Social uncertainty influences the optimal balance of quantity and quality of cooperative relationships

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Data Availability
NetLogo and R scripts and supporting data can be found at https://github.com/anonymousscientist8/social-bet-hedging (https://doi.org/10.5281/zenodo.17058021) with an additional large dataset used to determine average roost capacity is found at https://doi.org/10.5281/zenodo.15633664.

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We declare no competing interests.

Declaration of AI use
ChatGPT 3.5 and 4.0 was used to expedite writing chunks of NetLogo and R code, but AI did not contribute ideas or influence decisions or approaches to the coding. AI was not used during writing.

ABSTRACT

Many group-living animals develop and maintain stable affiliative social relationships. These 'social bonds' can benefit survival and reproduction, but they require significant investments of time and energy. How should individuals allocate those investments towards building new relationships (*"diversifying"*) versus maintaining existing ones (*"focusing"*)? The 'social bet-hedging' hypothesis states that conditions of greater social certainty (more reliable partner availability) favour greater "focusing", whereas conditions of social *uncertainty* favour "diversifying". This hypothesis is consistent with empirical findings in vampire bats, yet support from agent-based models is mixed. Here, we used an agent-based model to test the relative reproductive success of different "social-networking strategies" in vampire bats under conditions of greater or lower social uncertainty. To manipulate social uncertainty, we minimized or maximized roost-switching rates across simulations with realistic patterns of foraging, social behaviour, ageing, reproduction, and death. Virtual bats inherited one of six social-networking strategies, which varied in allocation of allogrooming across partners, from more focusing to more diversifying. We show that, under a range of conditions, greater social uncertainty favours diversifying strategies that invest relatively more in relationship quantity. Balancing the benefits of focusing and diversifying attention across social partners may be an important yet underappreciated factor explaining social network structure.

INTRODUCTION

In many socially complex birds and mammals, the health, survival, and reproductive success of individuals can depend on the *quantity* and *quality* of their affiliative or cooperative relationships (1,2). However, developing and maintaining cooperative relationships can require significant investments of time and energy. For example, female vampire bats (*Desmodus rotundus*) that are unrelated and unfamiliar can form social bonds that promote reciprocal helping in the form of regurgitated donations of food when one partner is starving (3). The bats develop these high-investment food-sharing relationships through an escalation of low-investment reciprocal allogrooming (3). Yet even after they establish reciprocal food-sharing relationships, female vampires continue to spend 5% of their active time allogrooming (4). Across many other group-living mammals and birds, individuals form and maintain similar cooperative relationships or 'social bonds' by allogrooming or allopreening (5).

However, many social animals face a necessary trade-off: individuals can invest each unit of time and energy in either developing new supportive relationships ('*diversifying'*) or maintaining existing ones (*'focusing'*). Although both the quantity and quality of these relationships are important, there are likely to be diminishing returns on investments in both forms of social integration. One can invest too little time across too many partners or too much time in too few partners, and the optimal balance of diversifying or focusing may vary across circumstances. A major open question in animal social behaviour is how individuals balance these social needs under different social and ecological conditions (6).

One hypothesis, originally called "social bet-hedging", states that, all else being equal, conditions of greater social uncertainty (where partner availability is less reliable) should favour relatively more diversifying (7). For instance, even if one or two social partners provide the greatest cooperative returns per unit of cooperative investment, one should not focus all investments in only those partners if they are often unavailable to help or provide benefits ("don't put all your eggs in one basket"). Note that this "social bet-hedging" hypothesis is a different concept than "altruistic bet-hedging" which is the hypothesis that altruistic helping is adaptive because it decreases the variance in reproductive success of genetic relatives in unpredictable environments (8-10). The social bet-hedging hypothesis is that individuals can reduce the variance in cooperative returns that come from cooperative investments (reciprocal help or byproduct benefits) by diversifying those investments across more partners in socially unpredictable environments. This process could apply at evolutionary or developmental timescales. Over evolutionary time, conditions of greater social uncertainty might select for individuals that are more likely to diversify cooperative investments across more partners. Within a lifetime, animals might respond to greater social uncertainty by shifting away from focusing their cooperative investments in the best partners towards diversifying investments across more partners. In either case, a key prediction is that social uncertainty should increase the success of diversifying strategies. In support of this prediction, experiments in food-sharing vampire bats showed that females that diversified their food-sharing investments by helping more nonkin in past years, did not typically receive more food donations, but they did cope better with the temporary removal of a major food-sharing partner, such as a mother or daughter (7). This finding is consistent with the idea that helping nonkin allows female vampire bats to build a wider social support network than would be possible from reciprocal helping among only kin (3,7).

However, theoretical support for the evolution of diversifying under social uncertainty has been mixed. One recent agent-based modelling study based on vampire bats revealed a trade-off between diversifying and focusing (11). The virtual bats in the simulations evolved a tendency to diversify their food-sharing network by building new relationships, and this diversifying was balanced against the need to also strengthen and focus cooperative investments in specific partners. However, the study was not designed to address if or how this trade-off was influenced by social uncertainty.

Another agent-based model found that, contrary to the prediction of social bet-hedging, greater social uncertainty favoured “focused” strategies (12). In this model, diversifying was beneficial for adult virtual bats under conditions of social uncertainty, but it was often fatal for juveniles, and only “focused” strategies allowed juvenile virtual bats to build new food-sharing relationships fast enough to survive (12). However, this apparent contradiction is at least partially semantic because the successful “focused” strategies survived *because they allowed juvenile bats to build new relationships*. That is, “focused strategies” were successful due to achieving an optimal balance of focusing and diversifying. An even more focused strategy that did not build new relationships beyond the mother would clearly fail. Furthermore, the contradiction with the social bet-hedging hypothesis was caused by a form of antagonistic pleiotropy that has not been observed in real vampire bats. In this model, juveniles that did not focus their helping starved to death, but empirical observations suggest that juvenile vampire bats experience extended maternal care that allows them to build new nonkin relationships gradually (4), and they can use low-cost allogrooming to ‘test the waters’ with multiple potential new partners (3)—factors missing from the model (12). It therefore remains unclear whether the logic of social bet-hedging in vampire bats holds under socially and ecologically realistic assumptions.

Here, we addressed this gap by creating an agent-based model of social-bond formation in vampire bats that includes empirically derived patterns of foraging success, roost switching, allogrooming, food sharing, maternal care, growth, weight loss, ageing, reproduction, and death. Our model confirms the logic of social bet-hedging. It shows that social uncertainty tends to push the optimal social-networking strategy towards cooperative relationship quantity at the expense of strengthening relationship quality. It also illustrates how and why social-networking strategies must avoid being too focused or too diversified.

METHODS

Model overview

In the model, virtual bats develop directed *relationship scores*, ranging from 0 to 100%, which define social preferences between all individuals, influencing which partners each actor grooms, feeds, and solicits for food donations when in need. Receiving allogrooming or food donations improves the recipient's relationship score to the giver. Virtual bats inherit one of six social-networking strategies which vary from most diversified to most focused (Figure 1). To test if and how social uncertainty changes the relative success of each strategy, we adjusted the bats' movements between roosts (roost-switching rate), which is the key factor in creating social unpredictability in vampire bats (13,14). We ran simulations with *rare roost switching* where virtual bats would switch only when their roost was "full", with *empirical roost switching* derived from field studies (13,14), or with *maximal roost switching* where bats switched roosts every night. Comparing these simulations estimates allowed us to determine the causal effect of social uncertainty on the reproductive success of different social-networking strategies.

