Title: Social uncertainty influences the balance of quantity and quality of cooperative relationships

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Short Title: Social uncertainty and the quality-quantity tradeoff

LAY SUMMARY

Social animals need to balance relationship quantity and quality. When is it better to invest in initiating new social connections at the expense of strengthening fewer, but stronger, social bonds? Here, we created a simulation of social-grooming and food-sharing strategies based on vampire bats. We found that bats investing in relationship quantity (rather than quality) were favored by social environments that were less predictable (due to greater movement between groups, food scarcity, and mortality).

ABSTRACT

Many group-living animals develop stable affiliative social relationships that benefit survival and reproduction but also require investments of time and energy (in activities like social grooming). These social investments serve two key functions: building new social relationships ("diversifying") and maintaining existing ones ("focusing"). The 'social bet-hedging' hypothesis states that the optimal balance of diversifying and focusing depends on the stability or predictability of the social environment: all else being equal, focusing is favored more when partners are reliably available, whereas diversifying is favored when it is more difficult to predict which partners will be available to help in the future (i.e. "social uncertainty"). To assess this idea, we created an evolutionary agent-based model of how vampire bats form cooperative relationships with realistic patterns of foraging, social behavior, ageing, reproduction, and death. To manipulate social uncertainty in our simulations, we adjusted the rates of roost switching, foraging success, and predation. We then determined how social uncertainty impacted the relative success of six "social investment strategies" that determined how much the bats diversified allogrooming across partners. We show that, under a wide range of conditions, (1) selective allogrooming creates new reciprocal food-sharing relationships which increase survival, (2) an optimal degree of diversifying balances the benefits of relationship quantity and quality, and (3) social

uncertainty consistently selects for more diversifying. Our model shows how species-specific social stability can determine the optimal social investment strategy for balancing relationship quantity versus quality.

Keywords: cooperation, social behavior, social relationships, vampire bats

INTRODUCTION

"Selection should favor those characters that promote the optimization of personal relationships."

-- Adaptation and Natural Selection by GC Williams (1966)

Over the last 50 years, long-term field studies of many species of social animals have shown that stable affiliative relationships often yield mutual benefits for health, survival, and lifetime reproductive success, but that these cooperative relationships also require significant investments of limited time and energy (Seyfarth and Cheney 2012, Snyder-Mackler et al. 2020, De Moor and Brent 2025). Many social birds and mammals strengthen their relationships using low-cost allogrooming or allopreening (Griesser et al. 2025), but even these low-cost behaviors require time and energy that could otherwise be used for resting or foraging. Individuals must also decide how to allocate that limited time and energy across multiple available recipients. A key challenge since the beginning social behavioral ecology has been to understand this "optimization of personal relationships" (Williams 1966).

Social evolution theory predicts that individuals should selectively invest in the cooperative relationships that provide the greatest returns, but the optimal partner choice strategy is not always to direct all of one's attention, grooming, or helping to the single most profitable relationship (Noë and Hammerstein 1994). This is because directed cooperative investments (like allogrooming) often serve two functions: maintaining existing cooperative relationships and building new ones. Greater relationship quantity requires "diversifying" grooming across more partners, whereas greater relationship quality requires "focusing" more grooming to fewer partners. In each moment of time, an animal can do either one or neither, but not both. An individual with multiple cooperative relationships can therefore

78 invest too little time in each partner across too many partners or too much time in too few
79 partners.
80 The relative importance of the quantity and quality of cooperative relationships—and
81 hence the optimal balance of diversifying or focusing— varies across species and ecological
82 circumstances (De Silva et al. 2011, Dakin and Ryder 2020, De Moor and Brent 2025). For
83 example, in barbary macaques (*Macaca sylvaus*), individuals appear to cope better with
84 harsh winters when they have *more* huddling partners (McFarland and Majolo 2013), and
85 survival in female giraffes (*Giraffa camelopardalis*) (Bond et al. 2021) and juvenile feral
86 horses (*Equus caballus*) (Nuñez et al. 2015) is predicted by greater social relationship
87 quantity. On the other hand, relationship strength and stability predicts longevity in female
88 chacma baboons (*Papio ursinus*) (Silk et al. 2010) and greater anis (*Crotophaga major*)
89 (Riehl and Strong 2018), and predicts helping behaviors in common vampire bats
90 (*Desmodus rotundus*) (Carter and Wilkinson 2013, Carter et al. 2020), monk parakeets
91 (*Myiopsitta monachus*) (O'Connell et al. 2025), and chimpanzees (*Pan troglodytes*) (Jaeggi
92 et al. 2013).
93 What kinds of social environments select for diversifying for partner quantity versus
94 focusing for partner quality? The "social bet-hedging" hypothesis (Carter et al. 2017, Carter
95 2021) states that the optimal balance of diversifying and focusing depends on social
96 uncertainty, or the difficulty in predicting which partners will be available to help in the future.
97 All else being equal, diversifying (investing in relationship quantity) is favored more by
98 conditions of social uncertainty, because each partner might be unavailable, whereas
99 focusing (investing in relationship quality) is favored more by conditions of greater social
100 certainty, because one's partners are more reliably available to help (Carter et al. 2017).
101 The social bet-hedging hypothesis was first described as an explanation for why
102 female vampire bats form reciprocal regurgitated food-sharing relationship with nonkin, even
103 when reciprocal sharing with kin was possible (Carter et al. 2017). Vampire bats form

104 reciprocal food-sharing relationships because, without donations from successful foragers,
105 each bat can starve to death after just 2-3 nights of failed hunting (Wilkinson 1984). Network
106 perturbation experiments found that female vampire bats that diversified their food-sharing
107 investments by helping more nonkin in past years coped better with the temporary removal
108 of a major food-sharing partner (Carter et al. 2017). This finding supports the idea that
109 helping nonkin allows the bats to build a wider social support network than would be possible
110 from reciprocal helping among only kin, avoiding the risk of investing only in one or a few
111 partners that might become unavailable ("don't put all your eggs in one basket").
112 Although vampire bats (e.g. Carter and Leffer 2015, Carter et al. 2020) are a good
113 illustrative example of how diversifying relationships can mitigate social uncertainty, the
114 hypothesis is consistent with evidence of within-individual tradeoffs between investing in
115 partner quantity and quality across a wide diversity of social vertebrates (e.g. Engh et al.
116 2005, Oishi and Kesebir 2012, Firth et al. 2017, Ellis et al. 2019, Dakin and Ryder 2020,
117 Testard et al. 2021, Earl et al. 2025). Most generally, social bet-hedging is the idea that
118 diversifying cooperative investments (e.g. helping more partners) can be adaptive because it
119 reduces the variance in cooperative returns in socially unpredictable environments (rather
120 than only increasing the mean return rate). To avoid semantic confusion, we note that this
121 concept is distinct from "altruistic bet-hedging", which is the idea that kin altruism is adaptive
122 because it reduces the variance in reproductive success of kin in ecologically unpredictable
123 environments (Kennedy et al. 2018, Capilla-Lasheras et al. 2021, Dos Santos et al. 2024).
124 Social bet-hedging has received mixed support from agent-based simulations, and it
125 remains unclear whether the logic of social bet-hedging holds under socially and ecologically
126 realistic assumptions (see Discussion). To address this gap, we created an agent-based
127 model of how cooperative relationships form and how different social conditions select for
128 different relationship-formation strategies. We used vampire bats as an illustrative example
129 by basing the model on empirically derived patterns of foraging success, roost switching,

allogrooming, food sharing, maternal care, growth, weight loss, ageing, reproduction, and death. To manipulate social uncertainty, we changed either (1) rates of roost switching, which shifts the probability that a potential donor is in a different roost when needed (Wilkinson 1985a, Hartman et al. 2024); (2) rates of foraging success, which determine the probability that a potential food donor is unable to share food (Wilkinson 1984); or (3) rates of predation, which determines the probability that each potential donor dies each night. We then determined how social uncertainty impacted the relative success of six "social investment strategies" that define how the bats diversified their allogrooming time across partners.

Our model confirms the logic of social bet-hedging: all three forms of social uncertainty consistently shifted the optimal social investment strategy towards diversifying. Although we use the social and ecological circumstances of vampire bats as a case study, many of our findings are relevant to a wide range of species that form individualized relationships under conditions of social uncertainty (e.g. fission-fusion dynamics, high mortality, or unpredictable availability to help).

METHODS

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 potential roosts. Some roosts may be empty by random initial assignment, and a maximum of 6 bats can initially fill a roost. Equal numbers of generated bats use one of 6 social investment strategies (see "Allogrooming" below). After startup, all bats proceed through a series of sub-models every time step (tick) representing one 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), and the order of bats performing each task is randomized except where otherwise mentioned.

