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By-product group benefits of non-kin resource-sharing in vampire bats

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Abstract. We develop an agent based model (ABM) to simulate the behaviour of a colony of vampire bats (Order: *Chiroptera*) and study the by-product group benefits that result from resource-sharing among related as well as unrelated members of the colony. Such cooperative behaviour can lead to unexpected group benefits; there is an increase the inclusive fitness of related members of the colony (namely *kin*) and can have direct benefit when shared with unrelated members (namely *non-kin*). Sharing can also provides by-product benefits when individuals have a shared (or *group*) interest.

Our study focuses on the contrast in the group estimates between sharing and non-sharing populations. For constant ecological resources, sharing behaviour can increase the sustainable population size, increase the total resource stored in the population, and reduce the average resource required per individual, compared to a non-sharing population. (The extent of the increase or decrease will depend on the parameters of the model). This increased carrying capacity due to resource sharing can increase the fitness of individuals in the group. The increase in cooperativity has a nonlinear effect on group benefits: Substantial group benefits are shown only after a cooperativity threshold, and it increases exponentially to a maximum thereafter.

1. Introduction

Agent based modeling (ABM) techniques are known to provide considerable insight into a number of different problems in different areas of enquiry, ranging from biology, physics, and chemistry, to economics and the social sciences [1, 2, 3]. In order to understand the emergence of properties in a complex system, its parts are modelled as interacting agents with a specified minimal set of properties and behaviours. As an example of such an approach, the properties of an ecology can be seen to derive from the populations of its constituent species [4, 5] and agent-based modelling has been usefully applied in to understand the complex process of the emergence of cooperation [6] among the species. In general, ABMs using simple local interactions can give insight into complex global patterns [7]. Our aim in this work is to use autonomous behaviours of vampire bats (such as foraging, starvation, death, breeding and blood sharing) in an ABM framework in order to understand the effect at a population level, particularly in respect of the inclusive fitness of the population.



Cooperating organisms often invest in partners preferentially so as to increase the inclusive fitness benefit [12]. Inclusive fitness is the sum of direct fitness and indirect fitness [8, 9, 10, 11]. The ability to identify close relatives, namely the phenomenon of kin discrimination, and reciprocity (a tit for tat strategy) are mechanisms that ensures that so-called cheaters do not benefit from cooperation. On the other hand, when the act of cooperation automatically provides so-called by-product benefits (which in general are shared group benefits) no specific enforcement may be required [9, 13]. In the present paper we explore such group benefits.

In the common vampire bat (*Desmodus rotundus*) food or blood sharing is a cooperative behaviour [14]. Vampire bats are obligate blood feeders and can store very limited resources for survival; a 72 hour starvation will kill the bat [15]. At the same time, bats regurgitate in order to share blood with kin, namely related members of the colony, as well as with others [16]. Cheaters, namely those who do not reciprocate help can be detected by social grooming [12, 17]. It has been observed that food-sharing with unrelated members of the colony, namely non-kin, occurs preferentially with individuals having high past reciprocation [14, 18].

Simulations by Wilkinson [16] have shown that the direct fitness benefit is low compared to indirect fitness benefit. A bat with 90% success rate of foraging takes 1110 days on average to miss three consecutive meals. Thus a typical bat may need no more than 3 to 5 donations of food through sharing in its entire lifespan. Considerable attention has been given to examine both primary (direct) fitness and indirect fitness benefits and mechanisms to maintain cooperation [12, 14, 16, 18]. By-product group benefits of food sharing in vampire bats have also been studied, although to a lesser extent. This is useful in understanding cooperation among non-kin individuals, and as has been seen in simulations, energy sharing as in vampire bats can bring substantial benefits to the group as a whole [19].

We present an agent-based model (ABM) of food sharing in vampire bats. Our simulations explore the group benefits of resource sharing with all individuals in the group. We find that within our model, for a given constant rate of ecological resources, both the carrying capacity as well as the total resources stored with the individuals in the population increase significantly. This increase in the sustainable population size with a small increase in resources gathered can reduce the resources required per individual. The increase in fitness due to the increased group size can result in the increased reproductive capacity of individuals.

