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The Evolution of Cooperative Breeding

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1 Introduction

Cooperative breeding defined as a situation where non-breeding individuals exhibit help in rearing offspring other than their own has arisen repeatedly across the animal kingdom (Koenig et al. 1992; Dey et al. 2017).

This kind of helping behaviour is energetically expensive and often means a renunciation of own reproduction (Heinsohn and Legge 1999). There exist different explanations trying to explain why cooperative breeding evolved despite these disadvantages (Heinsohn and Legge 1999). Basically all explanations agree on the point that disadvantages have to be exceeded by the benefits for a helping individual (Jennions and Macdonald 1994).

Benefits for helpers have shown to be diverse and can act both, directly and indirectly (Heinsohn and Legge 1999). Benefits directly increasing the helper's fitness, are for instance a reduced predation risk (due to staying in group), improved foraging efficiency or an increased chance for a helper to become breeder itself (Jennions and Macdonald 1994; Emlen 1997). Indirect benefits refer to Hamilton's inclusive fitness term, which explains how a non-breeding individual can increase its evolutionary success by indirectly promoting reproduction and survival of relatives carrying similar genes (Hamilton 1964; Hamilton 1970). The similarity of genes between a potential helper and its siblings (which it potentially help) is associated with the level of promiscuity (i.e. the number of mates of the breeder) (Cornwallis et al. 2010). Thus, a higher level of promiscuity decreases relatedness within family groups and would therefore decrease the level of helping. However, increased relatedness can also increase local competition and therefore decrease the level of helping (Hamilton 1964). Both ideas are supported by empirical observations (Cornwallis et al. 2010). In order to investigate the effect of promiscuity on the evolution cooperative breeding Leggett et al. 2012 developed an individual-based model (IBM) and showed that the level of promiscuity has either no, or a slightly positive effect on the level of helping.

However, there are certain assumptions behind their model. Since the ecology of cooperative breeding animal species is rather diverse (Emlen 1997), in this paper I modify the model from Leggett et al. 2012 in order to test for varied assumptions.

First, I present the structure and assumptions of the IBM from Leggett et al. 2012, which I call here Model 0 (M0). In this paper M0 serves as a basis for the construction of three models (Model 1 to 3) which structurally differ from M0. I

implemented these structural changes based on assumptions differing from those made in M0.

The assumptions I focus on in this paper are that (1) both, helpers and non-helpers compete for vacant spots after a breeder's death, that (2) the patches that the individuals inhabit are of constant quality and that (3) the breeders choose their mates from the global population of breeders. Model 1 focus on assumption (1), Model 2 deals with assumptions (1) and (2), and Model 3 is a variation of Model 2 additionally focusing on assumption (3).

2 Material and Methods

2.1 Model 0 - the reference model from Leggett et al. 2012

Model 0 (M0) represents the IBM from Leggett et al. 2012. For a more detailed presentation of their model refer to their paper and its supplementary material.

The modelled population in M0 consists of sexual hermaphrodites. The population inhabits a very large number of patches P (a list of all parameters appearing in this paper can be found in table 1). Each patch is of equal and constant quality and is occupied by one breeder plus K offspring at a time. It is assumed that the population is observed at discrete, evenly spaced points of time. The time between two observations represents one generation. Between each observation the following series of events occurs:

Each breeder chooses exactly M mates from the global population of breeders. The choice is made uniformly at random with replacement. Each breeder produces exactly K offspring. Each individual carries two chromosomes corresponding to two dispersal phenotypes: One maternally inherited from the breeder and one paternally inherited from one of the breeder's M mates (both chosen uniformly at random from one of the two chromosomes of the breeder and its mate, respectively). The mean of both dispersal phenotypes of an offspring determine d, its probability to disperse from its natal patch (a number between 0 and 1). It is assumed that each offspring has the choice between two options: (1) to disperse to another patch and compete there for the opportunity to breed, or (2) to remain on the patch where it was born and help its parents. Therefore, the probability to help is given by $1 - d$.