Social preferences and social network formation

Each bat has a relationship score directed towards every other bat which determines how much each bat prefers every other bat, ranging from 0% (unfamiliar) to 100% (closest possible relationship). These relationship scores are weighted directed network edges that are not always symmetric. The relationship score from bat A to bat B is increased by A's experiences of receiving allogrooming and food sharing from B, as described below under "Allogrooming" and "Food Sharing", and a greater relationship score from bat A to bat B causes A to form preferences for co-roosting, allogrooming, and allofeeding with B, similar to what we see in real vampire bats (Carter and Wilkinson 2013, Carter et al. 2020). When a bat is born, it has a 100% relationship score with its mother in both directions, and 0% relationship score with all other bats in the system. To focus on social bet-hedging, the model we present here does not incorporate social inheritance of relationships from its mother (Ilany and Akçay 2016), but future versions of the model will analyze that effect.

Foraging

At the start of each simulated day (tick), all virtual bats search for food if they are at least 120 days old, the approximate age vampire bats first feed on blood (Schmidt and Manske 1973). Virtual bats have an age-dependent probability of successfully feeding f, as shown by Eq. 1, 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%, the empirical foraging-success probability for common vampire bats older than 2 years of age (Fig. 1a, Wilkinson 1984).

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

The curve is designed so that at this maximum foraging-success probability, the average feeding probability of bats between 4 and 24 months is approximately 70%, matching the empirical foraging-success probabilities of bats in this age range (Wilkinson 1984). To assess the effect of foraging success on the relative success (survival) of social investment strategies, we also ran simulations with adult foraging success-probability set to 100%, increasing the social certainty that donors will be able to give food to younger bats in need. See "Model Testing" below.

Bats that successfully forage reach their maximum weight, w_{max}, derived from Eq. 2 which estimates weight over age in days (a). This curve (Fig 1b) is 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 (Crespo et al. 1970, Schmidt and Manske 1973, Schmidt 1978).

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

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, derived from the empirically estimated nonlinear relationship between weight and hours until starvation (Fig 1c, Wilkinson 1984, Freitas et al. 2003).

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

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 (Wilkinson 1984, Freitas et al. 2003). This equation is modified from the original equation (from Wilkinson 1984), such that at 100% weight, the time until starvation is approximately 72 hours (3 days) in our model, because vampire bats can survive for at least 72 hours without food (Freitas et al. 2003), and we want to account for a decrease in time until starvation caused by lactation down to 60 hours, about what is observed in Wilkinson (1984).

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

While foraging, bats were assigned a daily predation risk of 0.03%. Assuming predation is the only source of mortality, this risk corresponds to an approximately 17.3% probability of surviving to 16 years of age, the maximum observed lifespan of a female vampire bat in the wild (Delpietro et al. 2017). In the simulation, however, additional mortality sources such as starvation contribute substantially to overall mortality. To test the effect of predation on the relative success of different social investment strategies, we also ran simulations with a 0% daily predation probability.

[Fig 1]

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 wild common vampire bat roost-switching rates (see Hartman et al. 2024 for details, Fig

1d). This curve represents the average of all empirical bats' predicted daily roost-switching probabilities to create system-wide roost-switching rates dependent on time since last switch for all virtual bats, ranging from 33.9% on day 1 and 98.0% after 2 weeks. Virtual bats may also switch roosts if the roost was "full", with at least 6 adult bats present simultaneously (even if not cued to switch roosts based on time since last switch), although roost sizes of 7 adult bats were rarely seen occupying the same roost.

To determine how roost-switching rates influence the success of each social investment (allogrooming) strategy, the probability of switching roosts is modified via the roost-switching modifier, *m*, a value which controls whether bats move less, more, or the same amount as empirically observed, by being added to the daily probability of randomly switching roosts. For example, a virtual bat who would normally have an 80% chance of switching roosts on a particular day would have a 5% chance of switching roosts with a modifier of -0.75. Probability of movement is capped between 0% and 100%, such that a roost-switching modifier of -1 completely suppresses random movement and a roost-switching modifier of 1 guarantees daily roost switching. We compared results from 6 sets of scenarios, where the modifier was set to -1, -0.75, -0.5, -0.25, 0, and 1 (see Model Testing below).

Co-roosting ingroup bias

When visiting a roost, a bat decides whether to stay there. They do this by assessing the sum of the 'relationship scores' for bats in that roost. A virtual bat stays 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 continues 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 follow their mother's movements and die if their mother dies. Virtual bats of ages 4 to 10 months follow their mother to a roost whenever possible, but can move independently if their mother dies, following the same rules for adults described above. We chose these values because juveniles feed on blood at 4 months and are weaned at 10 months (Schmidt and Manske 1973). Search costs are not explicitly modelled. It should be noted that virtual adult or independent juvenile bats will not consider moving to a roost already occupied with 6 adult bats.

Allogrooming

After deciding where to roost, virtual bats allocate allogrooming across partners using one of six genetically-inherited social investment strategies or phenotypes (Fig. 2). All virtual bats spend the same total amount of time allogrooming, but each bat's "social investment strategy" is defined by its allocation of allogrooming across roostmates (Fig. 2). Female vampire bats spend about 5% of their awake time allogrooming (Carter and Leffer 2015), and allogrooming allows vampire bats to form and maintain food-sharing relationships (Carter et al. 2020). Compared to allogrooming, food sharing is relatively rare and occurs only when recipients are in dire need (Wilkinson 1984, Sopka et al. 2025).

Social investment strategies are listed here from least to most focused, based on the Gini coefficient (a standard measure of inequality where 0 is completely equal investment and 1 is maximally unequal). Note that, in most situations, there are no more than 12 virtual bats in a roost including adults and juveniles, however, there may be less. The Gini coefficient assumes a completely full roost (12 potential partners).

- Diversifying 3: groom up to 12 bats per day at equal rates (Gini coefficient = 0)

- Diversifying 2: groom up to 8 bats per day at equal rates (Gini coefficient = 0.333)
- Diversifying 1: groom up to 4 bats per day at equal rates (Gini coefficient = 0.667)
- Focusing 1: groom up to 12 bats per day at highly biased rates (see Eq. 6, Gini coefficient = 0.75)
- Focusing 2: groom up to 8 bats per day at highly biased rates (Gini coefficient = 0.751)
- Focusing 3: groom up to 4 bats per day at highly biased rates (Gini coefficient = 0.771)

We created these strategies to capture two dimensions of greater diversifying: investing in more partners and allocating investments more equitably across those partners. We chose to represent diversifying using both dimensions to highlight two different examples of how a quantity-quality tradeoff may present itself or be interpreted, but the Gini coefficient reduces these to a single measure of focusing. Gini coefficients are calculated using Eq. 5, where G is the Gini coefficient, n is the number of potential partners invested in, j is the partner, and y is proportional investment (making y_j proportional investment to a particular partner). Note that for our calculations of Gini coefficients, we assumed a full roost of 12 bats (6 adult bats and their children).

$$(5)\quad G = \frac{2\sum_{j=1}^{n} j y_j}{n\sum_{j=1}^{n} y_j} - \frac{n+1}{n}$$

Focusing strategies 1 to 3 allocate allogrooming at highly biased (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. 6, 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.

$$(6)\quad i = 0.5^{x} i_{total}$$

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, and the total amount a groomer can improve the total of recipients' relationship scores 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%).

333

334 [Fig 2]

335

336 **Food Sharing**

337 A virtual bat that failed to get blood while foraging asks each of its roostmates for
338 food donations in order of relationship score. All virtual bats that successfully foraged that
339 night can donate up to 2% of their body weight across multiple donation bouts of 0.5% each
340 (each donation bout can be given to only one individual). The 2% value was derived from
341 amount of food sharing estimated from the average total daily donation time towards fasted
342 bats (Razik et al. 2021, Razik et al. 2022) and the average weight of blood transferred per
343 minute sharing food (Carter and Wilkinson 2015). Virtual bats that donated usually donated
344 the full amount blood on any given time step.

345

346 **Food-sharing ingroup bias**

347 The probability that a potential donor gives a donation to a potential recipient (p_{donate})
348 is determined by Eq. 7 (Fig. 1e), where *r* is the relationship score from the potential donor to
349 the potential recipient, and *d* is the "food-sharing ingroup bias" which controls the average
350 relationship score needed to donate to partners. When *d* is higher, a stronger relationship
351 score is required to donate food. We chose levels of d based on preliminary analyses
352 revealing that populations collapsed when food donations were either too frequent or too
353 rare.

