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Evolution of Food Sharing Behavior and Social Grooming Networks in *Desmodus rotundus* with Agent-Based Models

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The common vampire bat, *Desmodus rotundus*, is an example of a non-primate social animal that shares food. Females live in social groups of 8-12, with their offspring and perform social behaviors, such as food sharing and social grooming. Vampire bats share food with other females in their social group by regurgitating their bloodmeals to certain group members. Vampire bats groom certain group members. While social grooming has been studied, its contribution to fitness is unknown. This behavior often occurs before food sharing, possibly to identify cheats, who accept food sharing but do not share. Excluding mother-daughter interactions, social grooming and food sharing usually occurs within subgroups of social groups. These subgroups within social groups are highly associated group members of 2 to 4 and their offspring. While many studies focus on entire social groups or populations, this paper lays the groundwork for investigating whether social grooming is a mechanism for assessing whether bats will share blood meals. The proposed investigation will be conducted by producing agent-based models of vampire bat social groups. These models represent individuals that behave in essential ways like vampire bats and will allow us to characterize by emergent behavior and population-level impacts of behavior. Our goal is to determine whether blood-meal sharing can evolve given or understand of the physiology, behavior, and population structure of vampire bats. We hypothesize that vampire bats with larger subgroups and more social grooming partners will evolve via higher food sharing. We also hypothesize that multi-level selection is one of the main mechanisms driving evolution of food sharing. But in this context, we propose to investigate social grooming as a mechanism to reduce the cost of cheating at the individual level.

Introduction

Desmodus rotundus, commonly known as the Common Vampire Bat, have a complex social system that involves blood meal sharing. Part of their social complexity is their roosting and social behaviors. When roosting in caves, vampire bat populations can number into the thousands. Tree-roosting vampire bats consist of eight to twelve females along with their offspring. At night, a social group breaks into subgroups of two to four individuals in separate trees (Wilkinson 1984). Among subgroup members, females engage food sharing (Wilkinson 1984) and social grooming (Wilkinson 1985). Most bloodmeal-sharing occurs between mother and offspring whereas non-mother-daughter sharing occurs between individuals that typically associate with each other (Wilkinson 1984).

Vampire bats live exclusively on blood. Common vampire bats feed exclusively on mammals and usually on large mammals such as horses and cattle (Wilkinson 1984). Their kidneys eliminate water faster than any other mammal so that they can drink as much blood as possible while still being able to fly back to the roost (McFarland and Wimsatt 1969). They do not store energy reserves well and their highly attuned physiology also leaves them vulnerable to foraging failures (Freitas et al. 2003). Even though the estimated foraging success for adult males and females over two-years old is 93%, they can rapidly starve to death if they fail to get two consecutive blood meals (Wilkinson 1984). Indeed, it has been estimated that vampire bats will starve to death in 60 hours without a blood meal (Wilkinson 1990).

Blood meal sharing with starving roost mates can solve the problem of failing to obtain a blood meal, but it has turned out to be difficult to explain using standard theoretical approaches in behavioral ecology. One proposed mechanism is reciprocity (Wilkinson 1986). On this explanation, bats reciprocate only with bats that have shared with them in the past, but research has failed to find evidence of direct reciprocity (Schank, personal communication). Another possible mechanism is kin selection (Wilkinson 1986). Bats only share with relatives, which would then provide indirect fitness benefits. However, genetic research has found that bats in social groups, which share, are often unrelated (Wilkinson 1984; Wilkinson 1986). Thus, blood meal share among unrelated adults in vampire bat social groups remains theoretically problematic.