We have also examined the effect of the rate of cooperativity on group size and find that considerable group benefits can occur only for large cooperativity. This suggests that such by-product benefits might be of use in maintaining the cooperativity, although this cannot explain the origin of cooperativity itself. Another factor in the model is the capacity to store food by an individual: this is varied from sufficient food for 3 days to sufficient food for 12 days. The increase in capacity to store food reduces the sustainable size for both cooperating and non-cooperating populations, but the population size ratio (sharing to non sharing) is nonmonotonic, increasing first and then decreasing. Our present results suggest that significant additional by-product group benefits accrue from food-sharing behaviour in vampire bats, and this aspect needs to be explicitly included in any estimation of the total fitness benefit of such cooperative behaviour.

2. Materials and Methods

The agent based model that we employ here is as follows. Each individual bat forages every day, and if successful will store three units of food resource. The success is probabilistic and depends on its own efficiency and resources available per individual. The rate of food resource in the

habitat (total resource per day) is taken to be constant and thus the resources available per bat per day is inversely related to the population size. If foraging is unsuccessful the bat's stored resource is reduced by one unit, and the particular bat survives only if the stored resources have a non-zero value. This is in keeping with the observation that a bat that is unsuccessful in foraging for three consecutive days is not likely to survive [14, 15]. The foraging efficiencies for initial individuals is randomly chosen in a range (for convenience between 1/2 and 1) and we further assume that each bat reproduces once every year at a random time [20], offspring inheriting the mother's foraging efficiency.

In a population with resources-sharing behaviour, individuals that are successful in foraging are considered donors and are denoted D: these have at least 3 units of stored food. Bats with only one unit of stored resources, namely those that are unsuccessful in foraging, are denoted N (for needy). So long as the total number of N bats is lower than the D, each will receive one unit of resource randomly from a donor. If N exceeds D, then each donor randomly selects one N bat to donate one unit of resources.

We find that in our simulations, the model bat populations stabilize after a transient time (which depends on the efficiency range chosen). Quantities such as the stable size of the population, the total food stored with individuals in each population and the resources available per individual can be measured, and compared between populations that indulge in food-sharing versus those that do not. For proper comparison, we take both populations to feed on the same amount of external resource, to have the same foraging efficiencies, and further, that both groups start with the same number of individuals. The efficiency of a strategy is measured by the size of the stable population that is eventually achieved.

In order to understand the effect of partial cooperativity, each resource-sharing event is taken to be probabilistic. If the index of cooperativity is w , only that fraction of resource-sharing acts will be successful, while others maintain the *status quo* by not sharing. Another parameter of interest is c , the capacity of an individual to store resources, and in our simulations we have varied its value from three to twelve. The model, data and NETLOGO code for reproducing the results can be downloaded from the <https://github.com/Donepudiraviteja/Resource-sharing/>.

3. Results

Results of our simulations for populations of equal size with each habitat having the same rate of resource availability are shown in Fig. 1. Transients are discarded and the different measures are calculated after the populations have stabilized.

The sustainable surviving population on the given constant food resource in the habitat for population with resources sharing behaviour is 417, where as for non-sharing behaviour it is 277 for this set of parameters, indicating that on average, the sustainable population size increases by approximately 50% due to resource-sharing, since this is the only difference between the two models. These results are typical: simulations for various levels of resource availability per day showed similar trends: both sharing and non-sharing populations have a linear population growth as a function of the resource availability, and with a similar size ratio (data not shown).

The total resources assimilated from the habitat in a single day is calculated by adding the resources available to all individuals. In our simulations, sharing behaviour actually increased the total resources assimilated by about 11% over non-sharing population since the cooperative behaviour allowed for more foragers and consequently, fewer N individuals. The resource required per individual, namely the total food resources assimilated divided by the population