354

355 $$(7)\ p_{donate} = \frac{100}{1 + e^{-0.1(r-d)}}$$

356

After a bat receives food, it continues to ask for subsequent donations with a probability of success dictated by Eq. 7 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 might build relationships faster than allogrooming, we kept the relationship score improvements comparable between food sharing and allogrooming for simplicity and to 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.

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. This order 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, which allows for pup survival, and which is also less than the weight loss caused by missing a day's worth of food calculated via Eq. 4 (about 16%).

383

384 **Birth and Death**

385 Surviving bats reproduce once every 10 months after reaching reproductive maturity
386 at the age of 12 months (Wilkinson 1985b). Newborn bats (age 0) inherit the social
387 investment strategy of their mother and are completely fed at birth. If any bat reaches zero
388 hours to starvation after the foraging or food-sharing sub-model, it dies and is removed from
389 the simulation. Any bat 16 years of age or older is also removed, because that age is the
390 oldest recorded in the wild (Delpietro et al. 2017).

391

392 **Statistical Testing**

393 To test if and how social uncertainty changes the relative success of each of the six
394 social investment strategies, we adjusted the bats' movements between roosts. We first
395 tested six roost-switching rates by manipulating the roost-switching modifier, which controls
396 the relative probability of roost switching: -1 (rare switching), 0 (empirical rate of switching),
397 and 1 (maximal rate of switching). Rare roost switching means virtual bats switch roosts only
398 when the roost has 6 other adult bats present, empirical roost switching means bats switch
399 roosts at empirical rates, and maximal roost switching means bats switch roosts every day.
400 For higher resolution, we added 3 additional values: -0.75, -0.5, -0.25. Finally, to identify
401 when populations transitioned from focusing to diversifying we modified the daily roost
402 switching probability from 0% to 0.5%, testing each 0.01% interval ten times.

403 We treat roost switching as exogenous to isolate its causal effect, but there might be
404 complex feedbacks between diversifying and roost switching (see "Future Directions" in
405 discussion). For this reason, we also manipulated social uncertainty in two other ways. We
406 compared simulations with empirical adult foraging-success probability (93%) to simulations
407 with maximal adult foraging-success probability (100%) and hence lower social uncertainty
408 (as younger, less skilled bats will have more reliable access to food from their older

409 partners). We also compared how the chances of predation influenced optimal investment
410 strategy, comparing 0.03% daily predation probability vs 0% which creates lower social
411 uncertainty because fewer partners go missing. Comparing these simulations allowed us to
412 determine whether other forms of social uncertainty influence the reproductive success of
413 different social investment strategies.

414 The effect of roost switching diversifying might also interact with other social traits.
415 To assess the stability of the effect of roost switching on optimal social investment strategy,
416 we measured how this effect changed with the tendency for virtual bats to co-roost with more
417 familiar bats (co-roosting ingroup bias) and to feed more familiar bats (food-sharing ingroup
418 bias) based on relative relationship scores. “Low” co-roosting ingroup bias means virtual bats
419 switched into any available roost with at least one familiar partner, whereas “high” means
420 they often preferentially select the roost containing the highest sum of relationship scores.
421 Similarly, a “high” food-sharing ingroup bias means a stronger relationship score is required
422 to donate food relative to a “low” or “medium” bias. Note that both ingroup biases impact
423 social uncertainty (high co-roosting ingroup bias could result in virtual bats following each
424 other even when roost switching is high, high food-sharing ingroup bias increases social
425 uncertainty by denying more familiar bats even when present), and food-sharing ingroup bias
426 may also directly impact the success of different levels of diversification. The expected
427 relationships between variables are shown in Fig. 3.

428 Combinations of these levels of roost switching and ingroup biases create 36
429 plausible scenarios, each simulated 1,000 times (36,000 simulations) with a 0.03% daily
430 predation probability and 93% adult foraging-success probability. To assess the effect of
431 predation and foraging success on diversifying, we ran 1,000 simulations with 0% daily
432 predation probability and 1,000 separate simulations with 100% adult foraging-success
433 probability, using empirical roost switching rates and low ingroup biases in both experiments.
434 All manipulations of the model were executed using NetLogo.

We ran each simulation for 200 years (about 109 generations). Within this period, most surviving populations (76.8%) had reached strategy fixation. For selected examples of simulation results showing the number of individuals using each social investment strategy, see Fig. S1. The success of strategies was principally determined using the average (and standard error) number of bats using each strategy across scenarios. All statistical analysis was ran in R.

[Fig 3]

RESULTS

An optimal degree of diversifying balances the benefits of relationship quantity and quality

Across 38,000 simulations, we found that the fitness (survival and reproduction) of vampire bats was influenced by how they allocated their allogrooming investments across available partners, because selective allogrooming created new reciprocal food-sharing relationships which increase survival. However, each of the six social investment strategies (Fig. 2) could be either too focused or too diversified, depending on the particular combination of social conditions: roost switching rate, co-roosting ingroup bias, and food-sharing ingroup bias (Fig. 4). If the virtual vampire bats focused their allogrooming in too few partners, they could develop fewer food-sharing partners and be less likely to survive than other bats. If they diversified their allogrooming across too many partners, those relationships might not be sufficiently strong to lead to reciprocal food sharing (Fig. 5).

Social uncertainty selects for more diversifying

When we increased social uncertainty via roost switching, we found that unstable social environments with greater roost switching selected for bats that allocate allogrooming more evenly across more partners each night. Across all sets of conditions, greater social uncertainty consistently shifted the optimal social investment strategy towards greater social diversifying (Fig. 5). This shift from focusing to diversifying occurred with only small increases in roost switching (Fig. S2); we observed a clear increase in diversifying with an increase in the realized roost switching rate from 0% to 3% daily (Fig. S3).

Besides roost switching, diversifying was caused independently by two other sources of social uncertainty (Fig. 6). Diversifying increased with reduced foraging success, when each donor was less likely to have food to give in the future (Fig. 6a). Diversifying increased with elevated predation rates where each donor was less likely to survive to give in the future (Fig. 6b). In sum, the optimal balance of diversifying and focusing depended on (1) the social certainty of available donors (caused by movement rates, predation rates, and food scarcity) and (2) the social traits (ingroup biases) in the population.

An optimal degree of diversifying is necessary for population survival

If the virtual vampire bats focused their food sharing in too few partners, conditions of social uncertainty could extinguish entire groups or populations (Fig 7). Under realistic amounts of foraging success and predation, the scenarios of highest population survival had frequent roost switching and rapid development of co-roosting and food sharing relationships (i.e. low ingroup biases for co-roosting and food sharing, Fig. 7a). Under these conditions, the best strategy was the second-most diversified (Fig. 4). However, population survival was also high under the opposite scenario of rare roost switching and selective co-roosting and food sharing (i.e. high ingroup biases, Fig. 7b), and the best strategy here was the most focused (Fig. 4). In other words, the effect of roost switching on population survival depended on how selective the virtual bats were in their food sharing. When we simulated

bats that were less restrictive in food sharing (low food sharing ingroup bias), stable groups had worse survival than groups with frequent roost switching (Fig. 7a). However, when we simulated vampire bats that only shared food within their strongest relationships (high food-sharing ingroup bias), roost switching had the reverse effect: the bats needed stable groups to reliably survive (Fig. 7b, 7c).

[Fig 4]

[Fig 5]

[Fig 6]

[Fig 7]

DISCUSSION

Cooperation in vampire bats is adaptive for multiple reasons

The virtual vampire bats in our agent-based model developed reciprocal food-sharing relationships through mutual social preferences that emerged via co-roosting and reciprocal allogrooming, similar to real vampire bats (Wilkinson 1984, Carter et al. 2020, Carter 2021, Razik et al. 2022, Carter et al. 2024). When a virtual bat gave grooming or food to a partner, this increased the recipient's preference for the giver, making the recipient more likely to co-roost with it, groom it, and feed it when in need.