To assess the stability of this causal effect, we measured how it changed with the tendency for virtual bats to co-roost with more familiar bats (*co-roosting ingroup bias*) and to feed more familiar bats (*food-sharing ingroup bias*). "Low" *co-roosting ingroup bias* means virtual bats switched into any available roost with at least one familiar partner, whereas "high" means they preferentially select the roost containing the highest sum of relationship scores. Similarly, a "high" *food-sharing ingroup bias* means a stronger relationship score is required to donate food relative to a "low" or "medium" bias. Combinations of these levels of roost switching and ingroup biases create 18 plausible scenarios, each simulated 1,000 times (18,000 simulations). We ran each simulation for 200 years (about 240 generations), a period in which 75% of surviving populations had reached strategy fixation.

Model details

Creation of agents

We used NetLogo to create an agent-based model that simulated the foraging, roost switching, allogrooming, and food-sharing of vampire bats. In the model, 24 unfamiliar virtual bats are generated into one of 12 roosts, with equal numbers of bats using one of 6 social-networking strategies (see Allogrooming Model below). After startup, all bats proceed through a series of sub-models every time step (day). Each sub-model (e.g. foraging) is completed by all virtual bats before any virtual bat proceeds to the next sub-model (e.g. roost switching).

Foraging

Each simulated day, virtual bats searched for food if they were at least 120 days old, the approximate age vampire bats first feed on blood (15). We used estimates from empirical studies (15-19) to estimate age-dependent probability of successfully feeding (Supplementary Information (SI), Fig. S1), weight gain and loss over time (SI, Fig. S2), and time until starvation (SI, Fig. S3). Foraging bats have a probability of being killed by predation of 0.03% per day, which allows an average of 17.3% of virtual bats to survive to the 16-year maximum lifespan for the virtual bats (the maximum observed lifespans of a female vampire bat in the wild (20)), ignoring any deaths from starvation.

Roost switching

After foraging, virtual bats older than 10 months move to a roost, deciding whether to return to the same roost as before foraging or move to a new roost. Whether virtual bats switch roosts is determined by the time since last switch, derived from empirical observations of vampire bat roost-switching rates (13,14,16). See Hartman et al, 2024 (14) for more details.

To determine how roost-switching rates influence the success of each allogrooming strategy, we compared the effect of empirical rates of roost switching to the minimum and maximum roost switching rate. We tested three sets of scenarios: bats switch only when their current roost is full (6 adult bats, rare roost switching); bats switch roosts at the empirically observed rate (empirical roost switching); and bats switch roosts every day, which is the maximum amount (maximal roost switching).

When visiting a roost, bats decided to stay there by assessing the sum of the 'relationship scores' for bats in that roost. Each *relationship score* is a percentage that determines how much each bat prefers every other bat, ranging from 0% (unfamiliar) to 100% (closest possible relationship). These relationship scores are directed network edges that are not necessarily symmetric, and they are updated by experiences of allogrooming and food sharing as described below. A virtual bat will stay at a given roost for that day if the sum of the relationship scores with all other bats currently occupying that roost is greater than a threshold called the **"*co-roosting ingroup bias*",** which defines how much bats prefer to co-roost with more familiar partners (a longer history of allogrooming and food sharing) rather than less familiar partners. If the co-roosting ingroup bias threshold is not met, the bat will continue to search roosts until it finds a roost that does meet that threshold. If no roost has a sufficient sum of relationship scores, the virtual bat moves to whichever roost had the highest relationship score.

Virtual juvenile bats younger than 4 months will die immediately if their mother dies but will otherwise follow their mother's movements. Since juveniles first feed on blood at 4 months and are weaned at 10 months (15), virtual bats of ages 4 to 10 months will follow their mother to a roost whenever possible, but can move independently if their mother dies, following the same rules for adults described above.

To estimate realized roost-switching rates across simulations and scenarios, we estimated the average days per switch for all bats starting after the first generation of bats all died (16 years after simulation start), by sampling 5 simulations per scenario (18 scenarios with different levels of roost switching and ingroup biases) at time step 10,000.

Allogrooming

The allocation of allogrooming across roostmates defined whether bats used a more focusing or more diversifying social-networking strategy. Although food sharing is relatively rare and occurs only when recipients are in dire need, female vampire bats spend about 5% of their awake time allogrooming (21), and allogrooming seems to allow bats to form and maintain food-sharing relationships (3).

After deciding where to roost, virtual bats allocate allogrooming across partners using one of six genetically-inherited social-networking strategies (Fig.1), listed here from least to most focused:

1. ***Diversifying 3:*** groom up to 12 bats per day at equal rates
2. ***Diversifying 2:*** groom up to 8 bats per day at equal rates
3. ***Diversifying 1:*** groom up to 4 bats per day at equal rates

4. ***Focusing 1:*** groom up to 12 bats per day at highly skewed rates (see SI Eq.5)
5. ***Focusing 2:*** groom up to 8 bats per day at highly skewed rates
6. ***Focusing 3:*** groom up to 4 bats per day at highly skewed rates

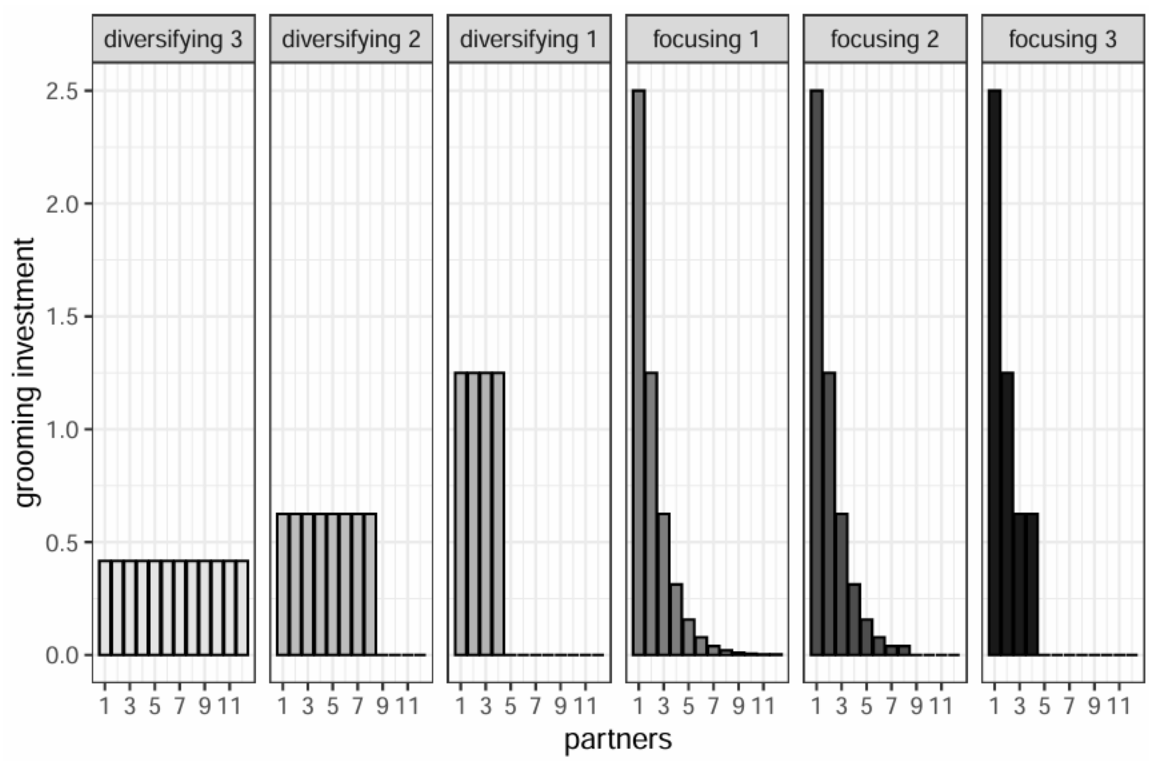

Figure 1. Allocation of allogrooming across preferred partners according to six social-networking strategies. Diversifying strategies uniformly allocate allogrooming across 12, 8, or 4 partners (left to right). Focusing strategies disproportionately allocate allogrooming towards top partners across 12, 8, and 4 partners (left to right).