In an agent-based model, Schank modelled the evolution of food sharing (Work in Preparation) with the aim of developing a theoretical explanation for blood meal sharing. Modelled vampire bats began sharing five percent of their blood-meals (measured in hours to survive). Over 10,000 simulated years, vampire bats evolved to sharing 20% of their meals (measured in hours to survive) (Fig. 1a). By observing the variance of food sharing at different population levels, Schank found the main evolutionary mechanism in food-sharing percentage change is multi-level selection. In this study, multi-level selection is represented as selection at the social group-level, in which an individual resides, and on the individual level. Variance was high both between groups and within groups. Selection was mainly driven at the group-level, indicated by a significantly greater variance between-groups than within-groups (Fig. 1b). The evolutionary time scale of Schank's food sharing model supports Wilkinson's proposal that food sharing evolved 50,000 years ago, as large mammals in South America went extinct during the Pleistocene (Wilkinson 1988). Schank's finding also corroborates that multi-level selection drives the evolution of food sharing behavior (Paolucci and Conte 2007).

Connected with food sharing events is social grooming behavior. Female vampire bats groom each other throughout the day, particularly before food sharing events. Wilkinson argued this pattern could cheating (Wilkinson 1986). Cheating vampire bats take food resources stored in the social group, but do not contribute food themselves (Wilkinson 1986). In contrast to storing body fat, vampire bats may be storing resources in their social groups (Schank, Personal Communication). Assuming food accumulates in a social group, cheating vampire bats would also take resources from the social groups they inhabit. Therefore, cheating can significantly impact vampire bat social group survival, since multi-level selection is primarily driven at the group level.

Mechanisms of how social grooming could prevent cheating are unknown, though explanations have been posited. Supporting evidence indicates that established social bonds could prevent cheating behavior in vampire bats. Carter and Wilkinson exposed oxytocin to *Desmodus rotundus*, increasing the duration of food sharing and social grooming (2015). Furthermore, Wilkinson recorded food sharing occurred either with between mother and offspring, or with individuals that are found in the same tree (1984). Social grooming possibly serves to facilitate olfactory and auditory recognition and is an immediate precursor to food sharing (Wilkinson 1986).