Reciprocal food sharing (from fed bats to unfed bats) helps both partners survive (Trivers 1971, Wilkinson 1984). In both virtual and real vampire bats, the return fitness benefits of investing in allogrooming and food sharing can be lumped into three categories: (1) increasing the fitness of your lineage including offspring, mothers, and their descendants ("kin selection", Hamilton 1964); (2) increasing the willingness of each partner to reciprocate future help ("reciprocity" or "responsiveness", Trivers 1971, Axelrod and Hamilton 1981, Van Cleve and Akçay 2014, Carter 2023); and (3) increasing the survival of each partner, which enables their existence and ability to provide future help (called "byproduct benefits",

518 “pseudo-reciprocity”, “synergy”, “group augmentation”, or “fitness interdependence”, Connor
519 1986, Kokko et al. 2001, Roberts 2005, Van Cleve and Akçay 2014, Carter 2023). Although
520 conceptually distinct, these factors are likely to interact in complex ways (Van Cleve and
521 Akçay 2014). However, the net outcome of these interacting benefits is that investments in
522 building social bonds are important for both individual survival and group/population
523 persistence.
524
525 **Different social investment strategies are adaptive in different social environments**
526 Rather than focusing on the classic question of how cooperative traits evolved (i.e.
527 Why does helping in vampire bats evolve?), our model focuses on a different question: Given
528 that bats should help others, how should they allocate that help across partners in each
529 social environment? All the virtual bats in each simulation were cooperative, they invested
530 the same total amount in building cooperative partnerships through allogrooming, and they
531 had equal thresholds for when to co-roost with partners and when to feed partners in need at
532 a cost to themselves (ingroup biases). They only varied in how they allocated their
533 allogrooming across partners, with some bats focusing more time per recipient in a few
534 partners and others diversifying less time per recipient across more partners (Fig. 2). This
535 variation led some social investment strategies to dominate others and for some populations
536 to persist while others went extinct. The social bet-hedging hypothesis predicts that
537 diversifying would increase with factors that cause greater social uncertainty, such as fission-
538 fusion dynamics and high mortality. However, prior to this study, there was no formal model
539 confirming this prediction.
540
541 **Support for the social bet-hedging hypothesis**
542 Our agent-based model supports the logic of the social bet-hedging hypothesis: more
543 diversified social investment strategies outcompeted more focused strategies under greater

social uncertainty due to either elevated roost switching (less reliable partner availability), reduced foraging success (lower probability that a partner can donate food even when present), or elevated predation (higher probability of permanent removal of partners). We also showed that the optimal social investment strategy must balance the trade-off between investing in the quantity versus the quality of social relationships. Bats with more focused social investment strategies could only dominate the population when group composition was very stable, and they could not survive with too much social uncertainty.

Consistent with the social bet-hedging hypothesis, we also found that medium or high food-sharing ingroup bias (which represents level of "focus" in sharing food) only resulted in increased population survival rates when roost switching (social uncertainty) was low. Under conditions of high social uncertainty, populations that were too selective in their food sharing could not reliably persist. Although populations with more deaths have more social uncertainty, we found that population survival rates did not consistently and clearly predict the frequency of focused or diversifying strategies, and population density (both within roost and across the colony) was not a major driver of strategy success. When inspecting the persistence of entire populations, we observed two possible kinds of successful societies: fission-fusion societies with diversifying individuals investing more in relationship quantity and stable groups with focusing individuals investing more in relationship quality. Although we did not originally predict this finding, it is entirely consistent with the social bet-hedging hypothesis.

In what other species do we expect social bet-hedging? We suspect that social uncertainty will favor the evolution of diversifying in relatively long-lived species (Silk and Hodgson 2021) where (1) individuals form preferred mutually beneficial relationships that benefit survival; (2) individuals make cooperative investments in these relationships that cause future reciprocal investments or byproduct benefits; and (3) the number of preferred relationships per individual is not highly restricted by a small group sizes. Social bet-hedging

570 is less likely when animals have less control over their social relationships, as when
571 relationships are driven almost entirely by passive processes such as family size and social
572 inheritance, rather than by allogrooming or helping.
573 In addition to the logic of social bet-hedging, our findings are consistent with the idea
574 that more “local” ecological pressures that impact specific individuals create a need for
575 focusing, whereas more “global” pressures that impact all group members necessitate
576 diversifying (“Adaptive Relationships Framework”, De Moor and Brent 2025). We see both
577 these forces at work in our simulations. Unsuccessful foraging creates a need for each bat to
578 focus enough to build strong social bonds that lead to food sharing, and at the same time,
579 social uncertainty from roost switching impacts all individuals and selects for diversifying
580 investments to a broader network of partners.
581
582 **Comparison to past agent-based simulations to address social bet-hedging**
583 Two previous agent-based models have addressed social bet-hedging in vampire
584 bats. Indirect evidence for a trade-off between diversifying and focusing emerged from one
585 agent-based model of the formation of cooperative relationships (Leimar and Bshary 2024).
586 The virtual bats in these simulations evolved a tendency to diversify their food-sharing
587 network by building new relationships, but this diversifying was balanced against the need to
588 also strengthen and focus cooperative investments in specific partners (Leimar and Bshary
589 2024). However, the simulations did not reveal if or how this trade-off is influenced by social
590 uncertainty.
591 A second agent-based model, which directly aimed to address social bet-hedging in
592 vampire bats, found that greater social uncertainty unexpectedly favored “focused” strategies
593 (Aubier and Kokko 2022), contrary to the prediction of social bet-hedging hypothesis.
594 However, this apparent contradiction is at least partially semantic. In that model, more
595 diversified strategies were more beneficial for adult bats under conditions of social

596 uncertainty (as predicted by social bet-hedging), but those strategies failed because they
597 were often fatal for juveniles, because only “focused” strategies allowed juveniles to build
598 new food-sharing relationships fast enough to survive to adulthood. Paradoxically, however,
599 only the “focused” strategies were successful at diversifying (building new relationships).
600 This is because only the “focused” strategies achieved the right balance of focusing and
601 diversifying necessary for both juveniles and adults to survive in the simulation. The
602 diversified strategies in the model by Aubier and Kokko (2022) were too diversified: they
603 failed at building new relationships and maximizing long-term benefits. However, our model
604 shows that it is also possible to create realistic strategies that are too focused.
605 Aubier and Kokko (2022) present a fascinating example of the potential role of
606 antagonistic pleiotropy in the evolution of cooperation strategies: diversifying was adaptive
607 for adults but maladaptive for juveniles. However, this form of antagonistic pleiotropy has not
608 been observed in real vampire bats. Instead, several observations suggest that focusing
609 social investments is not particularly necessary for juvenile vampire bats to survive to
610 adulthood. First, mother vampire bats provide extended maternal care well into adulthood by
611 staying with their offspring and creating a buffer against starvation while those offspring form
612 other relationships (Carter 2021), which is why we included this factor in our model. Second,
613 young bats can ‘test the waters’ with potential new partners using low-cost allogrooming
614 (Carter et al. 2020), which makes it easier for young bats to form relationships. This
615 phenomenon was missing from the model by Aubier and Kokko (2022), but it was a central
616 feature of our model. Third, juveniles can inherit bonds formed by their mother (Razik et al.
617 2021), which also makes it easier for them to form new nonkin relationships. Although we did
618 not incorporate social inheritance in our model, future versions will analyze its effects.
619 Finally, in contrast to the assumption of antagonistic pleiotropy (i.e. that partner selectivity is
620 a fixed trait across the lifespan and needs to be focused at an earlier age), studies across a
621 range of species suggest that animals can shift their social investment strategies with age,

and that focusing occurs more often in older individuals ("social ageing", Siracusa et al. 2022a, 2022b).

Future directions

Our model assumes that social investment strategies are fixed within a lifetime. However, diversifying in response to social uncertainty might occur on both evolutionary timescales and on ecological timescales (within a lifetime). This possibility is similar to the fact that partner choice can increase the evolution of cooperative traits and also immediately incentivize cooperative behavior by rewarding help. To the extent social investment strategies are not fixed, fluctuations in social uncertainty could select for more flexible strategies where individuals evolve the capacity to adjust their social investment strategies to recent or local social conditions. Increasing evidence from a diversity of species—including wire-tailed manakins (*Pipra filicauda*) (Dakin and Ryder 2020), great tits (*Parus major*) (Firth et al. 2017), rhesus macaques (*Macaca mulatta*) (Ellis et al. 2019, Testard et al. 2021), chacma baboons (*Papio ursinus*) (Engh et al. 2005), superb starlings (*Lamprotornis superbus*) (Earl et al. 2025), and humans (*Homo sapiens*) (Oishi and Kesebir 2012) is consistent with the hypothesis that animals attempt to diversify their relationships in response to cues of greater social uncertainty or changes in their social environment. Just as health, survival and reproduction can be influenced by "landscapes of fear" caused by predation cues (e.g. Zanette et al. 2011), mere cues of social uncertainty or social threat are likely to affect both individual health and social behavior.

A current major limitation of our model is the speed at which it runs. On a typical modern laptop, individual model runs take between seconds and a half-hour per core. Although the current version was created in Netlogo (and another version is in R), future versions can be translated to faster programming languages allowing us to run simulations

over longer periods of evolutionary time and to further extend the current model. However, the main findings that we present here are unlikely to change with more generations.

