

The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay?

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We used a reproductive skew framework to consider the evolution of parental and alloparental effort in cooperatively breeding groups. The model provides the first theoretical treatment of rent payment (the “pay-to-stay” hypothesis) for the evolution of helping behavior of subordinates. According to this hypothesis, not all helping behavior is kin selected, but group members help in order to be allowed to stay in the group and potentially gain breeding positions later in life. We show that reproductive concessions may be replaced by complete skew and voluntary, costly alloparental effort by subordinates once future prospects are included in fitness calculations. This suggests that incomplete skew observed in long-lived species is not due to dominant control over reproduction. Rent payment is predicted to occur when relatedness between subordinate and dominant is low, survival is high, ecological constraints are at least moderately tight, and retaining nonhelping subordinates harms the dominant’s fitness. Rent may also be required from related subordinates if helping is very costly (leading to low voluntary helping effort) and ecological constraints are moderately tight. However, related subordinates do not need to have a positive net effect on the dominant’s direct fitness to be accepted as group members. We also consider compensatory responses of dominant group members as a potential threat to the stability of renting behavior. If dominants trade off parental effort against their own survival, they may selfishly reduce their own parental effort as a response to increased help. As this improves their own survival, the prospects of territorial inheritance diminish for the subordinate, and subordinates should hence be less willing to accept the rent agreement. However, we show that compensatory responses by “lazy” parents prevent group formation only in borderline cases. *Key words*: alloparental care, cooperative breeding, helping at the nest, reproductive skew. [*Behav Ecol* 13:291–300 (2002)]

The apparent altruism of helping—parentlike behavior toward young that are not the genetic offspring of the helper—has inspired a number of alternative, but not mutually exclusive, evolutionary explanations (see Cockburn, 1998; Emlen and Wrege, 1989; Wright, 1997). The most well-known of these is kin selection (Hamilton, 1964; Maynard Smith, 1964), in which patterns of helping in many cooperatively breeding species are explained via indirect fitness benefits that helpers obtain from provisioning young to which they are related (see Bourke and Franks, 1995; Brown, 1987; Emlen, 1991). In addition, by investing in the production of younger members of their social group, helpers may obtain mutual benefits via improved future survivorship and/or reproduction upon inheritance of a breeding position (i.e., pseudo-reciprocity or group augmentation; Brown, 1983, 1987; Connor, 1986, 1995; Kokko and Johnstone, 1999; Kokko et al., 2001; Ligon, 1981; Ragsdale, 1999; Woolfenden and Fitzpatrick, 1978, 1984).

Among the various other hypotheses for helping is the intriguing suggestion that it represents the payment of a “rent” to dominant group members, and that subordinate helpers pay to stay in order to secure group membership and

its associated benefits (Gaston, 1978; Kazem and Wright, in press). In cooperatively breeding birds and fish, these benefits can include access to a communal territory, reduced susceptibility to predation, or enhanced intra- or extra-group mating opportunities (Balshine-Earn et al., 1998; Dunn et al., 1995; Gaston, 1978; Reyer, 1980, 1984). Any lack of effort on the part of the helper can be penalized via aggression from dominant breeders (e.g., superb fairy wrens, *Malurus cyaneus*; Mulder and Langmore, 1993), ultimately culminating in expulsion from the group. Dominant breeders should only tolerate helpers when they are needed (e.g., pied kingfishers, *Ceryle rudis*; Reyer, 1980, 1984). Therefore, below some minimum level of helping effort, it is not worthwhile for dominants to allow helpers in their group because of the potential reproductive and/or foraging competition that they represent (e.g., Florida scrub-jays, *Aphelocoma coerulescans*; Goldstein et al., 1998).

An assessment of the possibility of rent agreements between helpers and dominants should take into account the relative costs and benefits to the helper of membership of alternative groups within the population (Vehrencamp, 1979, 1983). Renting will not be evolutionarily stable if the subordinate benefits more by leaving the group than by providing the help required. In this respect there are obvious parallels with reproductive skew theory (Reeve, 1998; Johnstone, 2000). Here we use this modeling framework to develop the first formal treatment of the evolution of paying rent. The pay-to-stay hypothesis, or “renting” as we call it for simplicity, is intrinsically linked to the decision of staying in a group. Most models of cooperative breeding have simply linked the decision to stay

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Table 1
Symbols used in the model and their definitions

Symbol	Definition
h_0	Effect of presence of non-helping subordinate on dominant's fitness
h_D	Parental effort of dominant breeder
h_L	Parental effort of lone breeder
h_S	Alloparental effort (helping) of subordinate group member
H	Effort of subordinate as required by dominant
H_{min}	Minimum effort required that makes dominant accept subordinate
H_{max}	Maximum effort subordinate is willing to accept
k	Productivity of the group
p	Fraction of reproduction by the subordinate
r_S	Relatedness of subordinate to dominant
r_D	Relatedness of dominant to subordinate
s	Survival from one breeding season to the next
s_{max}	Survival of individual with no parental or alloparental effort
ϕ	Ease of helping (small ϕ means that even small amounts of help are costly to give)
a	Probability that lone breeder is joined by a helper
w_D	Direct lifetime fitness of dominant
w_L	Direct lifetime fitness of lone individual
w_S	Direct lifetime fitness of subordinate
W_D	Inclusive lifetime fitness of dominant
W_L	Inclusive lifetime fitness of lone individual
W_S	Inclusive lifetime fitness of subordinate

and the decision to help together by assuming that a retained subordinate automatically boosts the productivity of the group (e.g., Motro, 1993; Pen and Weissing, 2000; Reeve, 1998; but see also Johnstone and Cant, 1999; Kokko and Johnstone, 1999). However, it is clear that the benefits that a staying subordinate brings to the group will depend on its behavior, particularly on its eagerness to help. Thus, one of our goals in this study was to make the distinction between the staying and helping decisions within a modeling framework—a task whose importance empiricists have acknowledged for a long time (see Brown, 1987; Emlen, 1991, 1997).

Much of reproductive skew theory has focused on concessions, where dominants allow subordinates to have a share in reproduction. We include the possibility of concessions in our model, but our main focus is on coercive solutions (see also Crespi and Ragsdale, 2000), where subordinates do not reproduce and are instead required to help the dominant. We show that nonconcessive solutions can prevail, especially in long-lived species, in which indirect fitness and/or future fitness expectations can provide a reason for nonreproductive subordinates to remain as helpers (Ekman et al., 1999; Kokko and Johnstone, 1999; Pen and Weissing, 2000; Queller et al., 2000; Ragsdale, 1999; Stacey and Ligon, 1991).