We created these strategies to capture two dimensions of greater diversifying: investing in more partners and allocating investments more equitably across those partners. Diversifying strategies 1 to 3 allocate allogrooming at equal rates across expanding numbers of recipients. Focusing strategies 1 to 3 allocate allogrooming at highly skewed (unequal) rates across a shrinking number of maximum recipients, with the skew based on relationship scores, and with each partner in order given half the amount of allogrooming as the next most preferred partner until 100% is reached (Fig. 1). Allogrooming improves a recipient's relationship score to the groomer, but the total amount a groomer can improve recipients' relationship scores via allogrooming is 5% per day spread across all recipients. By increasing relationship scores, allogrooming influences food sharing.

Food Sharing

A virtual bat that failed to get blood while foraging asks each of its roostmates for food donations in order of relationship score. All virtual bats that successfully foraged that night could donate up to 2% of their body weight across multiple donation bouts of 0.5% each (each donation bout can be given to only one individual). The 2% value was derived from the amount of food sharing estimated from the average total daily donation time towards fasted bats (22,23) and the average amount weight of blood transferred per minute sharing food (24). The percentage probability that a potential donor gives a donation to a potential recipient depends on the relationship score from the potential donor to the potential recipient (see SI for details), and a **'*food-sharing ingroup bias*,'** which controls the average relationship score needed to donate to partners. When food-sharing ingroup bias is higher, a stronger relationship score is required to donate food. Food donations increase the receiving bat's relationship score to the donating bat.

Maternal care

To simulate the priority of females feeding their juvenile offspring over all others, all bats younger than 10 months ask for food first, followed by bats between 10 months old and 2 years old, then all bats older than 2 years old, which ensures that dependent juveniles get priority access to food donations from their mothers. Additionally, bats younger than 10 months that request food from their mothers receive food via lactation, feeding them until full or until the mother has given up to 11% of her body weight (sustaining juveniles without giving up a full day's worth of food).

Death and birth

If any bat reaches zero hours to starvation after the foraging or food-sharing sub-model, it dies and is removed from the simulation. Any bat 16 years of age or older is also removed (20). Surviving bats reproduce once every 10 months after reaching reproductive maturity at the age of 12 months (25). Newborn bats (age 0) inherit the allogrooming strategy of the mother, are completely fed at birth, and have relationship scores of zero with all other bats in the system except for their mother, which is set to the maximum (100%) in both directions.

For more information on this agent-based model or its sub-models, see the Overview, Design Concepts and Details (ODD) Protocol within the Supplemental Information (SI).

RESULTS

By manipulating roost switching among virtual bats, we shifted the social environment from (1) stable groups with rare roost switching (~0.004 to 0.04 switches/day) to (2) unstable subgroups with empirical rates of roost switching (~0.5 to 0.8 switches/day), observed in Costa Rican field studies (13,14), and to (3) maximally unstable subgroups with the maximal roost switching rate (1 switch/day). As expected by social bet-hedging, this increase in social uncertainty favoured the reproductive success of diversifying social-networking strategies, wherein virtual vampire bats spread allogrooming investments more evenly across more partners each night.

The optimal level of diversifying differed across social conditions: we observed that strategies could be either too focused or too diversified (Fig. 2). However, across all observed conditions, greater social uncertainty caused the optimal level of diversifying to evolve from more focusing towards more diversifying (Fig. 2). The overall effect was that social uncertainty selected for virtual bats that groomed more partners per night (Fig. 3).

In our simulations, allogrooming investments influenced the structure of food-sharing networks, which impacted both individual survival and population extinction. Conditions of social uncertainty could lead entire populations to extinction if virtual vampire bats focused their food sharing in too few partners (Fig. 3). For example, populations consistently went extinct if virtual bats switched roosts at maximal rates and only shared food within their strongest relationships (high food-sharing ingroup bias, Fig 3). In other words, social certainty is required for populations with high food-sharing ingroup bias to persist. The scenarios of highest population survival involved frequent roost switching with low ingroup biases for co-roosting and food sharing (Fig. 3). Under these conditions, the best strategy was the second-most diversified (Fig. 2), allocating grooming equally across 8 partners. This strategy outcompeted those which groomed either more or fewer partners (Fig. 2). Under the opposite scenario of rare roost switching and high ingroup biases, the best strategy was the most focused (Fig. 2): allocating grooming in a skewed distribution across only 4 partners (Fig. 1). These findings demonstrate that the optimal balance of diversifying and focusing depends on both the social stability (movement rates) and the social traits (ingroup biases) in the population.