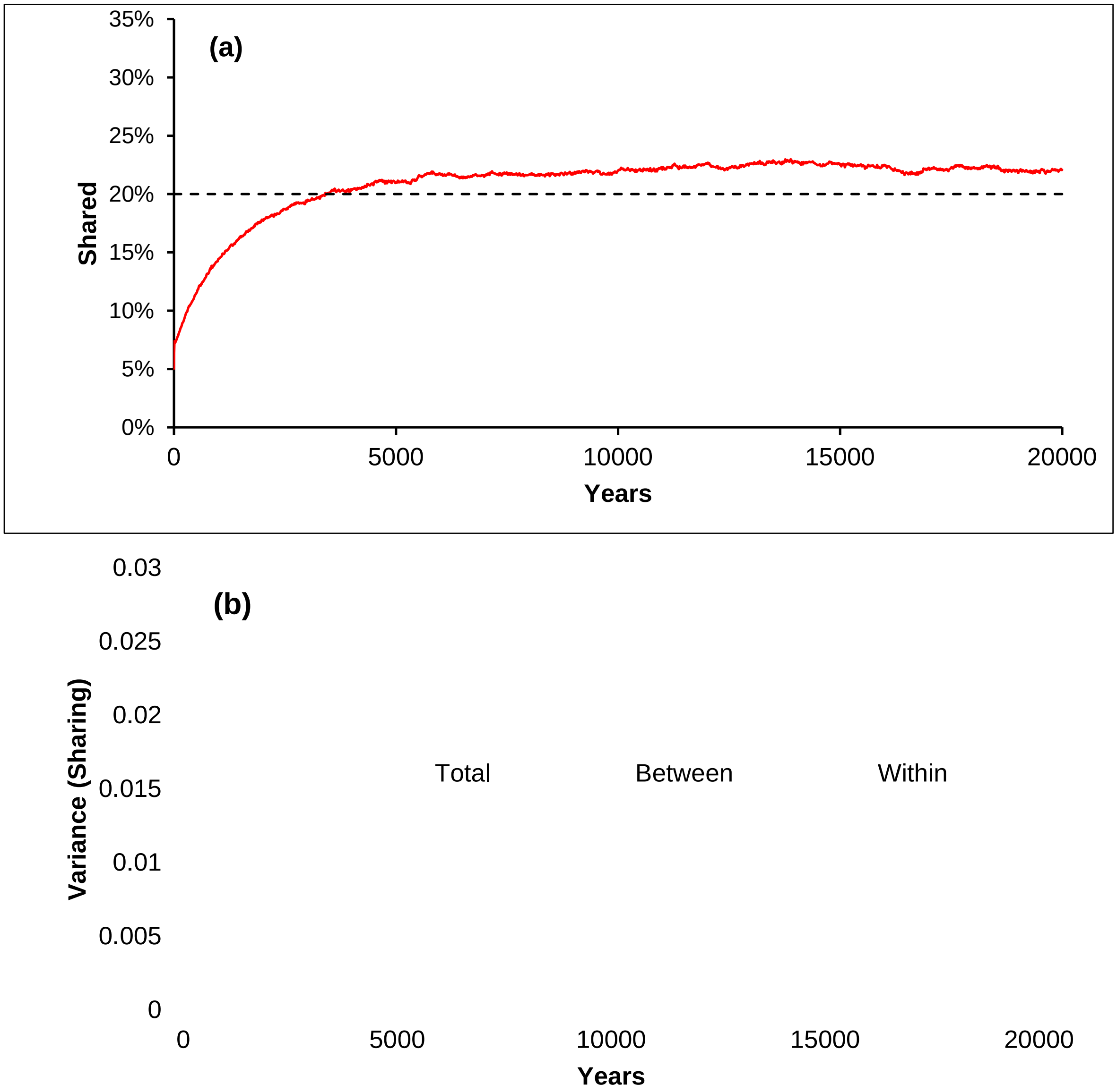

Figure 1 (Schank, Unpublished data, 2017)
a) Results of food sharing model. Vampire bats begin sharing five percent of their blood meals and evolve to 22 percent, higher than what is found by field ecologists. **b)** Results of food sharing model Variance within, between and total food sharing groups. Variance is above zero at between-group level and within-group level, indicating multi-level selection. Variance is highest between-groups, indicating selection is stronger at group level.

Previous research observed food sharing patterns of entire vampire bat groups or entire populations. Likewise, social grooming is usually observed in the whole population studied. Subgroup patterns of social grooming and food sharing have minimal research focus. This study will incorporate a scope that addresses the evolution of social behaviors in vampire bats while limited to subgroups. Our work further expands Schank's previous work on the evolution of food sharing. The previous model assumed vampire bats shared with other members indiscriminately that is, food sharing networks had full connectivity (Schank, Work in Preparation). In this model, connectivity of food sharing will be affected by social grooming connectivity.

Wilkinson claimed food sharing and social grooming behavior had a functional relationship (Wilkinson 1986). While this would be difficult to simulate, we will produce a model that attempts to include social grooming networks as part of the food sharing behavior and observe the evolutionary mechanisms. This model will produce potential mechanisms that social grooming can prevent cheats.

Methods

We will study vampire bats and their social behavior using agent-based models that simulate behavior. Agent behaviors and interactions are modelled as simple rules (e.g. conditional statements). We will describe the vampire bats and their behaviors using a meta-analysis of their ecology, ethology and physiology.

We will implement these models in MASON and MASONplus in the model (Luke, Catalin Balan, Panait, n.d.; Schank 2017). MASON and MASONplus were coded in Java, a language with relatively fast computation. Agents in this study represent individual vampire bats. We will code both individual behavior and daily events. A visual of the social groups in which vampire bats reside, will be produced by the graphical user interface of the model (Fig. 3, left).

Aspects of vampire bat ecology and physiology will be coded in the models as parameters. Specifically, we will incorporate values pertaining to hunting and starvation. Adults successfully hunt 93% of the time, and juveniles successfully hunt 67% of the time (Wilkinson 1984). Vampire bats die of starvation in 60 hours (Wilkinson 1990). This model assumes sharing events occur when vampire bats are close to starvation, around the 12-hour period. In the second stage of the model, we will incorporate social grooming as a precursor to food sharing behavior, which occurs among real vampire bats (Wilkinson 1986). Due to sparse information on reproduction patterns, intervals between reproduction will be tested at both 10 and 12 months.