We also consider a mechanism that might potentially hinder the evolution of paying rent. Parental effort often trades off with subsequent survival of the parent (Trivers, 1972; see also Clutton-Brock, 1991). Therefore, a dominant may respond to the presence of a helping subordinate by decreasing its own parental effort (Hatchwell, 1999; Hatchwell and Russell, 1996; Houston and Davies, 1985; Legge, 2000; Wright and Cuthill, 1989; Wright and Dingemanse, 1999). If this improves the dominant's survival, then the prospects of territorial inheritance may diminish for the subordinate that provides help.

The model

We evaluated the fitness of group members in the setting of Kokko and Johnstone (1999), in which individuals may be either alone or in a group comprising a dominant and a subordinate. If the dominant dies, the subordinate inherits its territory. This queuing for dominance establishes an incentive

to stay that is often enough to make the subordinate willing to remain without any direct immediate fitness benefits such as reproductive concessions (Kokko and Johnstone, 1999; Ragsdale, 1999). For the sake of completeness, we retain the possibility of concessions in the model, but we show that at equilibrium, concessions can often equal zero in stable groups. A list of symbols and their explanations is provided in Table 1.

To consider the possibility of rent payment, we extend the model by Kokko and Johnstone (1999) by assuming that the dominant and the subordinate can decide independently on the effort, h_D and h_S , that they put into raising offspring. Additionally, we assume that the presence of a nonhelping subordinate changes the productivity of the group by h_0 . Typically, nonhelping subordinates would decrease group productivity ($h_0 < 0$); this would occur as they consume resources of the territory (Brown, 1987). However, positive values of h_0 are possible—for example, if a subordinate aids in predator detection, even if it does not provide active altruistic help (Clutton-Brock et al., 1999; Connor, 1986, 1995; Hamilton, 1971; Wright et al., in preparation). We contrast the passive effect of the subordinate, h_0 , with active helping by the subordinate, h_S . The latter always increases the productivity of the group ($h_S > 0$). Finally, the dominant may also adjust its own parental effort, and therefore group productivity also depends on the effort, h_D , of the dominant. Thus, group productivity, k , equals $h_D + h_0 + h_S$. Reproduction is shared among group members so that the subordinate produces kp offspring, and the dominant produces $k(1 - p)$ offspring. The productivity of a lone individual depends only on its own parental effort: $k_L = h_L$. Between two breeding attempts, a lone individual is joined by a subordinate with a probability a , as in Kokko and Johnstone (1999).

The effort to raise offspring is costly for the individual, and survival, s , between breeding attempts therefore decreases with increasing effort, h_L , h_D , or h_S . We use a function which allows for varying costs of helping effort,

$$s(h) = s_{max}(1 - h^\phi).$$

This function implies that survival has its maximum value s_{max} when no effort is put into raising offspring ($h = 0$) and drops to zero at $h = 1$. We assume that alloparental and parental

effort are equally costly. The parameter ϕ scales the cost of giving small amounts of help. With large ϕ , small or moderate effort levels are relatively cheap, and the cost of raising offspring increases sharply only at high levels of effort, h . With small ϕ , helping is costly even at small help levels, h (see also Kokko et al., 2001). Because large ϕ implies that helping is cheap, we refer to ϕ as the ease of helping.

Kokko and Johnstone (1999) derived the direct lifetime fitness, w_D , w_S , and w_L of dominants, subordinates, and lone individuals, respectively. In each equation, the fitness of an individual equals the sum of current reproduction [e.g., $k(1-p)$ for the dominant] and the fitness of other states, scaled by the probability of ending up in these states after the current breeding attempt. For example, a dominant becomes a lone individual if it survives, the subordinate dies, and no new subordinate arrives. To examine the evolution of helping, we take equation 2 of Kokko and Johnstone (1999) and substitute $h_D + h_0 + h_S$ for the productivity of the group and h_L for the productivity of the lone individual. This yields

$$\begin{aligned} w_D &= (h_D + h_0 + h_S)(1-p) \\ &\quad + s_D\{[s_S + (1-s_S)a]w_D + (1-s_S)(1-a)w_L\} \\ w_S &= (h_D + h_0 + h_S)p \\ &\quad + s_S\{s_D w_S + (1-s_D)[aw_D + (1-a)w_L]\} \\ w_L &= h_L + s_L[aw_D + (1-a)w_L]. \end{aligned} \quad (1)$$

In these equations, the survival of individuals depends on their parental or alloparental effort: $s_D = s(h_D)$, $s_S = s(h_S)$, and $s_L = s(h_L)$. The parameter a specifies the probability that a lone breeder is joined by a helper, as in Kokko and Johnstone (1999).

We first examine the levels of parental effort that evolve voluntarily (that is, without any coercion by the dominant). We thus ask the question, how much would a subordinate help, if it had decided to stay in the group and if its acceptance in the group was independent of its help level? Similarly, we seek the dominant's optimal effort, given that it has a subordinate that decides independently on its effort. Equation 1 yields solutions for w_D , w_S , and w_L for each combination of effort levels h_D , h_S , and h_L (solutions derived in the same way as in Kokko and Johnstone, 1999). We seek the best response (cf. Houston and Davies, 1985) of a dominant by maximizing its inclusive fitness, $W_D = w_D + r_D w_S$:

$$\begin{aligned} W_D(h'_D) &= (h'_D + h_0 + h_S)(1-p) \\ &\quad + s(h'_D)\{[s_S + (1-s_S)a]w_D + (1-s_S)(1-a)w_L\} \\ &\quad + r_D[(h'_D + h_0 + h_S)p \\ &\quad \quad + s_S\{s_D w_S + (1-s_D)[aw_D + (1-a)w_L]\}]. \end{aligned} \quad (2a)$$

Here, r_D is the dominant's relatedness to the subordinate. Likewise, the best response of a subordinate to prevailing effort levels is obtained by maximizing

$$\begin{aligned} W_S(h'_S) &= (h_D + h_0 + h'_S)p \\ &\quad + s(h'_S)\{s_D w_S + (1-s_D)[aw_D + (1-a)w_L]\} \\ &\quad + r_S(h_D + h_0 + h'_S)(1-p) \\ &\quad + s_D\{[s(h'_S) + (1-s(h'_S))a]w_D \\ &\quad \quad + (1-s(h'_S))(1-a)w_L\}, \end{aligned} \quad (2b)$$

where r_S is the subordinate's relatedness to the dominant. The best response of a lone individual maximizes

$$W_L(h'_L) = h'_L + s(h'_L)[aw_D + (1-a)w_L]. \quad (2c)$$

Note that even a lone individual can have a best response to the behavior of other members of the population because it may gain a subordinate in the future, and it may be beneficial to adjust current parental effort in response to this possibility.