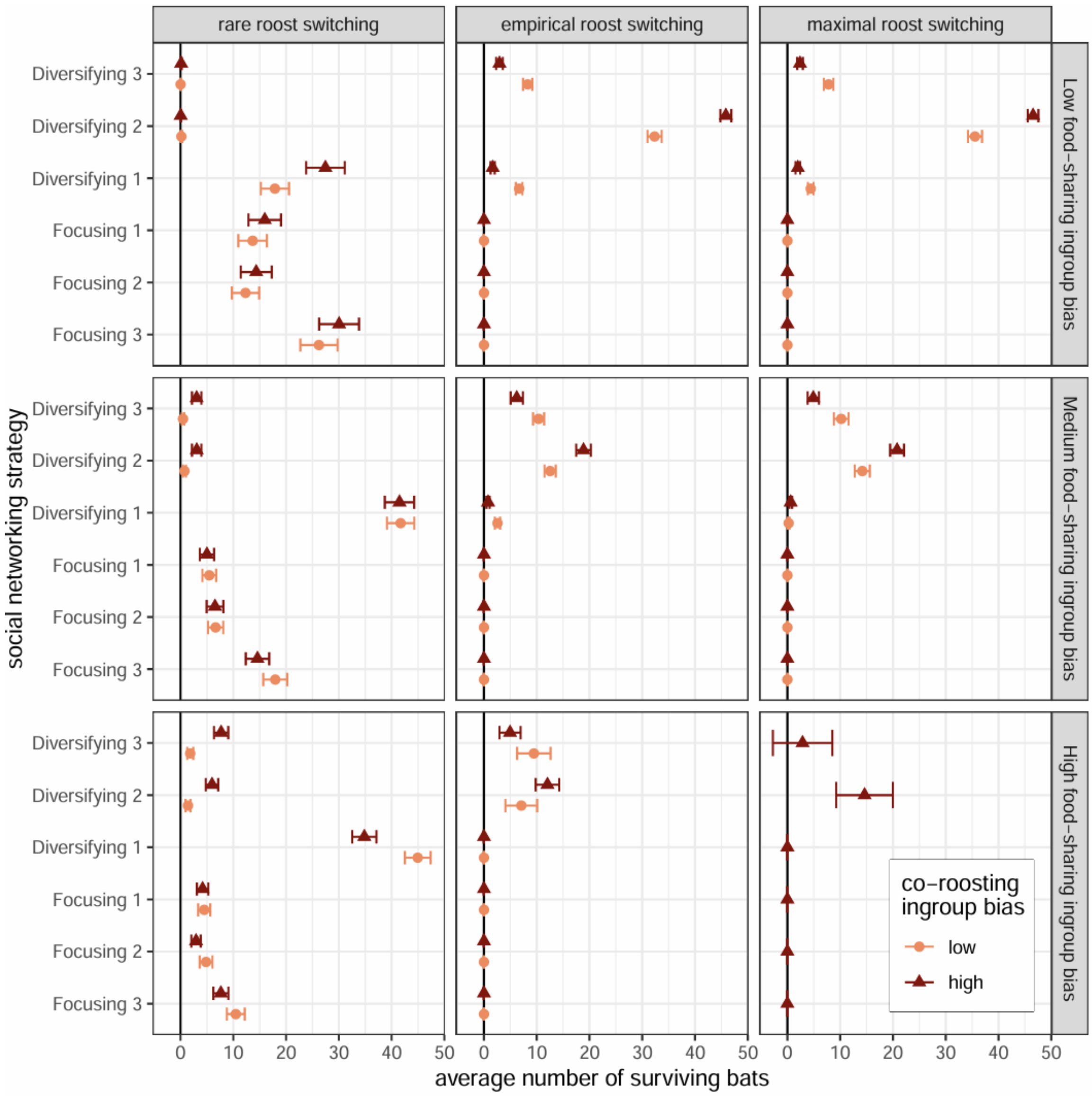

Figure 2. Greater social uncertainty influences optimal amount of diversifying of social investments. Columns show increasing roost switching from left to right. Social-networking strategies are listed top to bottom from most diversified to most focused. *Diversifying 3:* groom up to 12 recipients per day equally*; Diversifying 2*: same with 8 recipients*; Diversifying 1:* same with 4 recipients*; Focusing 1:* groom up to 12 recipients per day with strong bias by relationship score*; Focusing 2:* same with 8 recipients*; Focusing 3:* same with 4 recipients. Means and standard errors for number of surviving bats of each

strategy are shown for both levels of co-roosting ingroup bias (colours and shapes). Rows show levels of food-sharing ingroup bias.

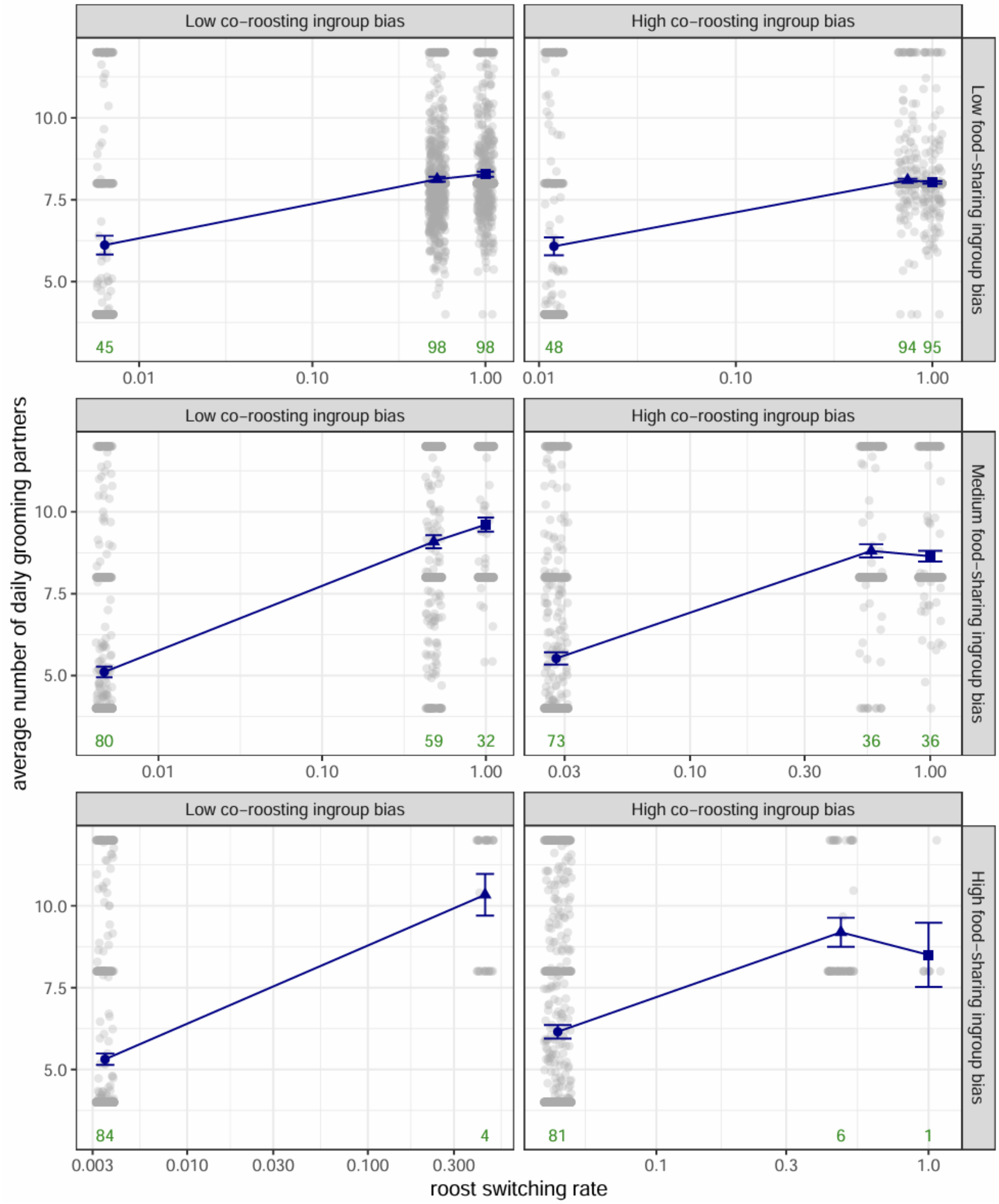

Figure 3. Rare roost switching selects for bats that groom fewer roostmates. Mean (with 95% confidence intervals) number of grooming partners per day for surviving bats is lower when roost switching is *rare* (circle) relative to *empirical* (triangle) and *maximum* rates

(square). Small green numbers just above the x-axis are the percentages of populations that survived. The x-axis is plotted on a $\log_{10}$ scale.

DISCUSSION

Our agent-based model confirms the logic of the social bet-hedging hypothesis. An optimal social-networking strategy must balance the trade-off between investing in the quantity versus the quality of social relationships. Stable social environments with greater social *certainty* selected for bats that focused their allogrooming relationships, whereas greater social *uncertainty* selected for diversifying, causing bats to have more allogrooming relationships. More focused social-networking strategies could dominate when group composition was more stable, but they could not survive with too much social uncertainty.

An individual's connectedness to a social network impacts its individual success (2), but individuals are not passive victims of their social networks—they can actively influence their own network connectedness through "social-networking strategies" that determine how to allocate time and energy across partners. The limited time and energy animals have for socializing can be put towards either strengthening existing social bonds (focusing) or choosing or building new ones (diversifying), and the optimal balance between diversifying and focusing is shaped by social uncertainty (or "unpredictability").