We focus most of our analysis on roost switching, because fission-fusion social dynamics is likely to be the main driver of social uncertainty in vampire bats (Hartman et al. 2024). However, social uncertainty is influenced by many other factors beyond fission-fusion social dynamics, mortality, and food abundance. Most notably, there are many demographic effects on social uncertainty including the amount and predictability of birth, death, emigration, and immigration (Daizaburo and Johnson 2020). These demographic effects on social uncertainty are themselves highly dependent on prior social structure, the social importance of the relationships (Daizaburo and Johnson 2020), and whether relationship formation depends social inheritance of parental ties (Ilany and Akçay 2016, African elephants (*Loxodonta africana*): Goldenberg et al. 2016, spotted hyena (*Crocuta crocuta*): Ilany et al. 2021) or cohort-biased associations (e.g. vervet monkeys (*Chlorocebus pygerythrus*): Jarrett et al. 2018).

To isolate its causal effect, we treat roost switching as exogenous variable in our model. The reasons for frequent roost switching in real vampire bats (and other bats) are unknown, and it is at least plausible that it is caused by non-social reasons such as parasite density or variation in microclimate (Patriquin and Ratcliffe 2016). Roost switching in bats likely pre-dates the common vampire bat because it is found in most forest-dwelling bats (Patriquin and Ratcliffe 2016). However, one possibility to explore further is that roost switching is both a cause of diversifying and consequence of it (e.g. a need to interact with more individuals). The result would be a positive feedback loop where more diversifying increases greater movement between roosts and greater social uncertainty, which favors more diversifying.

This idea begs another longstanding question about why fission-fusion dynamics exist in bats. What prevents vampire bats from simply forming one large stable group where

673 all partners are available every day? Identifying the function of fission-fusion dynamics
674 requires studying how it varies across ecological gradients both within and between species.
675 Our model was based on frequent roost switching rates observed in the most complete field
676 study of vampire bat social structure (Wilkinson 1984, Wilkinson 1985a, Wilkinson 1985b),
677 but group sizes and roost-switching rates in this species appear to vary across their range
678 (e.g. Wilkinson 1985a, Delpietro et al. 2017, Ripperger and Carter 2021).
679 Finally, it is important to note that trade-offs between diversifying and focusing
680 strategies are not straightforward to measure in observational field studies for several
681 reasons. Directed observations are necessary because associations do not indicate which
682 individual caused the interactions. Animals also spend different total amounts of time
683 socializing, meaning that measures of social connectedness or selectivity typically involve
684 individual differences in time spent socializing or not socializing, rather than the diversifying
685 or focusing of that social time across partners (e.g. Dakin and Ryder 2020). The within-
686 individual trade-off between diversifying and focusing cannot be simply measured as a
687 negative correlation between relationship quantity and quality across individuals or species,
688 because individuals that invest more total time in socializing (greater network strength) can
689 easily have both greater relationship quantity (greater network degree) and quality (stronger
690 ties to top partners) relative to others. Individuals in the field also have differential access to
691 partners, meaning that a diversifying individual might groom a greater-than-average number
692 of the partners that were available to it, while also grooming a smaller-than-average absolute
693 number of partners. It is therefore useful to use captive experiments that control the
694 opportunity and availability of interaction partners to be selected by a focal individual.
695
696 **Conclusion**
697 Social interaction structure is an emergent outcome of stochastic events and social
698 decisions by many members of the population. An individual's social integration is therefore

shaped by many forces outside its control. On the other hand, individuals are not passive victims of their social network; they can actively influence their connectedness by how much they socialize (or cooperate) and by how they direct that social attention (or help) across partners. Social animals make repeated investments in signaling, approaching, touching, grooming, or helping specific partners. Individuals consistently vary in the amounts of time and energy they dedicate to “socializing, and this variation forms the basis by which selection can acts on “sociability”. In each moment, however, individuals allocate their social investments of time and energy towards either maintaining existing social bonds (focusing) or building new ones (diversifying), and individuals might also consistently vary in how they navigate that trade-off. We showed that one important factor likely to influence the optimal balance between diversifying and focusing is social uncertainty—a factor likely to differ across species but also populations living under different ecological conditions. Further insight into animal societies will come from modelling the interplay between the ecological factors passively shaping animal social networks and the emergent outcome of what patterns of social integration (ego networks) each individual is actively trying to realize.

Conflict of Interest: none declared

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Data Availability

Supporting data and code (Netlogo and R) for this paper can be found at (https://doi.org/10.5281/zenodo.21480533), and the most recent version of the model can be found at https://github.com/anonymousscientist8/social-bet-hedging. An additional large dataset used to determine average roost capacity is found at https://doi.org/10.5281/zenodo.15633664.

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970

Figure Legends

Figure 1. Rates of successful foraging, growth, starvation, roost switching, and food sharing. Panel a shows age-dependent probability of successfully foraging per night with an expected adult foraging-success probability of 93% (horizontal blue line), reached after two years (vertical red line) based on empirical work (Wilkinson 1984). Panel b shows growth curve with empirical estimates of vampire bat weight at different stages of growth (points) based on published data (Crespo et al. 1970, Schmidt and Manske 1973, and Schmidt 1978) relative to adult weight (red line, fixed realized weight after 300 days). Panel c shows relationship between weight loss and time until starvation based on empirical work (Wilkinson 1984, Freitas et al. 2003). Panel d shows the probability of switching roosts given number of days since last switch (Hartman et al. 2024, Wilkinson 1985a). Panel e shows the probability of donating one bout of food based on the relationship score between virtual bats assuming an intermediate food-sharing ingroup bias of 50.

Figure 2. Allocation of allogrooming across preferred partners according to six social investment 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. Gini coefficients are a single measure of focusing (higher Gini = more focused). The similarity between the Gini coefficient for focusing 1 and focusing 2 demonstrates why number of grooming recipients with non-zero values (network degree) can be a poor metric of diversifying.

Figure 3. Causal diagram for drivers of the relative success of diversifying strategies in the agent-based model. Arrows show hypothesized causal effects which originated from variables that we controlled (blue boxes) and influenced outcomes that we estimated (white

ovals). The key prediction of social bet-hedging is that social uncertainty increases the relative success of diversifying strategies. However, the relative success of diversifying strategies might also be influenced directly or indirectly by food-sharing ingroup bias.

Figure 4. Success of each social investment strategy under 18 social conditions. Social uncertainty is shown by columns with increasing roost switching from left to right. Social investment 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 two levels of co-roosting ingroup bias (colors and shapes) and three levels of food-sharing ingroup bias (rows). A low ingroup bias indicates that bats are more willing to co-roost or feed bats with weaker relationship scores. For simplicity, the plot shows three levels of roost switching: from stable groups with rare roost switching, empirical rates of roost switching observed in field studies (Wilkinson 1985a, Hartman et al. 2024), and maximal rates of daily roost switching. Results for all 6 levels of roost switching are shown in Fig. S2.

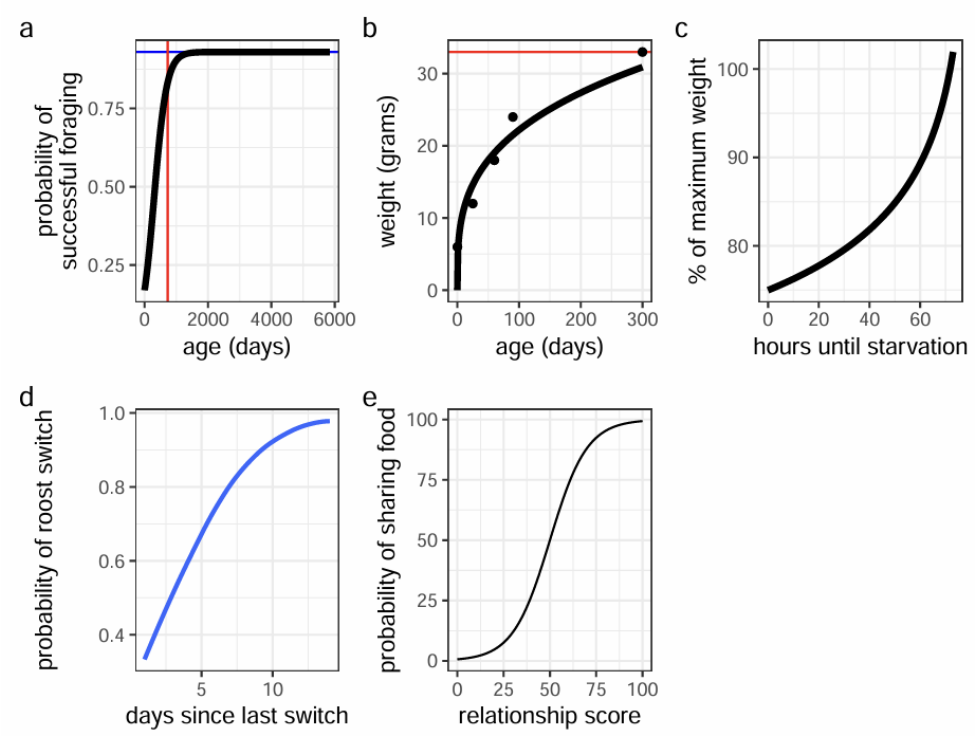
Figure 5. Greater social uncertainty changes the optimal amount of diversifying. When roost switching is rare (top panel a), the most successful social investment strategies are more focused (high Gini coefficient, x-axis). When roost switching is increased to higher rates observed in nature (middle panel b) or the highest rates possible (bottom panel c), the most successful social investment strategies are more diversified (lower Gini coefficient). A low ingroup bias indicates that bats are more willing to co-roost or feed bats with weaker