It is assumed that the benefits arising from the presence of helpers are indirect by promoting the survival of the breeder. Neither direct benefits such as increased foraging efficiency or decreased predator risk, nor the other possible

indirect benefit of increased reproductive success is considered. It is assumed that the survival of a breeder increases proportionally with the total number of helpers on its patch. The probability of breeder survival is modelled with the function

$$\mu(\bar{d}) = 1 - exp(-k(1 - \bar{d})) \tag{1}$$

where k is a positive constant that controls how fast breeder survival increases with increasing number of helpers, and where $\bar{d}$ is the mean probability to disperse among all current offspring of a breeder. The shape of $\mu(\bar{d})$ for different values of k is illustrated in figure 1.
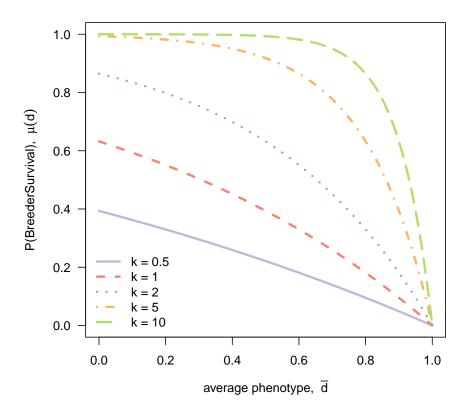

Figure 1: The probability of a breeder to survive (equation 1) is plotted against the average phenotype among all current offspring of a breeder $\bar{d}$ for different values of k.

If a breeder survives it remains on its patch and breeds there again in the next time step. However, if a breeder dies, the vacant patch is inhabited by either a helper from its own patch, or a disperser from another patch. Competition for vacant patches is modelled hierarchically: First, it is determined whether the winner comes from (1) the native patch (i.e. is a helper) or from (2) a non-native patch (i.e. is a disperser). The probability for case (1) is

$$\frac{1 - \bar{d}_{vp}}{c \cdot \bar{d}_{global} + (1 - \bar{d}_{vp})} \tag{2}$$

where $\bar{d}_{vp}$ stands for the average level of dispersal of the vacant patch and $\bar{d}_{global}$ for the global average level of dispersal. The parameter c determines the competitive ability of helper relative to a disperser. For $c > 1$ a disperser has a competitive advantage over a helper, for $c < 1$ a helper has a competitive advantage over a disperser. When $c = 1$ both are competitively equivalent. Accordingly, the probability for case (2) is

$$\frac{\bar{d}_{fp}}{c \cdot \bar{d}_{global} + (1 - \bar{d}_{vp})} \tag{3}$$

where $\bar{d}_{fp}$ stands for the average dispersal level of a specific foreign patch.

Secondly, after the natal patch of the winner is determined, the winner is identified by choosing randomly from among all the offspring from the patch. The probability of an individual j being chosen is $\frac{1 - d_{j,vp}}{\sum_{i=1}^{K} 1 - d_{i,vp}}$ in case (1) where the winner's natal patch corresponds to the vacant patch, and $\frac{d_{j,fp}}{\sum_{i=1}^{K} d_{i,fp}}$ in case (2) where the winner's natal patch is different from the vacant patch.

When the competition phase is complete the mean level of dispersal of all breeders is recorded, all unsuccessful offspring die and the cycle repeats.

2.2 Model 1

Model 1 (M1) is based against the background that in cooperative breeding animals individuals that help often forgo own reproduction (Heinsohn and Legge 1999). Therefore, M1 basically follows the structure and assumptions of M0, except for the competition phase following a breeder's death. While in M0 there is competition for free patches between helpers from the same patch and dispersers from other patches, in M1 only non-helpers (i.e. dispersers from other patches) can compete for free breeding spots. Thus, M1 is basically a variant

of M0 where the parameter c (see equation 2 and 3) is taken to infinite. Again, like in M0, the winner is determined hierarchically: First, one patch is chosen randomly from among all patches. The probability for patch s is assumed to be dependent on the average phenotype of the patch $\bar{d}_s$: $\frac{\bar{d}_s}{\sum_{i=1}^{P} \bar{d}_i}$. Then on the winning patch the winner is chosen randomly. The probability of an individual j from patch s to inhabit a free patch is $\frac{d_j}{\sum_{i=1}^{K} d_{i,s}}$.