In principle, the evolutionarily stable strategy is found by seeking the values of parental effort h_D , h_S and h_L for which it does not pay for any individual to alter its effort. Mathematically, such values have to satisfy $dW_D/dh'_D = 0$ at $h'_D = h_D$, $dW_S/dh'_S = 0$ at $h'_S = h_S$ and $dW_L/dh'_L = 0$ at $h'_L = h_L$. Equations 2a–c, unfortunately, do not yield an analytical solution. The evolutionarily stable effort values h_D^* , h_S^* and h_L^* are therefore obtained by iteration, where new effort values are a weighted sum of the previous prevailing effort and the new best response [e.g., $h'_D = \lambda h_D + (1-\lambda)h'_D$]. In practice, the iteration converges quickly (e.g., with $\lambda = 0.5$), and this value was used in the calculations.

When does rent-paying apply?

A dominant may potentially demand more help from a subordinate, whose voluntary help effort equals h_S^* (note that h_S^* may equal 0). We consider the rule where a dominant evicts a subordinate if its effort falls below H . Renting can be stable only if it is more beneficial for a subordinate to stay and spend the effort, H , than to leave. To evaluate the stability of renting, there are hence two values of effort that need to be specified: (1) What is the smallest value of H that the dominant accepts (H_{min})? (2) What is the highest value of H that the subordinate agrees to pay (H_{max})?

To find H_{min} and H_{max} , we need to take into account that the best effort of dominants and of lone individuals will depend on the help given by subordinates (Equations 2a,c). The calculation of H_{min} and H_{max} proceeds as follows: Substitute the subordinate's effort h_S in Equation 2b,c with H , and let H vary from 0 to 1. Seek the fitness-maximizing values of h_D and h_L according to Equation 2b,c for each H . Equation 1 then yields stable values of w_L , w_D , and w_S for each H . We want to find the range of acceptable values of H from the dominant's and subordinate's point of view. Assuming (as in reproductive skew models in general; Johnstone, 2000; Reeve, 1998) that a dispersing subordinate finds a breeding vacancy and becomes a lone breeder with probability x , the dominant benefits from retaining the subordinate if

$$w_D + r_D w_S \geq (1 + r_D x) w_L. \quad (3a)$$

The subordinate benefits from staying rather than leaving if

$$w_S + r_S w_D > (r_S + x) w_L. \quad (3b)$$

H_{min} is the smallest, and H_{max} the largest, value of H for which Equation 3a or 3b, respectively, applies. If $H_{max} \geq H_{min} > h_S^*$, subordinates accept paying rent.

There are four ways in which renting may be replaced by other types of solutions. First, renting may be replaced by voluntary helping if the voluntary effort by the subordinate, h_S^* , satisfies Equations 3a,b. Such solutions are characterized by $h_S^* > H_{min}$. Second, if the minimum effort required by the dominant exceeds the maximum that subordinates are willing to pay ($H_{min} > H_{max}$), renting is replaced by three alternatives, depending on the value of h_S^* . If at h_S^* subordinates and dominants both benefit from dispersal of the subordinate Equation 3, the group simply disbands. If the subordinate benefits from staying at h_S^* (but not at H_{min}), and if the dominant does not benefit from retaining the subordinate Equation 3, the dominant is expected to evict the subordinate. Finally, if the subordinate should leave at h_S^* (Equation 3b) but the dominant would benefit from retaining the helper (Equation 3a), the

situation has potential for staying incentives. Here, it may pay for the dominant to give a share of the reproduction to the subordinate ($p > 0$), to make staying and helping the preferred option. As our primary focus is on renting rather than on incentives, we do not solve the value of concessions p needed to stabilize the group (these would interact with the evolution of levels of helping, which makes the solution complicated), nor do we check whether dominants are willing to accept this increase in p . We merely note that in this last case, renting is excluded as an outcome, and it is replaced either by incentives or a failure of group formation.

Comparison to fixed parental effort by dominants

If survival trades off against parental effort, dominants may respond to increased effort by rent-paying subordinates by reducing their own effort. If “lazy” dominants survive better, selfish dominants reduce the subordinates’ prospects of territorial inheritance. To investigate whether this mechanism has a strong effect, we compared group stability in the above model to a hypothetical case where the dominant can set a minimum effort H_{min} as above, but the dominant’s own effort is fixed to h_D^* —the best response to a subordinate who does not pay rent (i.e., uses the effort h_S^*). The subordinate is free to choose any effort greater than H_{min} or to leave if the H_{min} is unacceptable to its. The dominant’s effort, h_D^* , is clearly evolutionarily unstable in this scenario because it is not the best response to the effort actually used by the subordinate. Yet, considering group formation under the artificial absence of adaptive effort adjustment of dominants allows us to evaluate the effect that this behavior has on group stability.

RESULTS

Stable groups are often found at complete skew with no reproductive concessions ($p = 0$). For example, consider the case with maximum survival $s_{max} = 0.75$, ease of helping $\phi = 2$, probability that a lonely breeder gains a helper $a = 0.5$, effect of nonhelping group member on productivity $h_0 = -0.2$, relatedness between dominant and subordinate $r = 0.25$, and complete skew $p = 0$. The model predicts evolutionarily stable effort by subordinates $h_S^* = 0.186$ and predicts that the subordinate would rather pay this than leave the group to breed on its own. The effort $h_S^* = 0.186$ is not sufficient to compensate completely for the negative effect on productivity, $h_0 = -0.2$, that the subordinate causes simply by being present. Yet, because the dominant shares an interest in the related subordinate’s future, it accepts this level of effort rather than evict the subordinate, whenever the probability that the subordinate finds a breeding position elsewhere falls below $x = 0.50$ (Figure 1).