Female vampire bats are philopatric, thus we assume that vampire bats in the simulation are female (Wilkinson 1985).

Our model expands Schank's work in 2019 (Work in Preparation). This study will be conducted in two steps. The first step will create grooming networks of vampire bats. Grooming networks are vampire bat groupmates, that perform social grooming with each other regularly (Fig. 4). The first model will investigate the evolution of food sharing with social grooming networks with different connectivity values. That is, we will simulate vampire bats a varying number of social group connections in their social grooming network.

The model programs the lifespan of each bat as the average life span of a vampire bat with a large standard deviation. The standard deviation is created in the model using a gaussian distribution. If a vampire bat goes without a blood meal for 60 hours, it starves to death. The individual dies and is removed from the simulation. The food that a vampire bat hunts is quantified as hours before starvation. Vampire bats have on average 60 hours of resources after every successful hunt (Wilkinson 1990). We will assume that hunting resources are normally distributed and simulate accordingly, which have implications on how the vampire bats will evolve in the model.

The maximum resources a vampire bat can gain is the highest percentile of the hunting distribution. Bats cannot accumulate resources and lose 24 units of blood resource every day. For example, if a vampire bat successfully hunted row and gained 60, they will have 60 hours on the first day. 24 hours is deducted, thus resulting in 36 hours until starvation. On the second day, the bat gains 60 hours, but she will not gain 96 hours total. She will only have 60 hours, the maximum amount a bat can store. In contrast, two consecutive, unsuccessful hunts are fatal, unless a vampire bat receives blood-meal sharing to successfully hunt a third night.

A starving bat will beg a maximum number of partners for food. The probability of an individual giving or receiving food depends on whether the two bats are connected on a social grooming network. Bloodmeal sharing is quantified as the percent of a bloodmeal a donor gives and can also be quantified as hours before starvation. The units of blood in this model are hours to survive to the next blood meal. The specific amount a donor vampire bat provides is based on a standard deviation of their blood-meal sharing percentage. E.g. if a vampire bat's sharing value is set to 10 percent, the 10 percent value is the mean, and a vampire bat may share a certain standard deviation away from the 10 percent. This normal distribution simulates mutations and creates variance of food sharing, which represents natural selection in the model.

We will start vampire bats sharing food relatively small percentage compared to percentages found in empirical research. In the model, average food shared begins at five percent and by sharing at different standard deviations during each bloodmeal sharing instance. Offspring inherit their parents average sharing percentage combined with a standard deviation. The model assumes all vampire bats are female, as they are the philopatric gender (Wilkinson 1985) and are the main performers of social interaction (Wilkinson 1984). Reproduction is asexual and occurs either 10 or 12 months, depending on the simulation.

Each vampire bat forms its own social grooming network (Fig. 3, right). The social grooming network is a subcommunity within a social group which contains a vampire bat's social grooming partners. Excluding mother-daughter connections, each network contains a unique set of randomly selected individuals in the social group. Mothers and offspring are automatically connected on their social grooming networks. Offspring inherit their parent's social grooming connections based on a standard deviation.

Model 1

Social grooming network size will be tested in two ways. Both tests will observe the evolution of food sharing from the previously described method. Social grooming connectivity is the number of groupmates, with whom a vampire social grooms occurs often.

Whether a potential donor shares food is determined by whether the donor and recipient are part of a social grooming network. Individuals connected on a social grooming network are more likely to share than unconnected bats. The probabilities of sharing while in a network or out of a network are unknown or perhaps non-existent. The correlation strength of social grooming and food sharing can be simulated by testing different probabilities in a parameter sweep. Along with food sharing, the bats will also have an evolvable social grooming connectivity size. Because we do not have specific information on social grooming network connectivity, we will apply two possible connectivity values.