2.3   Model 2

In Model 2 (M2) the following features are modified compared to M0: First, in M2 patches have an average lifetime p. This follows the ecology of cooperative breeding one-piece type termites (see Korb 2008). Termites of this group live in a single piece of wood that servers as both, food and shelter. Therefore, the availability of wood determines the longevity of colony. The probability of a patch to collapse is assumed to be normally distributed with $\mathcal{N}(\mu = p, \sigma^2 = 0.05 \cdot p)$. Patches that become free are assumed to regenerate and can be inhabited again in the next point of time by dispersers from other patches. The procedure of choosing a winner for the free patch is equivalent to the procedure following a breeder's death in M1 (see chapter 2.2).

Second, if a breeder dies only helpers from the same patch can compete for the free breeding spot. The likelihood of a helper j to inherit its natal patch is determined by $\frac{1-d_{j,vp}}{\sum_{i=1}^{K} 1-d_{i,vp}}$

2.4   Model 3

Model 2 (M3) is also based on the above-stated group of termites: Usually termites of this group mate among members of their own colony (Korb 2008). Thus, M3 is very similar to M2 with the only difference that the breeders choose their mates among their own offspring instead of from the global population of breeders. As a consequence *two* dispersers are required to inhabit a new breeding spot. Thus, in M3 two dispersers are chosen from the global population of offspring, likewise to the procedure following a breeder's death in M1 (see chapter 2.2).

2.5   Model parameters and technical details

All models were constructed in R (version 3.4.0). This includes M0 which was 'translated' from its original Matlab code into R. The codes of the models can

get on request from the author.

The initial conditions for the models were as follows: In all four models (M0 to M3) the population of breeders was initially assigned two random numbers per breeder. In M2 and M3 patches were first randomly assigned a boolean argument (true = is populated/false = is not populated) and an integer between 1 and the average lifetime p determining the age of the patch. In M3, since breeders choose their mates from their own offspring, also the population of offspring needs to be initialized. Likewise to the population of breeders this was done by assigning two random numbers per offspring.

The models were run with different parameter combinations. For descriptions and values of the parameters see table 1.

Table 1: Parameters included in the four models and their values.

Symbol	Description	included in	Value(s)
	varied parameters		
M	number of mates	M0 - M3	1, 5, 9
k	survival benefit conferred	M0	0.5, 1
	upon breeders	M1	2, 5, 10
		M2, M3	0.5, 1, 2
c	competitive ability of helpers	M0	0.75, 1, 1.25
	relative to dispersers		
p	average patch lifetime	M2, M3	10, 100
	fixed parameters		
P	number of patches	M0 - M3	1000
T	number of generations simulated	M0 - M3	500 - 3000*)
K	number of offspring	M0 - M3	100
*) depending on model and parameter combination			

Parameters that were varied in all models were on the one hand the number of mates M in order to investigate the effect of promiscuity on the evolution of cooperative. In contrast to Leggett et al. 2012 M was only taken to 1, 5 and 9 in order to decrease computation time. Also the parameter k describing the strength of the survival benefit for breeders through the presence of helpers is varied in all models, since they all include the same breeder survival function (equation 1). Values to which k was taken are dependant on the model. Additionally, in M0 the parameter c (the competitive ability of helper relative to a

disperser) was varied, and in M2 and M3 the average patch lifetime p. Following Leggett et al. 2012 the number of patches was fixed for each simulation at $P = 1000$ and the number of offspring of each breeder at $K = 100$ in order to avoid large fluctuations among runs.