That the subordinate stays with no concessions ($p = 0$) is in line with the recognition that territorial inheritance or other benefits of philopatry (see Brown, 1987) remove or reduce the need for reproductive concessions (Kokko and Johnstone, 1999; Ragsdale, 1999). Indeed, the above example shows that it is the dominant, rather than the subordinate, who is the first to benefit from the dispersal of the subordinate when the subordinate’s dispersal prospects improve. When the probability of a subordinate finding a breeding position exceeds $x = 0.50$, the dominant would rather have the subordinate dispersing than staying and helping at $h_S^* = 0.186$, while x has to reach 0.57 before dispersal becomes the preferred option for the subordinate (Figure 1). This means that our model captures the essential conflict that precedes paying rent: subordinates often benefit more strongly from staying in a group than dominants benefit from retaining subordinates.

Nevertheless, the situation does not immediately translate

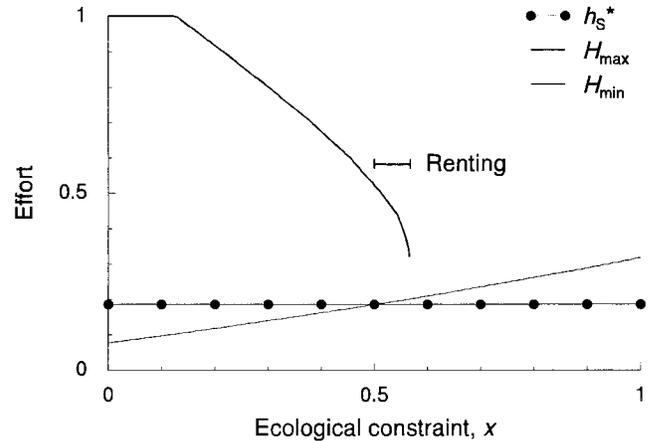


Figure 1

Solution of voluntary helping effort, h_S^* (dots), the minimum effort requirement, H_{min} (thin line), and the maximum that the subordinate is willing to pay, H_{max} (thick line), for parameter values $s_{max} = 0.75$, $\phi = 2$, $h_0 = -0.2$, $r_D = r_S = 0.25$, $a = 0.5$, and for ecological constraint x varying between 0 and 1. At $x < 0.50$ (tight constraints), voluntary helping exceeds the rent requirement and renting is not required. At $x > 0.57$, it is not optimal for the subordinate to stay at any level of help (H_{max} does not exist). Thus, renting only applies between $x = 0.50$ and $x = 0.57$, as is indicated. The amount of rent paid increases from $H_{min} = 0.186$ at $x = 0.50$ to $H_{min} = 0.202$ at $x = 0.57$.

into paying rent. Rent is paid if the maximum effort that subordinates are willing to pay, H_{max} , equals or exceeds the minimum that dominants require, H_{min} , and if subordinates would not pay this much without the rent requirement, $h_S^* < H_{min}$. In Figure 1, this situation only applies in a narrow range of ecological constraints, between $x = 0.50$ and 0.57 . When ecological constraints are tighter ($x < 0.50$), both the dominant and the subordinate benefit more from group formation than from the dispersal of the subordinate. The subordinate is allowed to stay, and its fitness is improved by prospects of territorial inheritance, but helping is nevertheless voluntary and based on indirect fitness benefits rather than on renting. On the other hand, when independent breeding is not strongly constrained ($x > 0.57$), the subordinate’s expected success by independent breeding is greater than the benefits of staying, and it will not stay as a helper or even as a nonhelping subordinate (Figure 1).

We now turn to the effect of different parameters on the prospects of renting.

Renting requires low relatedness or high costs of helping

Voluntary help levels h_S^* increase with relatedness, r_S , whereas effort requirements, H_{min} , decrease with r_D , as dominants have increasing interest in the subordinate’s survival and future reproduction. Therefore, renting is unlikely in kin groups, as it becomes replaced by voluntary, kin-selected helping when h_S^* exceeds H_{min} (Figure 2). Figure 2 also shows that individuals of different relatedness to the dominant may exhibit similar levels of alloparental effort, but for different reasons. For individuals with low relatedness to the dominant, voluntary effort is low, but renting may apply (in Figure 2, $r_D = r_S = 0$ leads to rent 0.2). Highly related subordinates do not need to pay as much to be allowed to stay, but indirect fitness benefits can favor an increase in helping effort (Figure 2: $r_D = r_S = 0.25$ leads to voluntary helping $h_S^* = 0.248$).

Because voluntary helping increases with the subordinate’s relatedness to the dominant (r_S), renting is especially unlikely

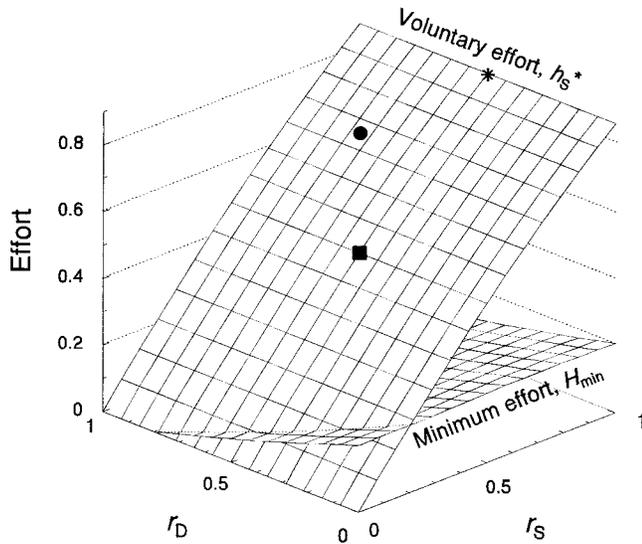


Figure 2 Voluntary helping, h_S^* , and minimum effort requirement, H_{min} , as a function of relatedness r_D of dominant to subordinate, and r_S of subordinate to dominant. To maintain generality, we allow relatedness values from 0 to 1, yet note that not all combinations are biologically meaningful. Other parameters: $\phi = 2$, $h_0 = -0.2$, $s_{max} = 0.5$, $a = 0.5$, $x = 0.2$. Groups are always stable at these parameter values ($H_{max} > H_{min}$ and $H_{max} > h_S^*$; H_{max} not shown for clarity). Rent is only required ($H_{min} > h_S^*$) when relatedness is low, and full compensation $h_S = 0.2$ is only required if dominant-to-subordinate relatedness (r_D) = 0. Three specially marked points indicate help levels in sister–sister association under diploidy (square: $r_D = r_S = 0.5$, $h_S^* = 0.478$, $H_{min} = 0.102$), sister–sister association under haplodiploidy (dot: $r_D = r_S = 0.75$, $h_S^* = 0.684$, $H_{min} = 0.078$), and mother–daughter association under either diploidy or haplodiploidy, when the mother is monogamously mated (star: $r_D = 0.5$, $r_S = 1$, $h_S = 0.866$, $H_{min} = 0.124$).

in mother–daughter associations, where relatedness asymmetry increases the effective relatedness of the daughter to the mother. If the mother is still mated to the daughter’s father and hence produces full sibs for the daughter, the daughter’s relatedness to the mother is effectively $r_S = 1$, while the mother’s relatedness to the daughter remains at $r_D = 0.5$ (Reeve and Keller, 1995). We conclude that mother–daughter groups should exhibit higher voluntary helping effort than sister–sister associations, and they should be less likely to require renting for the maintenance of group stability. With sufficiently monogamous mothers, this applies even if sisters are more related to each other than mothers to their daughters (Figure 2).