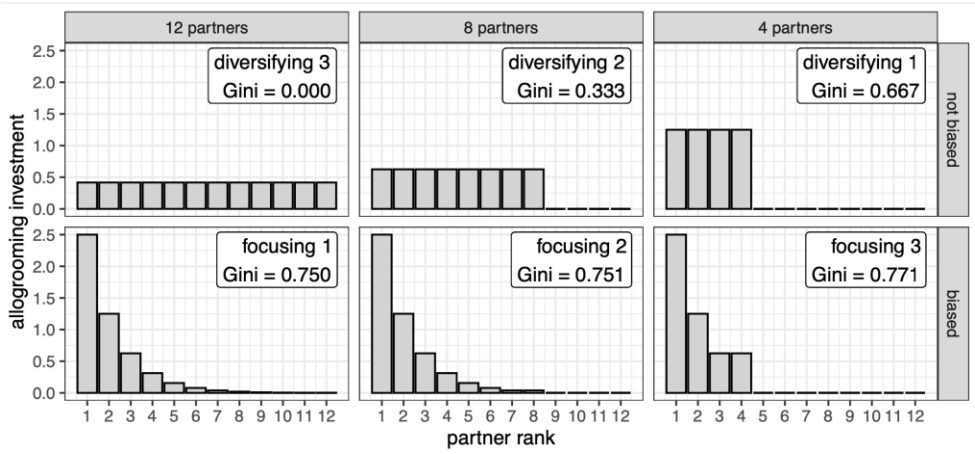
relationship scores. For simplicity, plot shows 3 levels of roost switching; results for all 6 levels of roost switching are shown in Fig. S2.

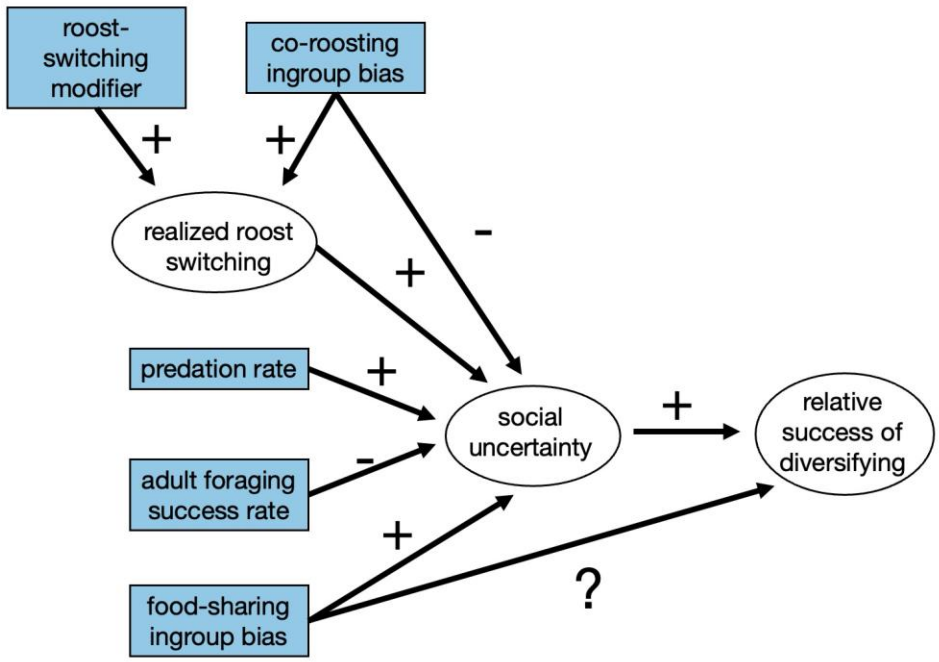
Figure 6. Diversifying is selected for by conditions of limited foraging success (a) and higher predation (b). Mean (with standard errors) are shown for each simulation test.

Figure 7. Effect of roost switching and food-sharing ingroup bias on population survival. The relationship between roost switching and population survival differs when food sharing ingroup bias is low (a), medium (b), or high (c). A low food-sharing ingroup bias indicates that bats are more willing to feed bats with weaker relationship scores.

Figures


a
probability of successful foraging
0.75
0.50
0.25
0
2000
4000
6000
age (days)
b
weight (grams)
30
20
10
0
0
100
200
300
age (days)
c
% of maximum weight
100
90
80
0
20
40
60
hours until starvation
d
probability of roost switch
1.0
0.8
0.6
0.4
5
10
days since last switch
e
probability of sharing food
100
75
50
25
0
0
25
50
75
100
relationship score


12 partners
8 partners
4 partners
diversifying 3
Gini = 0.000
diversifying 2
Gini = 0.333
diversifying 1
Gini = 0.667
not biased
focusing 1
Gini = 0.750
focusing 2
Gini = 0.751
focusing 3
Gini = 0.771
biased
allogrooming investment
2.5
2.0
1.5
1.0
0.5
0.0
1 2 3 4 5 6 7 8 9 10 11 12
partner rank


roost-switching modifier
co-roosting ingroup bias
realized roost switching
predation rate
adult foraging success rate
food-sharing ingroup bias
social uncertainty
relative success of diversifying
+
+
-
+
+
-
+
?