For each parameter combination 12 evolutionary trajectories were run (instead of 32 in Leggett et al. 2012 to reduce computation time). Each trajectory was simulated for as many generations T as were needed to reach a stable equilibrium level of dispersal d^*. In most cases $T = 500$ was sufficient. Convergence of the trajectories was checked visually.

3 Results

3.1 Model 0

The results of M0 are in accordance with the results from Leggett et al. 2012 (figure 2). The level of helping is negatively related to the competitive ability of helpers relative to dispersers c. When helpers have an competitive advantage over dispersers ($c = 0.75$) the level of helping ranges between 0.6 and close to 1 depending on the rate of c and M. With higher values of c the level of helping decreases; for $c = 1.25$ it ranges between 0.15 and 0.6. The value of k that controls how fast breeder survival increases with increasing number of helpers, has a positive effect on the level of helping. Promiscuity, described by the number of mates M has a positive effect on the level of helping. This effect is more distinct for a raise from 1 to 5 mates than from 5 to 9 mates. With higher values for c and lower values for k this trend gets flatter.
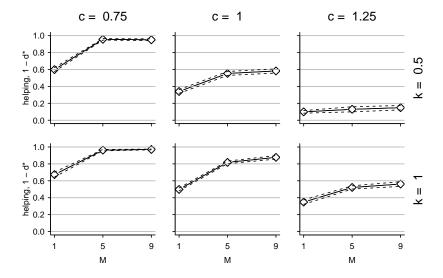

Figure 2: Results from the model M0, constructed according to Leggett et al. 2012. The average equilibrium level of helping $1 - d^*$ is plotted against the number of mates M for different values of c (the competitive ability of helpers relative to dispersers) and k (strength of the survival benefit for breeders through the presence of helpers). Dashed lines mark the 95% confidence interval.

3.2   Model 1

In M1 we can also observe an increased level of helping with higher values of k (figure 3). However, in order to reach levels of helping similar to M0 higher values of k are required. While for $k = 2$ the level of helping is still close to 0, for $k = 10$ it reaches almost 0.7. In contrast to M0 there is no effect of the number of mates M on the evolution of helping.
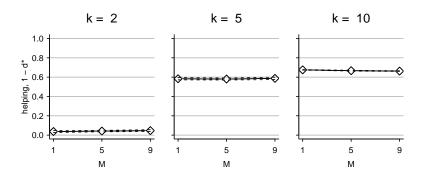

Figure 3: Results from the model M1. The average equilibrium level of helping $1-d^*$ is plotted against the number of mates M for different values of k (strength of the survival benefit for breeders through the presence of helpers). Dashed lines mark the 95% confidence interval.

3.3   Model 2

In contrast to M0 and M1 the value of k has a negative effect on the level of helping (figure 4, blue x). This trend is more distinct for an average patch lifetime of $p = 10$. The effect of the average patch lifetime p on the level of helping is positive. For $p = 10$ the level of helping is for all values of k lower than for $p = 100$. For $p = 10$ the number of mates M has a very slight positive impact on the level helping. This effect diminishes with increasing p and decreasing k.

3.4   Model 3

Simulations with M3 show a lower level of helping than in M2 (figure 4). Depending on the parameter combinations the level of helping in M3 ranges between 0.2 and and almost 0.4 compared to 0.5 to 1 in M2. In case of the

parameter k no effect on helping level can be observed. Similarly to M2 the average patch lifetime p has a positive impact on the level of helping, even though the trend in M3 is less distinct. The number of mates M has a very slight positive effect.
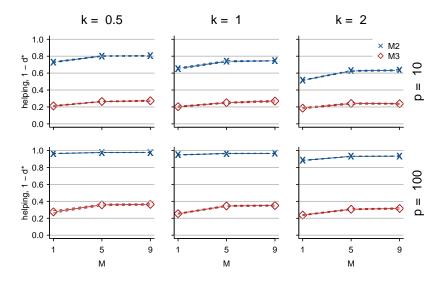

Figure 4: Results from the models M2 (blue, x) and M3 (red, ◇). The average equilibrium level of helping $1 - d^*$ is plotted against the number of mates M for different values of k (strength of the survival benefit for breeders through the presence of helpers) and p (average lifetime of the patches). Dashed lines mark the 95% confidence interval.