Minimum Connectivity

When using minimum connectivity, the model will create a social grooming network connectivity that is greater than or equal to the minimum value. All vampire bats are connected to the minimum number of bats. This model assumption could affect the sharing behavior of the vampire bats, thus affecting survival levels. In the case where a vampire bat falls below the minimum value, the model will automatically connect it to another vampire bats. The standard deviation of the social grooming network will pass down.

Mean Connectivity

When using the mean connectivity, the model will produce vampire bats with a connectivity greater or less than the mean. The mean connectivity will not produce the exact value specified but is accurate to the hundredths place. This is an alternative assumption of how vampire bats could form their grooming networks, which contrasts with minimum connectivity by allowing a lower value than the one set.

Model 2

The second model determines ways that social grooming could prevent cheats. In model 1, social grooming networks were simulated but not social grooming events itself. Model 2 will create these instances, which can affect the evolution of the model. Social grooming networks would then measure the strength of connectivity based on social grooming frequency. The probability of social grooming will be determined by a random number. Alternatively, social grooming strength can be based on time.

Expected Results

Model 1

We expect that vampire bats will evolve food sharing from five percent to around twenty percent (12 hours of blood to survive), since we assume that starving bats will have 12 hours left once donors share. This provides the starving bat at least 24 hours to survive until the next foraging bout. Because this model is based on Schank's prior model, it is likely the variance measured in vampire bats social groups will likely be found highest between social groups and to some extent found within social groups, reflecting Schank's prior results (Work in Preparation). Likewise, the variance of social group network size will likely have the highest variance between groups. Within social group variance may have a non-zero variance value. The social grooming network sizes will likely evolve to a stable value. Whether, social grooming networks will expand to full connectivity is not determined.

This hypothesis is based on the scope of the experiment and previous research. Food sharing models observe variances between within and total social groups (Schank, Work in Preparation) and social grooming instances are tied to food sharing events in this model. Thus, the selective mechanism of social grooming is connected to food sharing. How social grooming networks truly relate to food sharing networks is unknown. Empirical research does not explicitly state the total number of vampire bats that socially groom, aside from stating that it only occurs among subgroup members. However, individuals could be part of several subgroups at a time, which makes the total number of group members with whom individuals socially groom or share food, are vague. There may be a stable value at which social grooming networks lie. Empirical work indicates that not all social group members socially groom or food share with each other (Wilkinson 1984; Carter and Wilkinson 2012). The results of this model may produce partial or full social grooming network connectivity.

A saturated connectivity level occurs when an individual can share with all members of its subgroup. This value may be detrimental when individuals are also connected with cheats. Partial connectivity, where vampire bats create a subgroup of those with whom they share, may also be a viable result. The vampire bat donors partitioned the burden of donating 20 percent bloodmeals in relatively equal amounts to their recipient (Schank, Unpublished data, 2017).

Model 2

The second model will be based on the survival rate of the vampire bat populations. The system will be stressed until the populations go extinct. The type of stress monitored and the point at which the vampire bats go extinct will determine which possible mechanisms are most effectively used for social grooming preventing cheats. The stress could be based on the influx of cheats into social groups, with or without a waiting period for cheating. This could also be simulated by connectivity strength, wherein vampire bats must perform significant amounts of grooming to benefit from sharing.