Although we focused here on individual movement, social uncertainty is influenced by multiple other factors including demography, predation, movement, and resource abundance. Our findings are therefore consistent with the recently developed "Adaptive Relationships Framework" (6), which posits that "local" ecological pressures that impact individuals create a need for focusing, whereas pressures that impact all group members necessitate diversifying. In this case, unsuccessful foraging creates a need for individuals to invest in strong social bonds which can lead to food sharing, whereas uncertainty in the social environment impacts all individuals and encourages diversifying investments to a broader network of partners.

One possibility to explore further is whether roost switching in vampire bats is not only a cause of diversifying but also a consequence of it. One way for an individual to socially diversify is to move more often between sub-groups. However, because such movements create social uncertainty, the result might be a positive feedback loop where more diversifying increases social uncertainty, which favours more diversifying.

This idea begs another question. Our model was based on studies of vampire bats in Costa Rica by Wilkinson (13,16,25), but observed group sizes, roost-switching rates, and social dynamics of vampire bats appear to vary across their range (13,20,26). What prevents the vampire bats in Wilkinson's study from forming one large stable group with all partners available on every day? It remains unclear which of many possible factors most encourage fission-fusion dynamics and switching among roost trees in vampire bats and in bats more generally (reviewed by (27)).

Our model focused on the process of social bet-hedging over evolutionary time, and the social-networking strategies in our simulations were therefore fixed. In this case, fluctuations in social uncertainty over time could increase variation in social-networking strategies across individuals, because both diversifying and focusing strategies might thrive under different conditions over time. On the other hand, if social-networking strategies are not fixed, then fluctuations in social uncertainty could favour the evolution of more flexible strategies where individuals evolve the capacity to adjust their social-networking strategies to recent or local social conditions. That is, animals might attempt to diversify their relationships in response to cues of greater social uncertainty. This hypothesis is consistent with increasing evidence from a diversity of species—including wire-tailed manakins (*Pipra filicauda*) (28), great tits (*Parus major*) (29), rhesus macaques (*Macaca mulatta*) (30,31), chacma baboons (*Papio ursinus*) (32), and humans (*Homo sapiens*) (33)—that individuals respond to changes in the social environment such as the loss of partners by changing their social networking. The trade-off between the benefits of focusing on one's best relationships and the benefits of diversifying attention across partners to develop new relationships might be an important yet still underappreciated factor explaining how animal social network structure emerges from individual behaviour.

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Supplementary Information (SI)

OVERVIEW, DESIGN CONCEPTS, AND DETAILS (ODD) PROTOCOL

1. **Purpose**

   The model is designed to explore how social uncertainty, in the form of variation in roost switching rate, influences the evolution of more "focusing" or "diversifying" social-networking strategies (i.e. investment into quality and quantity of relationships, respectively) under a realistic range of conditions for the common vampire bat (*Desmodus rotundus*).

2. **Entities, state variables, and scales**

   The model has two types of entities: mobile vampire bat agents and 48 stationary, square patches. The patches are arranged in an 8 x 6 grid and are grouped into 12 2 x 2 square patch group. Patches have one state variable: roost number, which is shared between all patches in the same 2 x 2 square (visualized by alternating colours), which represents distinct roosts. The number of bats occupying a roost (any patch with a particular roost number) is also kept track of.

   The vampire bat agents have multiple state variables:

   a. ID: A number unique to each bat in a simulation.
   b. Relation: a vector of relationship scores (see Allogrooming Sub-Model) representing how familiar bats are with each other. Influences the probability that a bat chooses to share food with other vampire bat agents (with more familiar bats being more willing to share food, see Food Sharing Sub-Model), the order in which other vampire bats are solicited for food (from greatest to smallest, see Food Sharing Sub-Model), the order in which other vampire bat agents are groomed (from greatest relationship to smallest relationship, see Allogrooming Sub-Model), and the probability of moving to roosts occupied by other vampire bats (more likely to visit roosts with higher total relationship score between all bats occupying that roost, see Roost Switching Sub-Model). Relationship scores are arranged in ascending order based on the ID number of all bats currently alive the simulation, updating when bats die or are born. Relationship scores range from 0% (completely unfamiliar) to 100% (max familiarity), and are non-symmetric. That is, bat a's relationship to bat b is not necessarily the same as bat b's relationship towards bat a. Each relationship score models a virtual vampire bat's preference towards another virtual bat.
   c. Age: How many ticks (representing days) a bat has been alive. This influences probability of successfully finding food (see Foraging Sub-Model) and order in which food is received, with bats younger than 120 ticks receiving food first, then bats between 120 ticks and 300 ticks, then bats older than 300 ticks (see Food Sharing Sub-Model). It also dictates the maximum weight of the bat, influencing how much bats weigh alongside foraging success rate and, subsequently, weight percentage and time until starvation. Finally, age dictates whether a bat may give birth or not, which occurs every 10 months (300 ticks) if the bat is greater than 1 year old (365 ticks)
   d. Fed: Whether a bat fed or not, which is determined by an age-dependent probability of successfully foraging for food. Also influences the actual weight and weight percentage of the virtual bat (see Foraging Sub-Model).
   e. Mother: The ID of the mother of the child (see Birth Sub-Model).

f. Child: The ID of the most recently born child from the bat.
g. Last Switch: The number of days (ticks) since last switch, which influences roost-switching probability for that day (1).
h. Strategy: Whether bats use Diversifying 3, Diversifying 2, Diversifying 1, Focusing 1, Focusing 2, or Focusing 3 as their investment strategy (see Allogrooming Sub-Model).

Vampire bats occupy the centre of each patch, so the position of the bats are represented in discrete units. Roost number (which roost is being occupied) affects the behaviour of the virtual bats, rather than specific position. The model is not spatially explicit, but is temporally explicit. All Sub-Models run sequentially on each tick such that all bats must complete a prior Sub-Model before the next is completed. The simulation runs for 73,000 ticks (200 years), or until the population goes extinct, with the global environment keeping track of days passed and the number of living bats. The number of bats in the system is dynamic, starting out with 4 bats using each of the 6 strategies (see Initialization), but changing with birth and death thereafter. The simulation ends if there are no bats left in the simulation, and the maximum number of bats is limited by a roost occupancy limit, set to 6 for all run simulations, which dictates the number of adult virtual bats that can occupy a roost at a time (see Roost Switching Sub-Model).

3. Process Overview and Scheduling

Unless otherwise stated, all bats in random order perform each sub-model in the same sequence as listed below, and each sub-model must be completed by every virtual bat before moving onto the next sub-model. Virtual bats start off each tick foraging for food (Foraging Sub-Model). Afterwards, those who did not find food and who have less or equal to 0 hours until starvation die and are removed from the system (Death Sub-Model). Bats then decide where to roost, starting with the adults (Roost Switching Sub-Model), then all bats with an age of less than 300 ticks. Bats then build relationships via allogrooming (Allogrooming Sub-Model), then ask for food, with virtual bats less than 120 ticks getting to request food first, then virtual bats between 120 and 300 ticks, and finally virtual bats older than 300 ticks (Food Sharing Sub-Model). There is then a second check for starvation (Death Sub-Model). Surviving bats may give birth afterwards, passing on their social-networking (allogrooming) strategy (Birth Sub-Model). The model then ages the bats by one tick, counts the number of surviving bats using each strategy, stops the model if 200 years (73,000 ticks) have passed or there are no bats in the simulation left.