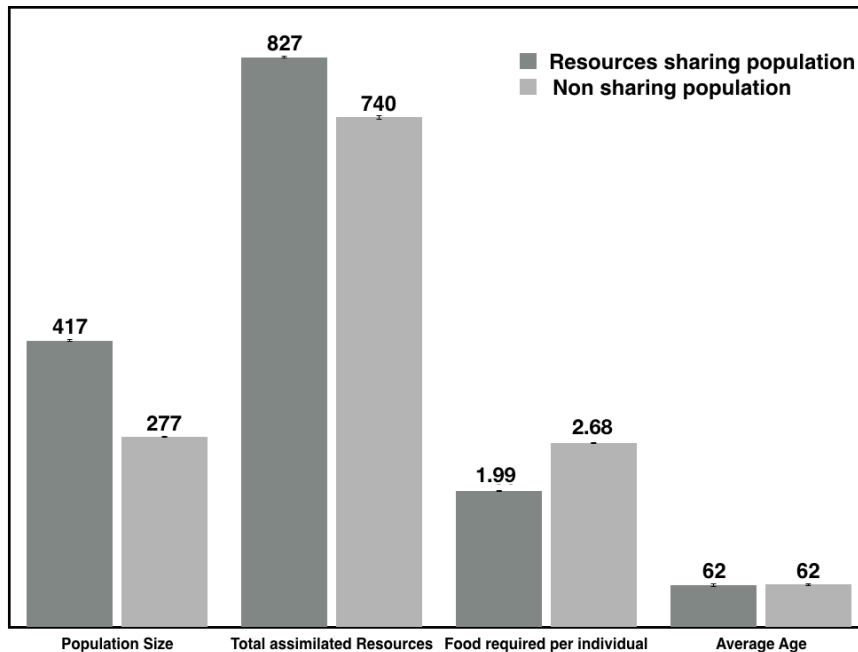


Figure 1. Comparison of measured quantities for the sharing and non-sharing populations, starting with 200 individuals and 600 units of ecological resources. A transient time of 100 days is taken, and simulations have been averaged and rounded over an ensemble of 12 realizations. The sample to sample variation is small and does not show up on this scale.

size is about one fourth *less* for food sharing population.

We also considered the case when individuals were pre-classified as resource sharing or non-sharing, and allowed them to compete for resources. An equal number of both types of individuals was considered, and in steady state, we find (see Fig. 2) that resources sharing individuals eventually take over the population: this is the dominant strategy. We keep the populations distinct, namely there are no resource transfers between sharing and non sharing individuals, and there are no defectors between the types in the population. Simulations show that an increase in cooperativity leads to a nonlinear increases in group benefits: substantial benefits are shown only after the cooperativity parameter is 60%, and it increases exponentially to a maximum thereafter.

The sustainable group size is strongly dependent on the maximum capacity c that an individual possesses to store resources. Group sizes were measured for c varying between 3 and 12. The effect of increasing capacity is, paradoxically, to *reduce* group size in both sharing and non-sharing populations (see Fig. 3). The ratio between sharing and non sharing populations has a nonmonotonic dependence on c whereas the total resources stored by both sharing and non sharing populations has the inverse effect.

Finally, to see whether the increased population size effects the lifespan, we measure the average age and the average age at death for both the populations. (In this simplified model, we only consider death to occur via resource-deprivation). For both average age and average age at death the food-sharing population is statistically similar to the non-sharing population. And

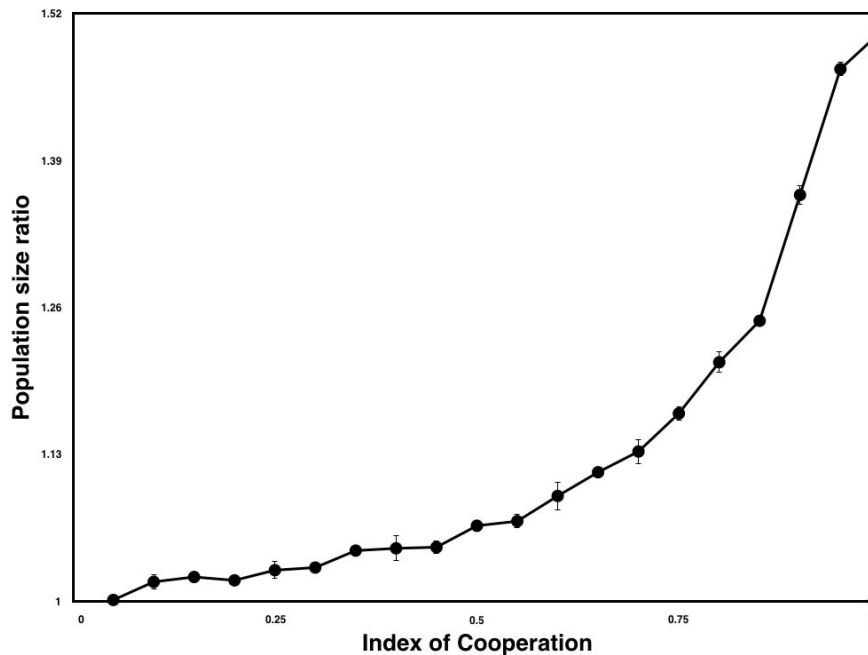


Figure 2. Group benefits with increasing cooperativity. The cooperativity of the population is varied on the abscissa, and the resulting population size ratio (between populations of sharers versus non-sharers) is on the ordinate. All results are averaged over 5 realizations, and the error bars are shown.

the average age for both food-sharing population and non-sharing population are not affected by the amount of ecological resources available or the initial population size.