4   Discussion and Conclusion

The models in this paper predict either no impact of promiscuity on the evolution of cooperative breeding (in the case of M1) or a (very) slightly positive (in the case of M2 and M3). The first finding is in concordance with Leggett et al. 2012 (here: M0) who stated a decreased effect of promiscuity when helpers are less likely to inherit a vacant patch (higher c). When c is taken to infinite, like it is the case in M1, this effect vanishes completely.

The model predictions with respect to the strength of the survival benefit that breeders have from the presence of helpers (k) vary among the models.

The impact of k on the level of helping is positive in M0 and M1, negative in M2 and neutral in M3. In case of M0 and M1, the more distinct the impact that helpers have on the survival of their breeder (higher k) the higher are the model predictions of the level of helping. This might be explained with a higher personal fitness of a breeder that has many helpers. The higher values of k which are required in M1 to obtain similar levels of helping to M0 can be explained by the fact that in M1 helpers have no more chance to become breeders. Thus, since their only benefit is through boosting the survival of the breeder, this 'boost' needs to more distinct than in M0.

In contrast to M0 and M1, M2 predicts that a decreased survival benefit that breeders have from the presence of helpers (lower k) leads to higher model predictions of the level of helping. This results from the structure of M2: the shorter a breeder lives, the better the chances for an offspring with high level of helping to become a breeder itself, as only helpers from the same patch can inherit dead breeders (with a probability of $1 - d$). However, if a breeders lives for several generations, helpers in-wait that only live for one generation have no chance to become a breeder. In contrast, dispersers have - irrespective of the breeder's mortality - always the same chances to become breeder as due to the limited lifetime of patches they continuously become free.

The results of M3 show an independence of the value of k on the level of helping, indicating that the evolution of helping in this model is unrelated to the breeders' mortality. The reason for this could be that due to inbreeding (resulting from the mating of own offspring) the common gene pool of a colony is very homogeneous and therefore, it does not matter which individual from a colony produces offspring. Since the only benefit of helping is through the boost of breeder survival, also the lower absolute level of helping compared to M2 can be explained.

Both models that assumed a limited patch lifetime (M2 and M3) predict a positive impact of the average patch lifetime on the evolution of cooperative breeding. This follows the logic that the shorter the average patch lifetime, the more patches become free in each time step. And the more free patches, the more likely it is for a disperser to become breeder itself, which favours dispersing on the cost of helping. The reason why this effect is more distinct in M2 than in M3 could be that through inbreeding in M3 the entire population is very homogeneous so that the effect of the patch lifetime on the level of helping becomes less important.

In this paper I modified the IBM from Leggett et al. 2012 against the back-

ground of assumptions differing from those made by the authors. However, there are still several assumptions that I did not take into account in this paper but may be modified, too. First, all models presented here are locally implicit which means that the patches have no local coordinates. Thus, breeders find their mates (at least for M0 to M2) from within the global population of breeders irrespective of the local conditions, or dispersers inhabit free patches independent of their native patch. Including local explicit structures into the models could help to better understand the phenomena that within the same animal species the level of cooperative breeding varies from group to group (Riehl 2013).

Secondly, none of the models contains a cost of inbreeding. However, it was shown that inbreeding under most circumstances decreases fitness (Ralls et al. 1988). Especially in the case of M3 where breeders select their mates among their own offspring the implementation of a cost of inbreeding (e.g. in form of a decreased survival rate with increasing similarity of the two genotypes of an individual) would allow us to study the evolution of cooperative breeding for different rates of inbreeding-costs.