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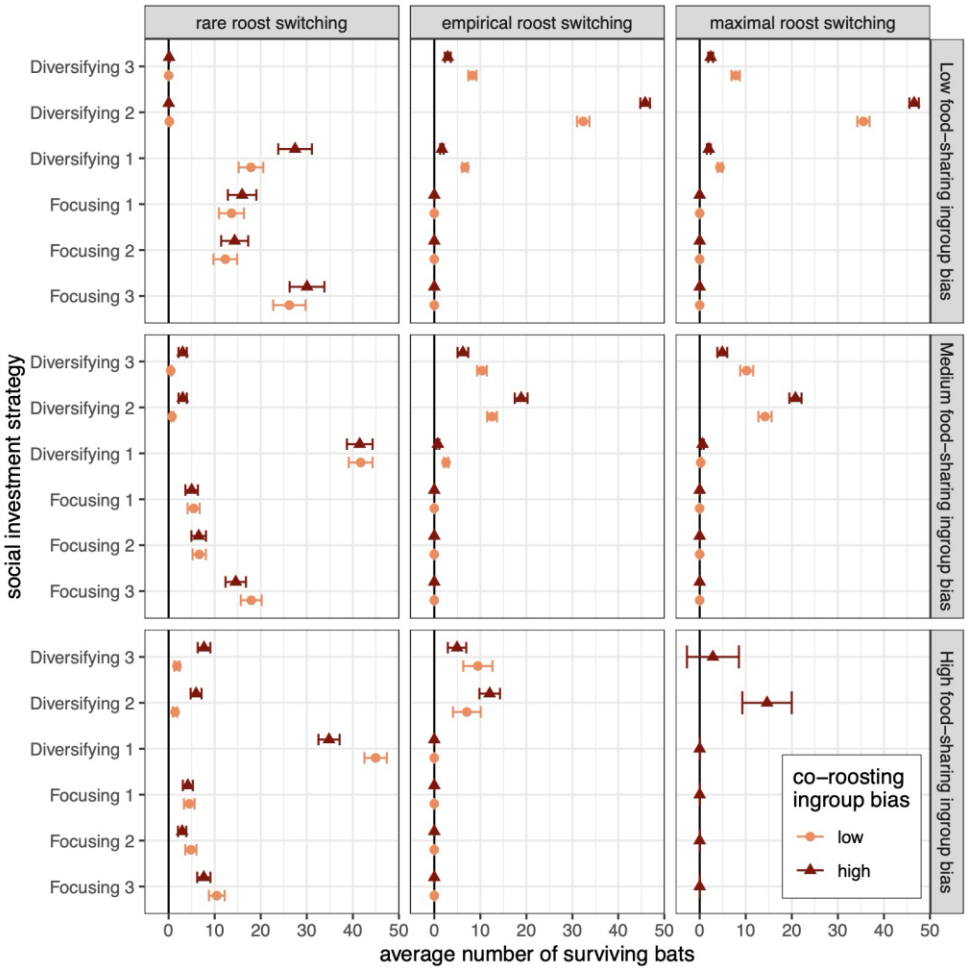
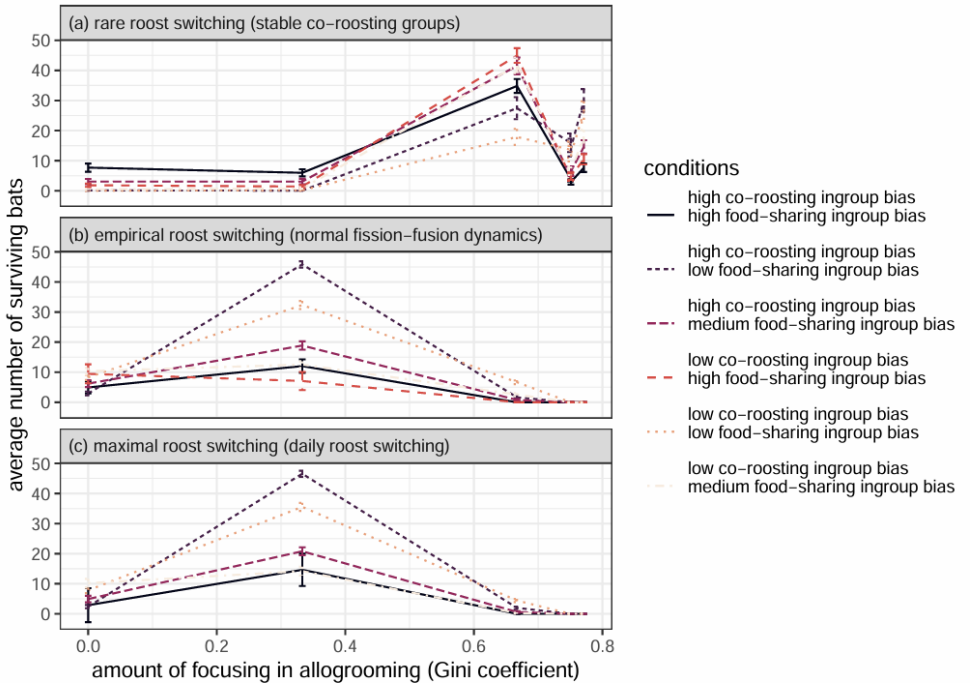
1040


rare roost switching
empirical roost switching
maximal roost switching
Low food−sharing ingroup bias
Medium food−sharing ingroup bias
High food−sharing ingroup bias
social investment strategy
Diversifying 3
Diversifying 2
Diversifying 1
Focusing 1
Focusing 2
Focusing 3
0
10
20
30
40
50
average number of surviving bats
co−roosting ingroup bias
low
high

1041

1042



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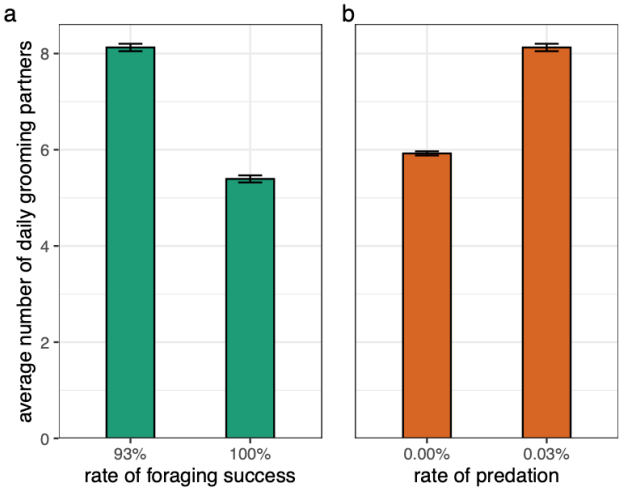

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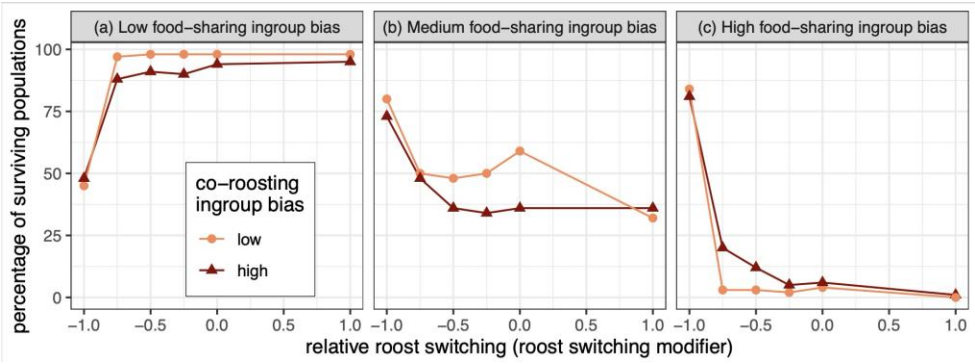
(a) Low food–sharing ingroup bias
(b) Medium food–sharing ingroup bias
(c) High food–sharing ingroup bias
percentage of surviving populations
100
75
50
25
0
co–roosting ingroup bias
low
high
−1.0
−0.5
0.0
0.5
1.0
relative roost switching (roost switching modifier)

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Supplementary Information (SI) for…

Hartman CRA, Salles A, Carter G. 2025. Social uncertainty influences the balance of quantity and quality of cooperative relationships. Behav Ecol. In Review.

Supplementary Figures

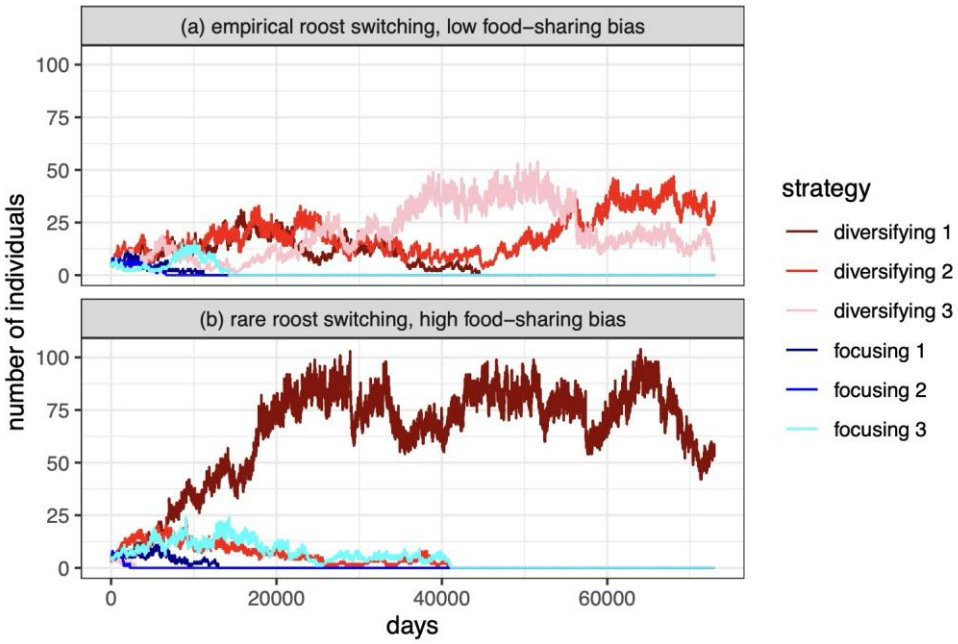

Figure S1. Social investment strategy success over simulated time. Colored lines show the number of bats using each social investment strategy over time in two selected simulations. In one simulation (a), the two most diversifying strategies become dominant at empirical roost switching and low food-sharing ingroup bias. In the other (b), a more focused strategy dominates when roost switching is rare and food-sharing ingroup bias is high. Both simulations had low co-roosting ingroup bias.