4. Basic Principles

The *basic principle* being tested by this model is the social bet-hedging hypothesis, which states that, all else being equal, as social uncertainty (or, how unpredictable the availability or success of partners is) increases, then individuals or populations will be more likely to diversify investment over time (invest in quantity of relationships) rather than focus investment (invest in quality of relationships) given the same amount of time to invest in relationships (2).

To test this hypothesis, we manipulated a simulation-wide average roost-switching rate, dictating how often individuals decide to switch roost and, therefore, determine the likelihood that a familiar partner will be available for prolonged periods of time.

Roost-switching rate can be set to occur at empirical rate, but can range anywhere from switching every day to only switching roosts when a roost was full (based on a roost-capacity limit which defines how many adults can occupy a roost at a time; a limit of 6 was used for the study), thus allowing for direct control over social uncertainty. We also included various genetically-determined social-networking strategies in the form of variation in the level of focusing or diversifying in daily allogrooming time. Diversifying bats invest equally in all selected partners, and focusing bats invest preferentially in familiar bats (see Allogrooming Sub-Model). Additionally, there is more variation in level of diversification in social-networking strategy resulting from how many virtual bats investment is split between (see Allogrooming Sub-Model). These strategies are passed down from mother to child. By monitoring the number of bats using each strategy over a prolonged period (200 years in the study) with various levels of roost switching (empirical and both extremes in the study), we could determine how social uncertainty influences diversification in social-networking strategy, controlling all other influences,

In addition, we tried to emulate realistic birth rates, growth, foraging, roost switching, grooming, food sharing, death, and maternal care to test this hypothesis under reasonably realistic conditions (see appropriate sub-models). Further, to test the robustness of the model, we altered simulation-wide “food-sharing ingroup bias” (determines how familiar bats need to be to share food reliably, see Food Sharing Sub-Model) as well as simulation-wide “roostmate ingroup bias” (determines how likely bats are to choose to roost with more familiar bats, see Roost-Switching Sub-Model).

The virtual bats do not *adapt* their allogrooming strategy within their lifetime, rather, we look at how the population evolves. Still behaviour does change in relation to their environment depending on relationship scores, both their own and others. Bats start out completely dependent on their mother, having only that maximized relationship. As they groom (and eventually, share food), they improve relationship scores with other bats, influencing others to invest in them back. This causes agents to begin to rely on a differing array of other virtual bats throughout their life depending on strategy and circumstance, which dictates where they choose to roost, who they choose to groom, who they decide to ask for food from, and whether they donate food to others. As all bats in the model have fixed grooming strategies, the bats do not make decisions to directly influence their fitness (e.g., how many offspring they are expected to have); rather, they are simply reacting to the conditions around them. As such the *Objectives* and *Predictions* of the virtual bats are not considered.

In addition to monitoring their own internal state (including weight, maximum weight, and weight percentage, see Entities, State Variables, and Scales) and remembering relationship score between themselves and all other living bats (not necessarily based on a history of events, but by increases in impression caused by said events), virtual bats may detect (*Sense*) whether other virtual bats are full or not (whether they have fed) and the identity of other individuals (including where other virtual bats are when deciding where to roost and who their current roostmates are). Virtual bats can detect the identity of their mother or their youngest child, and mothers detect the age of their youngest child (whether it is a juvenile, adolescent, or adult). Finally, virtual bats can detect when a bat is born or dies, establishing a new relation with new bats and removing relationships with dead ones. Initial relationship scores established with newborn bats are symmetrically 0, except for initial mother-daughter relationships, which is symmetrically 100.

Interaction is key in this model. Virtual bats interact principally by preferentially associating with each other (see Roost Switching Sub-Model), grooming each other (see Allogrooming Sub-Model), and sharing food with each other (see Food-Sharing Sub-Model), the latter two of which improves the recipient's relationship score towards the donor. This, in turn, increases the likelihood that the original recipient associates with, allogrooms, or shares food with the original donor. These relationships generally start with association and allogrooming preferentially favoured individuals (depending on strategy, see Allogrooming Sub-Model), eventually leading to individuals sharing food with each other, a resource that directly impacts survival (see Foraging and Food Sharing Sub-Models). These interactions may dictate which virtual bats end up surviving or dying when they are unable to find food for multiple days in a row (see Death Sub-Model).

Stochasticity is also central to the model. The order in which virtual bats are called within each Sub-Model is randomly determined (except the Roost Switching Sub-Model, where adults move first, and the Food Sharing Sub-Model, where juveniles beg for food first, followed by adolescents, then adults). Whether virtual bats are successful at foraging for food (dependent on age) and whether they die while foraging via predation are determined via a probability of occurrence (see Foraging Sub-Model). The order in which bats check roosts for partners to determine if the occupying bats are familiar enough is determined via random sampling without replacement, and whether they move at all from their original roost is determined by a probability based on time since last switch (see Roost Switching Sub-Model). Whether a virtual bat donates food to a hungry bat is also determined by a probability, this time based on the potential donor's perception of the potential receiver (see Food Sharing Sub-Model).

To determine the success of each strategy over time, the model *observes* and reports the number of virtual bats using each strategy, as well as the total number of bats in the system.

5. Initialization

On startup, the grid is split into 2x2 squares, each representing a different roost. 24 virtual bats are also created, including 4 bats using each of the 6 strategies, each bat having no relationship to each other, a random starting position (random roost), an age drawn from a uniform distribution between 2 and 9 years old, an initial age-based weight, weight percentage (100%, assumed fed), and time until starvation based on said weight percentage, a roost switching probability based on days since last switch (0 days, 33.9% chance of switching).

6. Input Data

This model does not explicitly use any data external to the program itself. Probability of predation per day, roost size, foraging success rate, the amount that relationship improves via food sharing and allogrooming, roost switching rate, co-roosting ingroup bias, food-sharing in-group bias, and the maximum number and size of food-sharing donations may all be edited on the interface before startup.

7. Sub-Models

a. Foraging Sub-Model

At the start of each tick (day), all virtual bats at least 120 days old search for food, the approximate age vampire bats first feed on blood (7), with an age-dependent probability of successfully feeding *f*, as shown by Eq. 1 (Fig. S1), where *a* is age in days, and f_{max} is the maximum probability that a bat could acquire food on a given night, which we set to 93%. When f_{max} = 93%, the average feeding probability of bats between 4 and 24 months is 70% matching the empirical age-dependent probabilities of feeding (8).

$$(1)\ f = \frac{f_{max}}{1 + e^{-0.005(a-300)}}$$

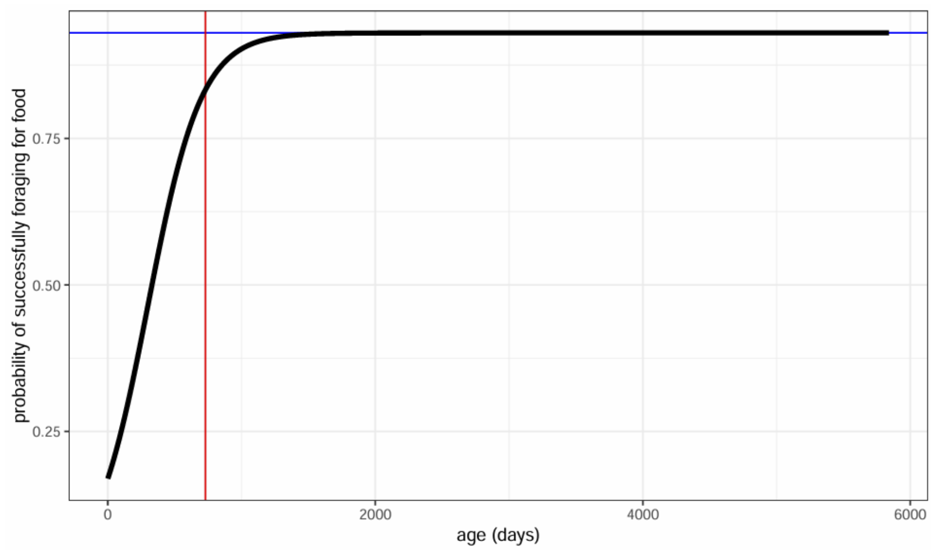

Figure S1. Age-dependent probability of successfully foraging for food per night. The black curve shows the modelled relationship, the blue line is the expected adult foraging success rate of 93% (8), and the red line shows two years. The maximum foraging success rate largely overlaps with the relationship after the bat reaches two years of age.