Highly related subordinates may, however, be required to pay rent if their willingness to provide help voluntarily is reduced. Such a reduction may be caused by high costs of helping behavior. Subordinates and dominants are asymmetric in their prospects of current versus future fitness. In subordinates that help while waiting to inherit a breeding position, the future represents a major fitness component, and they are expected to be more sensitive to survival costs of current helping effort. Therefore, if survival costs of helping effort are high (ϕ is low), the model predicts a strong asymmetry in the amount of care provided: reproductive dominants show much more effort than the nonreproductive subordinates. If some degree of effort is relatively cheap (indicated by high ϕ), effort is more evenly distributed among reproductive and nonreproductive group members (Figure 3). To summarize, decreasing the cost of helping (increasing ϕ) shifts some part of parenting effort from dominants to helpers. Because min-

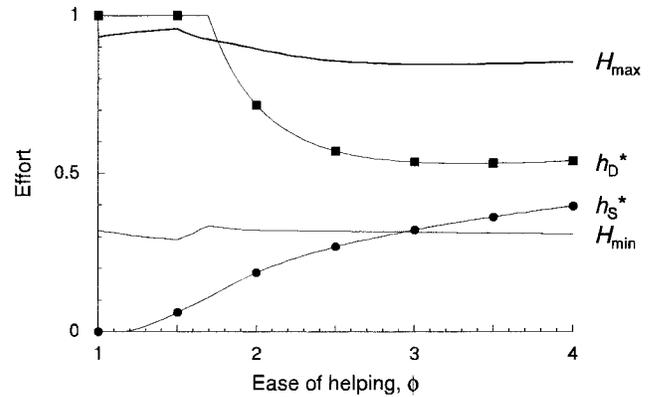


Figure 3 Alloparental (helping) and parental effort, h_S^* (dots) and h_D^* (squares), minimum effort requirement, H_{min} (thin line), and maximum that subordinates are willing to pay H_{max} (thick line), for varying values of ease of helping, ϕ . Other parameters: $s_{max} = 0.8$, $r_D = r_S = 0.25$, $h_0 = -0.4$, $a = 0.5$, $x = 0.2$. If cost of helping is high (low ϕ), the subordinate’s voluntary effort falls much below that of the dominant, and rent is required. If survival decreases less strongly with alloparental effort (high ϕ), the alloparental effort by the subordinate is more similar to the parental effort of the dominant, and no rent is required as voluntary helping, h_S^* , exceeds minimum rent, H_{min} .

imum effort requirements by dominants do not appear to respond strongly to costs of helping (Figure 3), the net effect is that renting in kin groups is more likely if helping is very costly.

Renting requires high survival

According to life-history theory, a long life span means that the relative importance of future fitness increases compared with the current reproductive event (e.g., Roff, 1992). This has several implications for the evolution of renting. Benefits of philopatry, such as the prospects of inheriting a territory, are of greater importance in species with high survival (Kokko and Johnstone, 1999; Pen and Weissing, 2000). Therefore, the willingness of subordinates to stay and queue for breeding positions is stronger if survival, s_{max} , is high. In addition, renting requires that the voluntary effort by subordinates is low, as it is otherwise replaced by voluntary helping. Life-history theory predicts that individuals with a long life span should be less willing to trade off their survival for a fixed current benefit (Roff, 1992). Thus, both parental and alloparental effort decrease with increasing survival (Figure 4), which enhances prospects for renting in long-lived species. Yet rent requirements may also decrease when survival improves: in long-lived species, a decrease in current productivity becomes less important for the parent than ensuring that the (related) subordinate has good prospects to inherit the territory. However, this drop in the minimum effort requirement is less strong than changes in voluntary effort levels, so that the net effect is that long-lived species are more likely to exhibit renting behavior (Figure 4).

In long-lived species, potential benefits of increasing life span are also greatest, and we might expect that long-lived dominants reduce their own effort as a response to rent payment by subordinates. However, with the parameters of Figure 4, dominants would spend maximally only 5% more effort if they were unable to adjust their behavior to increased help by subordinates (at $s_{max} = 0.9$; for clarity, evolutionary unstable efforts are not shown in Figure 4). Likewise, the maximum effort that subordinates are willing to pay would increase by

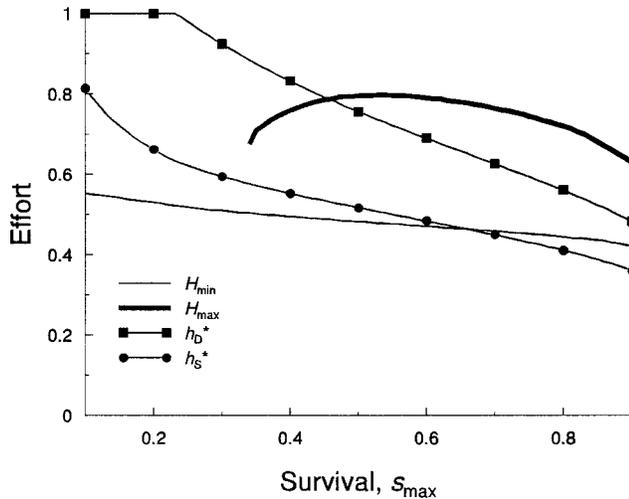


Figure 4

Alloparental (helping) and parental effort, h_S^* (dots) and h_D^* (squares), minimum effort requirement, H_{min} (thin solid line), and maximum that subordinates are willing to pay, H_{max} (thick solid line), for varying values of survival, s_{max} . Other parameters: $\phi = 4$, $r_D = r_S = 0.25$, $x = 0.3$, $h_0 = -0.5$, $a = 0.5$. Groups disband if $s_{max} < 0.34$ (H_{max} does not exist; short-lived subordinates do not accept queuing positions), subordinates stay and help voluntarily ($H_{max} > h_S^* > H_{min}$) at intermediate survival, $0.34 < s_{max} < 0.66$, and rent is paid ($H_{min} > h_S^*$) if $s_{max} > 0.66$.

less than 6%. With relatively tight ecological constraints as in Figure 4, adaptively lazy dominants do not therefore threaten group formation.

