_{\mathrm{L,HS}} = (1 + 0.5\bar{v}_2 + r_3\bar{v}_{\mathrm{H}} - \bar{v}_{\mathrm{HS}} - 0.5\bar{v}_3 - r_3\bar{v}_{\mathrm{HD}}). \tag{D3}$$

In intact families, the differences are

$$\Delta w_{\mathrm{L,H}} = (1 + 2r_1\bar{v}_1 - 2r_1\bar{v}_2 - \bar{v}_{\mathrm{H}}), \tag{D4}$$

$$\Delta w_{\mathrm{L,HD}} = (1 + 2r_2\bar{v}_2 + r_3\bar{v}_{\mathrm{H}} - \bar{v}_{\mathrm{HD}} - 2r_2\bar{v}_3 - r_3\bar{v}_{\mathrm{HS}}), \tag{D5}$$

$$\Delta w_{\mathrm{L,HS}} = (1 + \bar{v}_2 + r_3\bar{v}_{\mathrm{H}} - \bar{v}_{\mathrm{HS}} - \bar{v}_3 - r_3\bar{v}_{\mathrm{HD}}). \tag{D6}$$

For staying as a helper to be net beneficial, these measures must be negative at the evolutionarily stable equilibrium.

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