Bats that successfully foraged reach their maximum weight, w_{max}, derived from Eq. 2 (Fig. S2) which estimates weight over age in days (a), based on empirical data from vampire bats at various stages of adolescence (6 g at birth, 12 g at 25 days, 18 g at 2 months, 24 g at 3 months, and 33 g at 10 months (7,9,10)).

$$(2)\ w_{max} = 5.5453a^{0.3012} + 0.00001$$

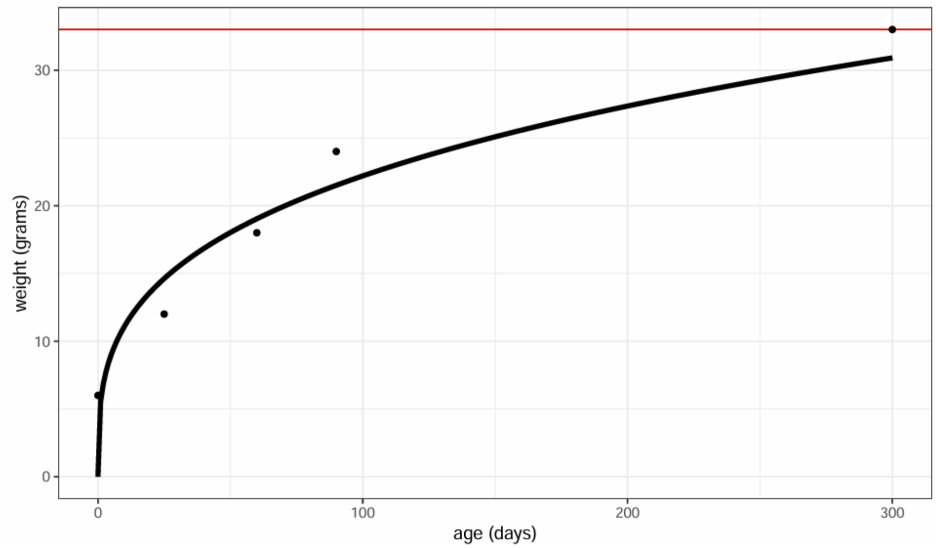

Figure S2. Growth curve of virtual vampire bats. The data points represent empirical estimates of vampire bat weight at different stages of adolescence (7,9,10). The black curve is an estimated growth curve based on the empirical data points. The red line represents adult weight (fixed realized weight after 300 days).

If a virtual bat feeds, its time left until starvation in hours (*t*) is updated based on its body weight in grams (*w*), via Eq. 3 (Fig. S3), derived from the empirically estimated nonlinear relationship between weight and hours until starvation (8).

$$(3)\ t = \frac{\left(-521^{7}2^{\frac{8}{63}}521^{\frac{59}{63}} + 5242880\left(\frac{w}{w_{max}}100\right)^{\frac{500}{63}}\right)}{65536\left(\frac{w}{w_{max}}100\right)^{\frac{500}{63}}}$$

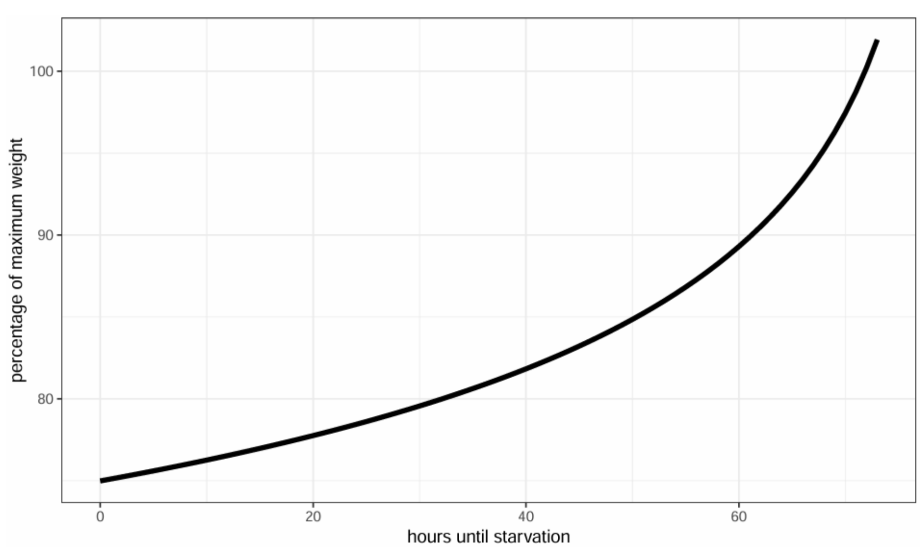

Figure S3. Relationship between weight loss and time until starvation (8).

If a bat fails to feed, 24 hours is subtracted from the total time until starvation, *t*, and the proportion of the fed weight of the virtual bats is updated via Eq. 4 (Fig. S3) (8). This equation is modified from the original equation (presented in (8)), as at 100%, the time until starvation was 72 hours (3 days). This accounts for a decrease in time until starvation caused by lactation (down to 60 hours, about what is observed in (8)). Further, there is evidence that bats can survive for at least 72 hours (11).

$$(4)\ \frac{w}{w_{max}}100 = 130.25(80 - t)^{-0.126}$$

While foraging, bats have a probability of being killed by predation of 0.03% per day, which allows an average of 17.3% of virtual bats to survive within the 16 year maximum lifespan for the virtual bats (the maximum observed lifespans of a female vampire bat in the wild (12)), ignoring any deaths from starvation.

b. Roost Switching Sub-Model

After foraging, virtual bats older than 10 months move to a roost, deciding whether to return to the same roost as before foraging or move to a new roost. Whether virtual bats switch roosts is determined by the time since last switch, derived from empirical observations of vampire bat roost-switching rates (1,13,14). See Hartman et al, 2024 (1) for more details.

To determine how roost-switching rates influence the success of each allogrooming strategy, the probability of switching roosts is modified via the *roost-switching modifier*, *m*, which controls whether bats move less, more, or the same amount as empirically observed. We compared the effect of empirical rates of roost switching to the minimum and maximum. When *m* is -1, bats switch only when their current roost is full (6 adult bats, rare roost switching, approximately 0.0035 to 0.043 switches per day, depending on scenario); when *m* = 0, they switch roosts at the empirically observed rate (empirical roost switching, 0.45 to 0.75 switches per day); when *m* = 1, they switch roosts every day, which is the maximum amount (maximal roost switching).