Renting requires tight or moderate ecological constraints in non-kin groups and moderate ecological constraints in kin groups

Tight ecological constraints (low x) describe a situation in which dispersing individuals face difficulties in finding a breeding position. If constraints are tight, subordinates are willing to pay more to be allowed to stay. However, in the case where dominants are related to their subordinates, dominants will demand less rent if the subordinate's dispersal chances are poor. This is because dominants compare the benefits of retaining a subordinate to the benefits of evicting it, and the latter diminishes if a related, evicted subordinate fares badly. Therefore, for related individuals, voluntary helping will exceed rent requirements at tightest ecological constraints (low x), whereas benefits of dispersal will exceed benefits of staying if independent breeding is unconstrained (high x). Renting, if any, will be required at intermediately strong constraints. Because the minimum acceptable rent is set by the dominants, the highest rent appears at relatively good dispersal prospects (i.e., constraints that are mild [high x] but not mild enough to lead to dispersal to the subordinate; Figure 5; see also Figure 1).

In unrelated subordinates, voluntary helping is absent (but see Discussion), and renting is not replaced by voluntary helping at the tightest constraints. Also, in cases where the subordinate benefits from staying and the dominant benefits from its dispersal, subordinates are more tenacious if unrelated, as they do not need to take the dominant's fitness into account. Therefore, the conflict that underlies renting applies at a wider range of values (both low and moderate) of ecological constraint if relatedness between dominant and subordinate is low (Figure 5).

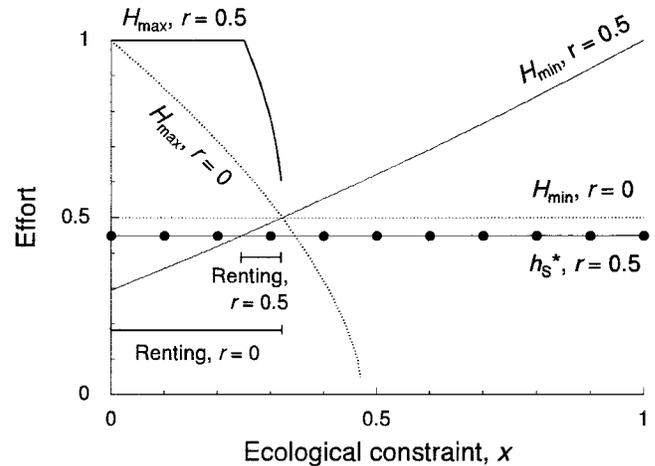


Figure 5

Voluntary helping, h_S^* (dots), minimum effort requirement, H_{min} (thin lines), and maximum effort accepted by the subordinate H_{max} (thick lines) for various values of ecological constraint, x . Relatedness is either $r_D = r_S = 0$ (dotted lines; voluntary helping $h_S^* = 0$) or $r_D = r_S = 0.5$ (solid lines). Other parameter values: $\phi = 1.5$, $h_0 = -0.5$, $s_{max} = 0.5$, $a = 0.1$. Renting applies for all $x \leq 0.32$ when group members are unrelated, but only between $x = 0.25$ and $x = 0.32$ when relatedness equals 0.5. At low x (tight constraints), voluntary helping of related subordinates exceeds the rent requirement. The conflict over staying, where subordinates would be willing to stay though not compensating fully for the negative effect of their presence, extends up to $x = 0.47$ if subordinates are unrelated to the dominant, but only to $x = 0.32$ if subordinates are related to the dominant.

Renting requires that nonhelping subordinates are harmful

If it is beneficial for a dominant to have subordinates even if these do not help (i.e., if $h_0 > 0$); dominants will not require any rent-paying. From related subordinates, rent will not be required even if they are slightly harmful for the dominant (Figure 6). Unrelated subordinates are required to fully compensate for the harm ($h_0 + h_S \geq 0$), to be accepted as group members, whereas partial compensation suffices for related subordinates. Additionally, because of the voluntary helping effort by related subordinates, subordinates that are kin will only need to pay rent if they are extremely harmful to the dominant's reproduction, and even then they do not need to fully compensate for the harm caused. This is seen in Figure 6, where $h_0 + H_{min} = 0$ for an unrelated subordinate (full compensation), but $h_0 + H_{min} < 0$ for a related subordinate (i.e., the dominant tolerates some reduction in its own fitness). Kin groups are therefore expected to be less productive overall if help is rent-based. However, when help by related individuals is voluntary, kin groups are more productive than non-kin (Figure 6).

Summary of results

We have shown that renting can be expected in some situations but can be overridden by several alternatives such as voluntary helping or eviction. Especially in kin groups, payment of rent is only stable under rather restrictive conditions. Figure 7 summarizes the effect of survival s_{max} , relatedness, r (assuming symmetrical relatedness $r_D = r_S = r$), ecological constraint, x , and passive subordinate effect, h_0 , on the solutions. Payment of rent requires tight or moderate ecological constraints in non-kin and moderate constraints in kin, and is most widely established if survival is high. Related subordinates pay rent only if they would otherwise be very harmful