If p is the probability of unsuccessful forages the average number of days before there are three consecutive unsuccessful forages (TCUF), is clearly given by

$$\text{TCUF} = \frac{1 + p + p^2}{p^3}.$$

For the reported probability of 10% unsuccessful forages [14, 16], therefore, on average TCUF will occur after more than three years; the average lifespan of a vampire bat being about 10 years.

4. Summary and Discussion

Pseudo-reciprocity [13, 21] results when the cheaters (in the sense used here) indirectly benefit those individuals who share resources. This is a *by-product* group benefit, and in the present work we study a model of resource-sharing between individuals in a bat colony where such behaviour can lead to substantial group benefits. Mechanisms such as kin recognition and reciprocity ensure and reinforce cooperative behaviour. The by-product group benefits that result in our simulations has the effect of increasing the effective total fitness of individuals and thereby might also help in maintaining the fitness through pseudo-reciprocity.

Increasing the maximum capacity of resources that can be stored affects the quantifiers we have focussed upon for both sharing and non-sharing populations. However, the ratio of their

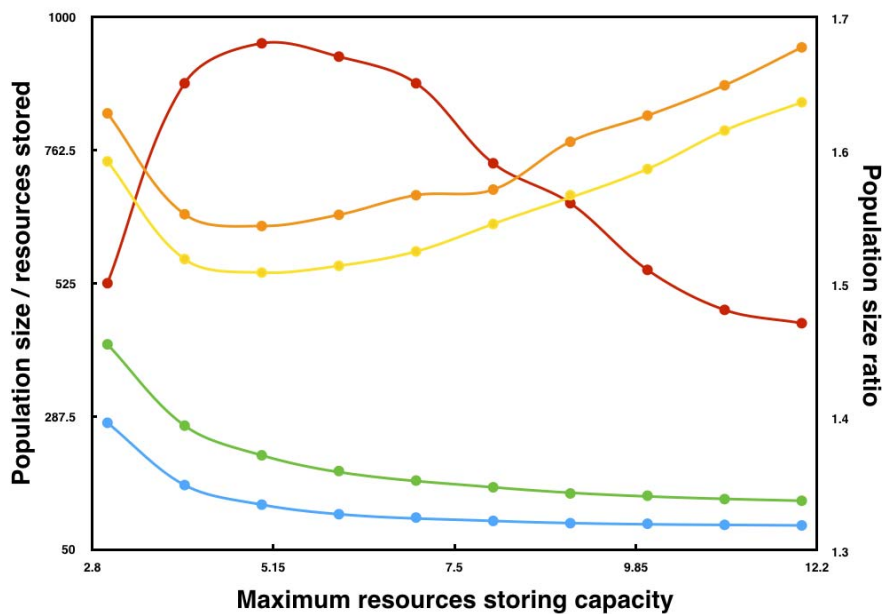


Figure 3. Group benefits with increasing maximum resource storing capacity, c plotted along the abscissa. Red curve represents population size ratio between sharing and non-sharing populations, blue and yellow curves represent the population size and total resources stored for non sharing population. The green and orange curves represents the population size and total resources stored for a sharing population. All results are averaged over 5 realizations.

respective population sizes is a nonmonotonic function of storage capacity, suggesting that for a species that can store resources for sufficiently long, there is unlikely to be any added benefits due to cooperation.

Cooperativity has a nonlinear effect on benefits. For low levels of cooperativity the benefits are also low, but after the cooperativity increases to about 60% benefits rapidly increase. In the evolution of food-sharing behaviour, in the initial stages, when the co-operativity is low, the by-product benefits would be minimal, but once significant co-operativity is established, the consequent benefits help in its maintenance.

In summary, our simple application of agent based models to understand cooperative behaviour of vampire bats suggests that resource-sharing between unrelated individuals in vampire bat colonies can yield substantial by-product benefits. Such behaviour has not been explored in previous studies, and this suggests that more specifically defined resource-sharing models need to be developed and studied, particularly to understand better the differential advantages of various strategies of foraging and resource allocation.

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