When visiting a roost, bats decided to stay there by assessing the sum of the 'relationship scores' for bats in that roost. Each relationship score is a percentage that determines how much each bat prefers every other bat, ranging from 0% (unfamiliar) to 100% (closest possible relationship). These scores are directed network edges that are not necessarily symmetric. Relationships scores are updated by allogrooming and food sharing as described below. A virtual bat will stay at a given roost for that day if the sum of the relationship scores with all other bats currently occupying that roost is greater than a threshold called the "*co-roosting ingroup bias*", which defines how much bats prefer to co-roost with more familiar partners (a longer history of allogrooming and food sharing) rather than less familiar partners. If the co-roosting ingroup bias threshold is not met, the bat will continue to search roosts until it finds a roost that does meet that threshold. If no roost has a sufficient sum of relationship scores, the virtual bat moves to whichever roost had the highest relationship score.

Virtual juvenile bats younger than 4 months will die immediately if their mother dies but will otherwise follow their mother's movements. Since juveniles first feed on blood at 4 months and are weaned at 10 months (7), virtual bats of ages 4 to 10 months will follow their mother to a roost whenever possible, but can move independently if their mother dies, following the same rules for adults described above.

To estimate realized roost-switching rates across simulations and scenarios, we estimated the average days per switch for all bats starting after the first generation of bats all died (16 years after simulation start), by sampling 5 simulations per scenario (18 scenarios with different levels of roost switching and ingroup biases) at time step 10,000.

c. Allogrooming Sub-Model

The allocation of allogrooming across roostmates defined whether bats used a more focusing or more diversifying social-networking strategy. Although food sharing is relatively rare and occurs only when recipients are in dire need, female vampire bats spend about 5% of their awake time allogrooming (15), and allogrooming helps bats to form and maintain food-sharing relationships (6).

After deciding where to roost, virtual bats allocate allogrooming across partners using one of six genetically-inherited social-networking strategies, listed here from least to most focused:

1. ***Diversifying 3***: groom up to 12 bats per day at equal rates
2. ***Diversifying 2***: groom up to 8 bats per day at equal rates
3. ***Diversifying 1***: groom up to 4 bats per day at equal rates
4. ***Focusing 1***: groom up to 12 bats per day at highly skewed rates (Eq. 5)
5. ***Focusing 2***: groom up to 8 bats per day at highly skewed rates
6. ***Focusing 3***: groom up to 4 bats per day at highly skewed rates

We created these strategies to capture two dimensions of greater diversifying: investing in more partners and allocating investments more equitably across those partners. Diversifying strategies 1 to 3 allocate allogrooming at equal rates across expanding numbers of recipients. Focusing strategies 1 to 3 allocate allogrooming at highly skewed (unequal) rates across a shrinking number of maximum recipients, with the skew based on relationship scores, and with each partner in order given half the amount of allogrooming as the next most preferred partner until 100% is reached. For instance, the "Focusing 3" strategy dictates that the most preferred partner (by relationship score) receives 50% of the bat's daily allogrooming, the second most preferred partner receives 25%, the third and fourth receives 12.5%. Focusing bats therefore allocate allogrooming across partners according to Eq. 5, where i represents the total amount of allogrooming given to a particular partner, x represents the rank of the partner's relationship score (i.e. the most preferred partner has a rank of one), and i_{total} represents the total amount of allogrooming that can be given in a day.

$$(5)\ i = 0.5^x i_{total}$$

This equation holds for all but the least preferred partner, which is given the same level of investment as the second-least preferred, as in the example above. These strategies determine how allogrooming time is divided among recipients, but bats always choose to invest in their most preferred partners (highest relationship scores) within their roost, regardless of strategy.

Allogrooming improves the recipient's relationship score to the groomer, but the total amount a groomer can improve the recipient's relationship score via allogrooming is 5% per day. The amount that relationship scores can improve is directly proportional to the time that a bat spends allogrooming the other bat. For example, a bat with a Diversifying 1 strategy would groom 4 partners equally on a given day, improving each partners' relationship score towards it by 1.25 percentage points. A bat with a Focusing 3 strategy would give the most preferred partner 50% of its daily allogrooming investment and increase its relationship by 2.5 points, give the second most preferred partner 25% of its investment and increase its relationship score by 1.25 points and so on. If there are less than the maximum number of allogrooming partners sharing a roost (say 6 potential allogrooming partners for a Diversifying 2 bat, which can groom up to 8 bats per day), then the virtual bat recycles the remaining allogrooming investments back towards the most preferred partners (so those two top partners would receive 25% of the investment, and the other 4 partners would receive the normal 12.5%).

d. Food Sharing Sub-Model

All virtual bats that successfully foraged that night could donate up to 2% of their body weight across multiple donation bouts of 0.5% each (each donation bout can be given to only one individual). The 2% value was derived from amount of food sharing estimated from the average total daily donation time towards fasted bats (16,17) and the average amount weight of blood transferred per minute sharing food (18). Preliminary analyses showed that virtual bats who donated usually donated the full amount blood on any given time step.

A virtual bat that failed to get blood while foraging asks each of its roostmates for food donations in order of relationship score. The percentage probability that a potential donor gives a donation to a potential recipient (p_{donate}) is determined by Eq. 6, where *r* is the relationship score from the potential donor to the potential recipient, and *d* is the **'*food-sharing ingroup bias*,'** which controls the average relationship score needed to donate to partners. When *d* has higher values, a stronger relationship score is required to donate food. We chose levels of *d* based on preliminary analyses revealing that populations collapsed when food donations were either too frequent or too rare.

$$(6)\ p_{donate} = \frac{100}{1 + e^{-0.1(r-d)}}$$

After a bat receives food, and the bat continues to ask for subsequent donations with a probability of success dictated by Eq. 6 until 1) the donating bat refuses to give 2) the donating bat has given its maximum possible donation amount, or 3) the receiving bat reaches a 100% of total full weight. For each successful donation, the receiving bat's relationship score to the donating bat increases by 0.5 percentage points. The maximum relationship score increase towards the donating bat is 2 percentage points for food received that day. Although in real bats food donations are likely to build relationships faster than allogrooming, we kept the relationship score improvements comparable between food sharing and allogrooming to simply highlight the effect of diversifying or focusing investments.

If a virtual bat is not full after receiving donations from a particular bat or being refused, the bat moves on to the next most preferred partner and repeats the process until it is full or has requested food from every bat in the roost. If its final weight is less than the maximum for its age (Eq. 2), then the hours until starvation is updated via Eq. 3 and the bat will proceed to the next day with a reduced time until starvation.

To simulate the priority of females feeding their juvenile offspring over all others, all bats younger than 10 months ask for food first, followed by bats between 10 months old and 2 years old, then all bats older than 2 years old, which ensures that dependent juveniles get priority access to food donations from their mothers. Additionally, bats younger than 10 months that request food from their mothers receive food via lactation, feeding them until full or until the mother has given up to 11% of her body weight. This number was chosen because it is a significant decrease in average condition for mothers caring for young pups, that allows for the survival of the pups, and that is also less than the weight loss caused by missing a day's worth of food calculated via Eq. 4 (about 16%).

Death Sub-Model

If any bat reaches zero hours to starvation after the foraging or food-sharing sub-model, it dies and is removed from the simulation. Any bat 16 years of age or older is also removed (12).

Birth Sub-Model

Surviving bats reproduce once every 10 months after reaching reproductive maturity at the age of 12 months (19). Newborn bats (age 0) inherit the allogrooming strategy of the mother, are completely fed at birth, and have relationship scores of zero with all other bats in the system except for their mother, which is set to the maximum (100%) in both directions.

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