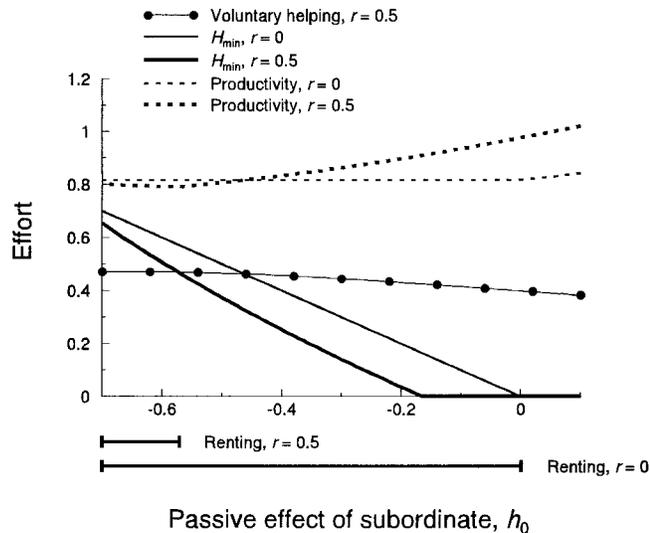


Figure 6

Voluntary helping, h_S^* (dots), minimum effort requirement, H_{min} (solid lines), and total productivity of the group on the dominant's reproduction, h_0 . Other parameter values: $s_{max} = 0.6$, $\phi = 2$, $r_D = r_S = 0$ (thin lines) or $r_D = r_S = 0.5$ (bold lines), $a = 0.5$, $x = 0.2$. These values lead to a stable group at any value of h_0 . Rent is not required if subordinates are beneficial to the dominant even if they do not help (i.e., if $h_0 > 0$). From related subordinates, rent is not required even if they are slightly harmful when nonhelping ($h_0 > -0.17$), and when rent is required, a full compensation of their passive negative effect, h_0 , is not needed for group stability. However, they often help voluntarily to more than compensate for this ($h_S^* > -h_0$), and only fail to do so when their harmful effect is very great (lowest h_0). Renting will apply to non-kin as soon as they will otherwise harm group productivity, but related subordinates will pay rent only if retaining them is otherwise extremely harmful for the dominant. Where related subordinates provide much voluntary help, kin groups are more productive than non-kin groups; otherwise, the reverse is true because kin pay less rent.

for the dominant ($h_0 \ll 0$), whereas rent is required from unrelated subordinates at the slightest negative effect $h_0 < 0$. At the borderline between stable, cooperative groups and instability of group formation, there may be a region in which rent-paying groups can only exist if dominants are not adaptively lazy (i.e., if they do not reduce their own parental effort as a response to help by the subordinate). If dominants are lazy, the subordinates' benefits of staying are reduced to such a degree that they opt for dispersal instead. Dominant laziness, however, seldom hinders group formation (Figure 7; regions marked with U_R are small).

DISCUSSION

This model confirms arguments for the evolutionary stability of a pay-to-stay system of helping (Gaston, 1978; Kazem and Wright, in press). By exploring this possibility within a reproductive skew framework, we have been able to formulate predictions concerning the existence of rent paying in cooperative groups. Rent paying applies most widely when the relatedness between the subordinate and the dominant is low, but related subordinates may also be required to pay rent under restricted conditions. This happens especially if helping is costly, in which case the voluntary effort of related subordinates will be low. There is a possibility that dominants may destroy the stability of rent paying by selfishly decreasing their parental effort in favor of their own survival (thereby dimin-

ishing prospects of territorial inheritance), but this only applies to borderline cases in which mild ecological constraints begin to favor independent breeding of subordinates. We may thus expect to see rent being paid in groups where relatedness between group members is low, subordinates potentially reduce the fitness of dominants unless they compensate by helping, ecological constraints are moderately tight, and survival from one breeding season to the next is high.

High survival also means that breeding vacancies occur less often in the environment. We have modeled the probability of acquiring a breeding vacancy, x , and the probability of acquiring a new subordinate, a , as independent parameters, whereas in reality they interact with the population parameters, including survival (Arnold and Owens, 1998; Kokko and Lundberg, 2001; Pen and Weissing, 2000). Because subordinates are more willing to stay under tight ecological constraints (low x), our conclusion that high survival favors staying and renting would have been strengthened even more if our model had included a link between low x and low mortality of territory owners.

Our conclusions appear to be broadly consistent with examples of pay to stay in the cooperative bird literature. These tend to involve unrelated male helpers in potential reproductive competition with the breeding male, being tolerated only because they are needed, and benefiting via access to one of a limited number of dominant breeding positions in subsequent breeding seasons (e.g., Dunn et al., 1995; Kazem and Wright, in preparation; Mulder and Langmore, 1993; Reyer, 1980, 1984). However, rent payment explanations may only have been invoked in exactly these cases where a lack of relatedness and reproductive concessions already excluded the more obvious possibility of fitness benefits from kin-selected helping. It is only through models such as ours that rent payment can be identified as one of a number of factors responsible for the level of helping seen in a particular system. We have outlined the conditions under which renting should be observed. In empirical tests of the pay-to-stay hypothesis, renting can potentially be distinguished from other forms of helping by its involuntary nature, where too little help leads to punishment.

In agreement with earlier results (Kokko and Johnstone, 1999; Ragsdale, 1999), our model predicts that concessions are not necessarily very important in groups with prominent future fitness benefits: despite the possibility of concessions, our model often predicts complete skew. Helping in many species is not restricted to nonbreeding individuals, however (Bourke and Franks, 1995; Brown, 1987; Emlen, 1991), and the evolution of such cooperative breeding is associated with longevity (Arnold and Owens, 1998). That concessions are evolutionarily unstable in long-lived species (see also Kokko and Johnstone, 1999) suggests that any observations of incomplete skew in real cooperative systems might be the result of a lack of dominant control over reproduction (see also Clutton-Brock et al., 2001). A natural extension of the present model would therefore be to solve the optimal allocation of parental and alloparental care in groups without dominant control of reproduction. This would require one to focus on the trade-off between helping and an individual's own breeding effort, instead of, or in addition to, the trade-off between helping and survival. The former has been addressed, albeit indirectly, in a recent model of reproductive skew (Cant and Johnstone, 1999), which incorporates a link between the division of reproduction among group members and total productivity; the latter is the focus of results presented here. The joint treatment of helping and skew may be particularly relevant to payment of rent because the amount of reproduction that a subordinate claims will strongly influence the level of