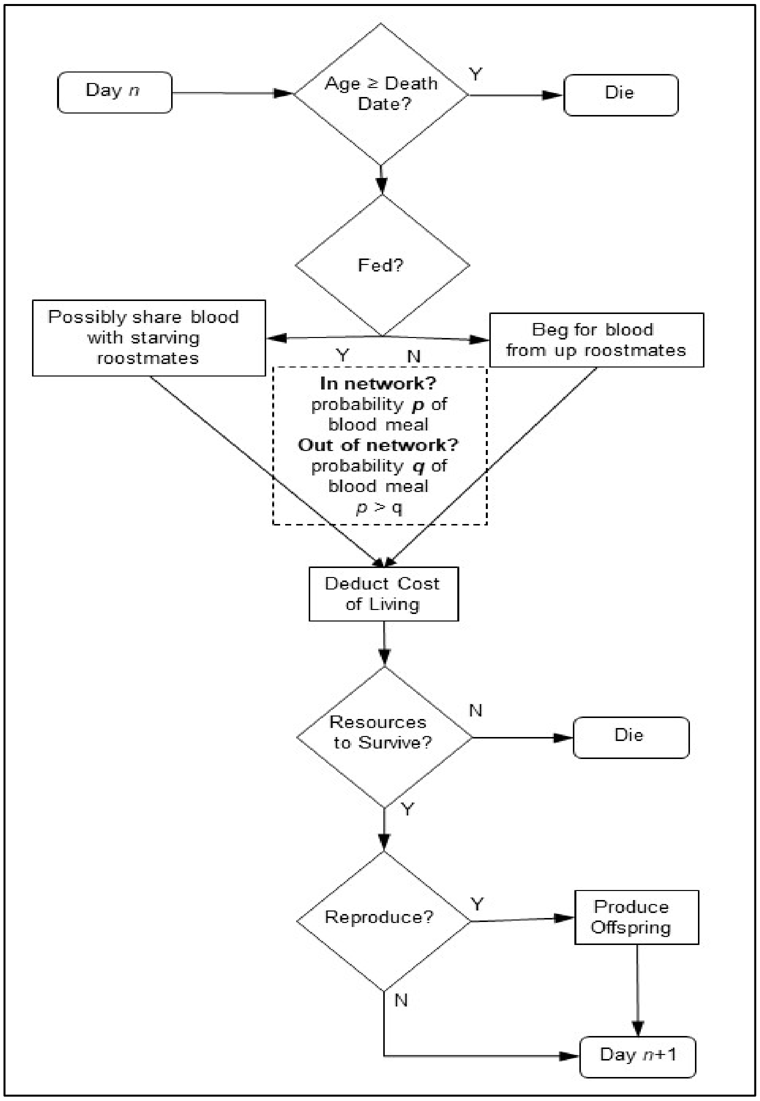

Figure 4
Daily event diagram of vampire bat behavior. If vampire bats are older than death date, die. If fed, the vampire bat might share If not fed, beg max number of vampire bats. If connected, sharing or receiving food is based on probability *p*. If not connected sharing or receiving based on probability *q*. Deduct daily cost of living 24 units of food. If resources are less than 0, die If resources over 0 and time since last gestation is 10 or 12 months, reproduce.

Discussion

The variance of food sharing determines which form of natural selection is occurring in vampire bats. For the first model, we assume multi-level selection will drive the change in food sharing. Previous research corroborates this result, particularly Schank’s model (Work in Preparation), upon which this research is based. Previous results indicate that the group level variance is the main level at which selection occurs with small variance levels within group selection (Schank, Work in Preparation). The social grooming network will increase possibly through variance found between groups and within groups as well.

This research also predicts the stable size for social grooming networks. Models with weak low standards for social grooming connectivity or having low prerequisites for sharing against cheating likely will have partial connectivity. Partial connectivity would limit the exposure of cheating bats in the social grooming network. Social groups may have high or fully saturated social grooming networks. This saturation is sustainable if vampire bats have no cheats or have strong preventive mechanisms (e.g. social grooming, waiting periods before individuals initiate sharing) in place to prevent cheating. Vampire bats represent cooperative societies. In all such systems, cheating is a latent possibility.

Applied to game theory and perhaps human systems, these results can indicate stable numbers of individuals with whom to cooperate. Cooperative systems often prevent cheating through retaliation, which requires energetic expense for cooperative members (Hamilton 1970). Social grooming as a deterrent or a requirement for receiving the benefits of cooperative systems ensures that shared resources are received by cooperating members. Of course, cheating in social grooming may exist. These social grooming cheats participate in the grooming, invalidating the notion that social grooming indicates cooperative behavior. These grooming cheats' ability to gain benefits depends on the relative densities of grooming cheats and cooperative groomers. When a significant number of grooming cheats occur in the population, the assumption that social grooming indicates a cooperative nature is obsoleted.

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