Thirdly, in all models the only benefit of helping is on the survival rate of the breeder. However, as stated in the introduction the benefits of helping can be rather diverse. For instance, a benefit of helpers on the reproduction of the breeder could be included into the models. But not only indirect benefits following Hamilton's inclusive fitness theory, also direct benefits of helping were observed for cooperative breeding animals (Balshine-Earn et al. 1998). Kokko et al. 2001 for example investigated group augmentation (e.g. decreased predator risk) as a driver in the evolution of cooperative breeding. They found that group augmentation can 'potentially explain the weak relationships between relatedness and helping behaviour that are observed in some cooperatively breeding species' (Kokko et al. 2001).

In order to gain a more comprehensive understanding of the evolution of cooperative breeding local explicitness, costs of inbreeding and other (also direct) benefits of helping could be incorporated into the here presented models.

References

Balshine-Earn, Sigal, Franics C Neat, Hannah Reid, and Michael Taborsky (1998). "Paying to Stay or Paying to Breed? Field Evidence for Direct Benefits of Helping Behavior in a Cooperatively Breeding Fish". In: *Behavioral Ecology* 9.5, pp. 432–438.

Cornwallis, Charlie K, Stuart A West, Katie E Davis, and Ashleigh S Griffin (2010). "Promiscuity and the Evolutionary Transition to Complex Societies". In: *Nature* 466.7309, pp. 969–972.

Dey, Cody J, Constance M O'Connor, Holly Wilkinson, Susanne Shultz, Sigal Balshine, and John L Fitzpatrick (2017). "Direct Benefits and Evolutionary Transitions to Complex Societies". In: *Nature Ecology & Evolution* 1, p. 0137.

Emlen, Stephen T (1997). "Predicting Family Dynamics in Social Vertebrates". In: *Behavioural ecology: an evolutionary approach* 4, pp. 228–253.

Hamilton, William D (1964). "The Genetical Evolution of Social Behaviour. II". In: *Journal of theoretical biology* 7.1, pp. 17–52.

— (1970). "Selfish and Spiteful Behaviour in an Evolutionary Model". In: *Nature* 228.5277, pp. 1218–1220.

Heinsohn, Robert and Sarah Legge (1999). "The Cost of Helping". In: *Trends in Ecology & Evolution* 14.2, pp. 53–57.

Jennions, Michael D and David W Macdonald (1994). "Cooperative Breeding in Mammals". In: *Trends in Ecology & Evolution* 9.3, pp. 89–93.

Koenig, Walter D, Frank A Pitelka, William J Carmen, Ronald L Mumme, and Mark T Stanback (1992). "The Evolution of Delayed Dispersal in Cooperative Breeders". In: *The Quarterly Review of Biology* 67.2, pp. 111–150.

Kokko, Hanna, Rufus A Johnstone, and TH Clutton-Brock (2001). "The Evolution of Cooperative Breeding through Group Augmentation". In: *Proceedings of the Royal Society of London B: Biological Sciences* 268.1463, pp. 187–196.

Korb, Judith (2008). "The Ecology of Social Evolution in Termites". In: *Ecology of Social Evolution*. Springer, pp. 151–174.

Leggett, Helen C, Claire El Mouden, Geoff Wild, and Stuart West (2012). "Promiscuity and the Evolution of Cooperative Breeding". In: *Proceedings of the Royal Society of London B: Biological Sciences* 279.1732, pp. 1405–1411.

Ralls, Katherine, Jonathan D Ballou, and Alan Templeton (1988). "Estimates of Lethal Equivalents and the Cost of Inbreeding in Mammals". In: *Conservation biology* 2.2, pp. 185–193.

Riehl, Christina (2013). "Evolutionary Routes to Non-Kin Cooperative Breeding in Birds". In: *Proceedings of the Royal Society of London B: Biological Sciences* 280.1772, p. 20132245.