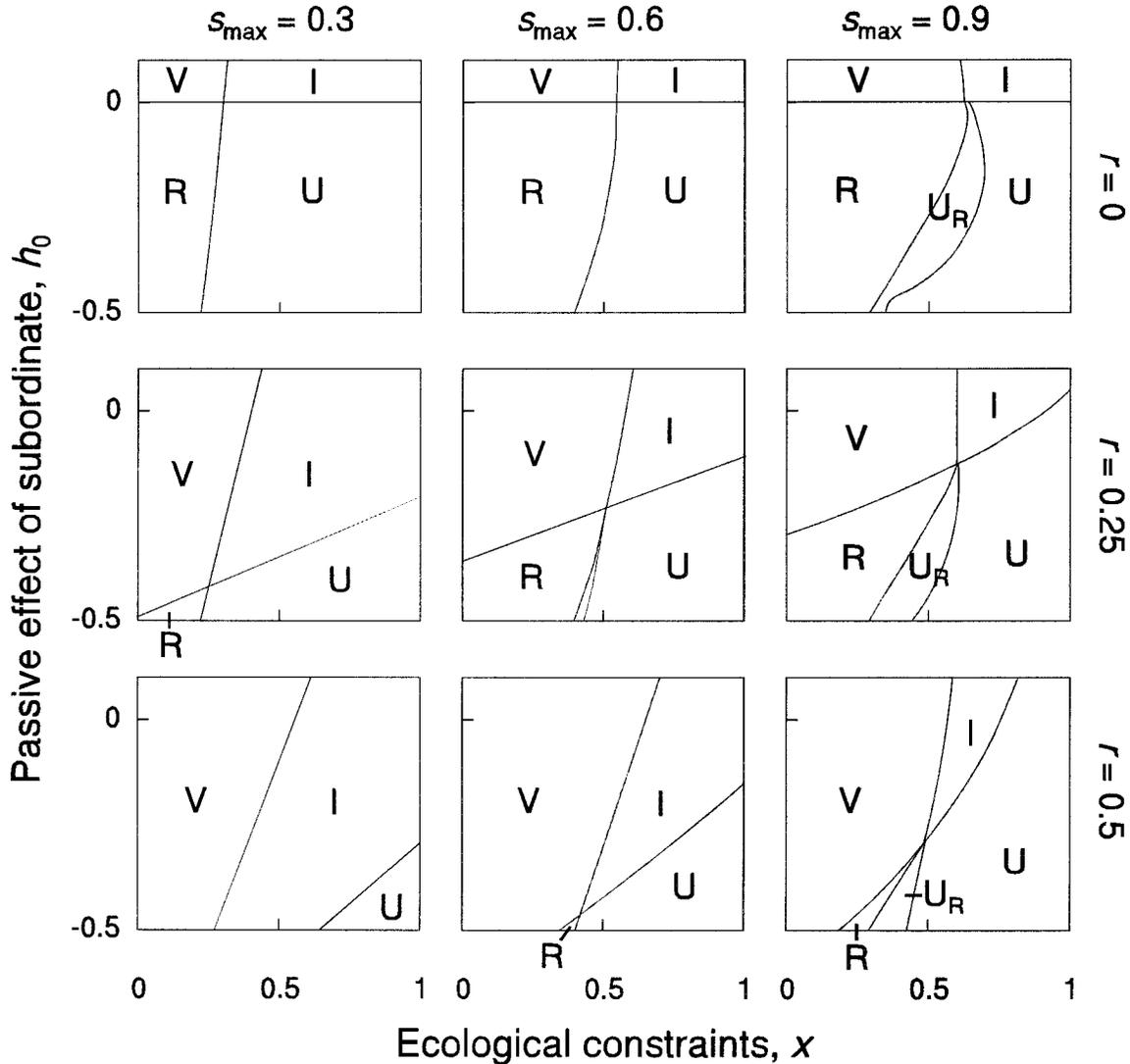


Figure 7

Classification of solutions into nonrenting stable groups where voluntary helping exceeds rent requirement (V), unstable groups (U), potentially stable groups if incentives are given (I), and rent-paying groups (R), according to values of ecological constraint $0 \leq x \leq 1$ and passive effect of a nonhelping subordinate $-0.5 \leq h_0 \leq +0.1$. Other parameters: $\phi = 2$, $a = 0.5$, and $r_D = r_S = 0, 0.25$, or 0.5 as indicated, and $s_{\max} = 0.3, 0.6$, or 0.9 as indicated. In certain parameter regions, renting groups are stable only if dominants do not adjust their own breeding effort as a response to increased help by rent-paying subordinates; these regions are marked as U_R .

help that it must give to render tolerance profitable for the dominant (Johnstone and Cant, 1999).

How general are our conclusions, given that we have shown the evolutionary stability of rent paying in nonconcessive groups only? Our model may provide a conservative view on rent paying: the model shows that rent paying is evolutionarily stable but relevant only under fairly restricted conditions. Imperfect dominant control over reproduction may mean that subordinates have the option of breeding and may do best by claiming some reproduction for themselves, while simultaneously offering help in order to defray the costs their breeding imposes on dominants. Payment of rent could, in this case, prove to be significant in a wider range on natural systems than has previously been acknowledged.

We conclude by discussing two other processes not included in our model that may influence the prevalence of rent paying: nonevictive enforcement of helping behavior and delayed benefits of helping. Enforcement of helping behavior (Clutton-Brock and Parker, 1995; Reeve, 1992) might be a widely

used strategy by dominants. The levels of effort calculated in the present model represent the minimum effort required to persuade a dominant to accept otherwise harmful subordinates. If independent breeding is constrained, this is often less than the maximum that subordinates will tolerate rather than leaving the group (Johnstone and Cant, 1999). Indeed, in our model, the maximum help, H_{\max} , accepted by the subordinate is often much higher than the minimum, H_{\min} , that enables group stability: related subordinates should often accept even suicidal help levels ($H_{\max} = 1$). This means that subordinates can be coerced to pay more than the minimum if dominants use an eviction rule with a large H , even in cases where renting is not required for group stability. Still, such eviction rules may be unlikely to spread because it would not be beneficial for a single mutant dominant to evict subordinates if they are helping sufficiently to have a positive net effect on the dominant's fitness. However, it seems that a more detailed treatment of the use of behaviors such as punishment without evicting (e.g., Mulder and Langmore, 1993) could lead to

higher rent levels. Therefore, if dominants can potentially punish subordinates that want to stay (by means other than eviction), they could potentially enforce higher help levels from subordinates. A game-theoretic negotiation approach (McNamara et al., 1999) would shed more light on this issue.

Finally, we note that any process that increases voluntary help levels will reduce the need for rent paying. We have considered kin selection as the only reason to provide help voluntarily, but delayed benefits of helping, such as pseudoreciprocity or group augmentation, may provide a reason to help even for unrelated subordinates (Brown, 1983, 1987; Connor, 1986, 1995; Kokko et al., 2001; Ligon, 1981; Woolfenden and Fitzpatrick, 1978, 1984). Hence, with the inclusion of direct fitness benefits from increasing group size, the prospects of renting would decrease.

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