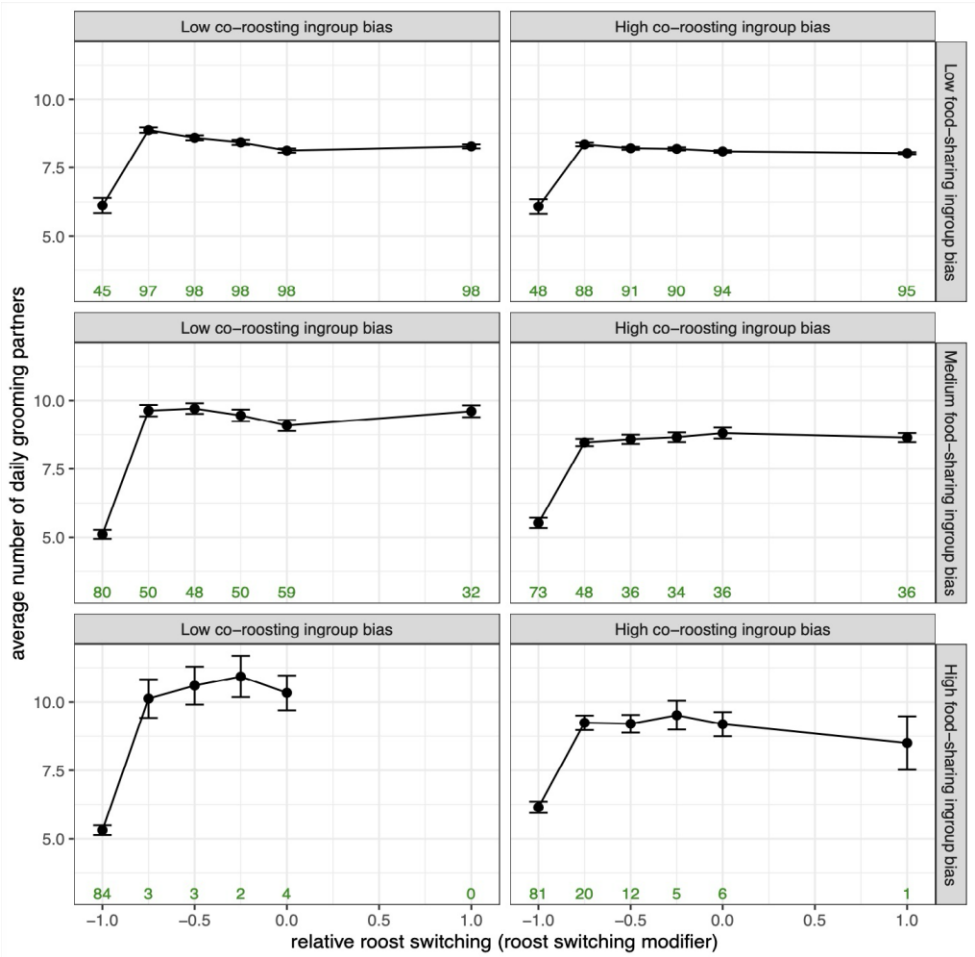

Figure S2. Greater roost switching selects for bats that groom more roostmates (diversifying). Mean (with standard error) number of intended daily grooming partners for surviving bats is lower when roost switching is *rare* (modifier of -1, or 0% probability of random roost switch) compared to more frequent roost switching. A low co-roosting/food-sharing ingroup bias indicates that bats are more willing to co-roost/feed bats with weaker relationship scores. Small green numbers just above the x-axis are the percentages of populations that survived (see Fig. 7). For an analysis of small degrees of variation in realized roost switching, see Fig. S3.

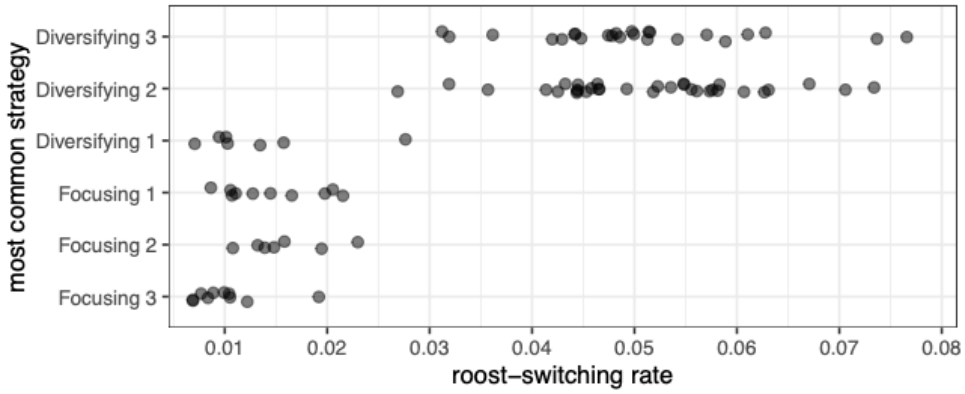

Figure S3. Shift in optimal amount of diversifying (y-axis) with increasing realized roost switching rate in switches per day (x-axis). The most common surviving strategy shifts from focusing to diversifying at a daily roost-switching rate of around 3%.

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, predation rate, and maximum foraging-success rate influences the evolution of more "focusing" or "diversifying" social investment 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 in Methods) 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 in Methods), the order in which other vampire bats are solicited for food (from greatest to smallest, see Food Sharing), the order in which other vampire bat agents are groomed (from greatest relationship to smallest relationship, see Allogrooming), 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 in Methods). 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 in Methods) 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 in Methods). It also dictates the maximum weight of the bat, influences how much bats weigh alongside foraging-success probability 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 in Methods).
e. Mother: The ID of the mother of the child.
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 (Hartman et al. 2024 Proceedings B).
h. Strategy: Whether bats use Diversifying 3, Diversifying 2, Diversifying 1, Focusing 1, Focusing 2, or Focusing 3 as their investment strategy (see Allogrooming in Methods).

Vampire bats occupy the center of each patch, so the position of the bats is represented in discrete units. Roost number (which roost is being occupied) affects the behavior 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 order of completion by each bat is random unless otherwise stated (see Process Overview and Scheduling). 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 in Methods).

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 cooperation (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 (Carter et al. 2017 Biology Letters).

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. Further, we manipulated system-wide daily predation rate and maximum (adult) foraging-success rate, both of which affect the potential for partners to reliably aid others in the future and, therefore, control social uncertainty. We also included various genetically-determined social investment 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 in Methods). Additionally, there is more variation in level of diversification in social investment strategy resulting from how many virtual bats investment is split between (see Allogrooming). 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, both extremes, and three other points), predation (existing or non-existing), and foraging success (empirical or near guaranteed for sufficiently old, skilled virtual bats) we could determine how social uncertainty influences diversification in social investment strategy, controlling for other influences.

In addition, we tried to emulate realistic birth rates, growth, foraging, roost switching, allogrooming, food sharing, gestation, 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 Ingroup Bias in Methods) as well as simulation-wide “co-roosting ingroup bias” (determines how likely bats are to choose to roost with more familiar bats, see Co-Roosting Ingroup Bias in Methods), which we anticipated might influence the success of different cooperative strategies either directly or indirectly through adjustment of social uncertainty.

The virtual bats do not *adapt* their social investment strategy within their lifetime, rather, we look at how the population evolves. Still behavior 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 potential relation with new bats and removing relationships with dead ones. Initial relationship scores established with newborn bats are symmetrically 0 (i.e., no relationship), except for initial mother-daughter relationships, which is symmetrically 100 (maximal relationship).

Interaction is key in this model. Virtual bats interact principally by preferentially associating with each other (see Roost Switching in Methods), grooming each other (see Allogrooming in Methods), and sharing food with each other (see Food-Sharing in Methods), 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 favored individuals (depending on strategy, see Allogrooming), eventually leading to individuals sharing food with each other, a resource that directly impacts survival (see Foraging and Food Sharing). 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 Birth and Death in Methods).

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 in Methods). 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 in Methods). 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 in Methods).

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 probability, the amount that relationship improves via food sharing and allogrooming, roost switching rate, co-roosting ingroup bias, food-sharing ingroup bias, and the maximum number and size of food-sharing donations may all be edited on the interface before startup.

7. Sub-Models

Foraging Sub-Model

See the Foraging subsection of the Methods.

Roost Switching Sub-Model

See Roost Switching and Co-Roosting Ingroup Bias subsections of Methods.

Allogrooming Sub-Model

See Allogrooming subsection of Methods.

Food Sharing Sub-Model

See Food Sharing, Food-Sharing Ingroup Bias, and Maternal Care subsections of Methods.

Death Sub-Model

See Birth and Death subsection of Methods.

Birth Sub-Model

See Birth and Death subsection of Methods.