The ‘social microbiome’ can fundamentally shape the costs and benefits of group living, but understanding social transmission of microbes in free-living animals is challenging due to confounding effects of kinship and shared environments (e.g. highly associated individuals often share the same spaces, food and water). Here, we report evidence for convergence towards a social microbiome among introduced common vampire bats, Desmodus rotundus, a highly social species in which adults feed only on blood, and engage in both mouth-to-body allogrooming and mouth-to-mouth regurgitated food sharing. Shotgun sequencing of samples from six zoos in the USA, 15 wild-caught bats from a colony in Belize and 31 bats from three colonies in Panama showed that faecal microbiomes were more similar within colonies than between colonies. To assess microbial transmission, we created an experimentally merged group of the Panama bats from the three distant sites by housing these bats together for four months. In this merged colony, we found evidence that dyadic gut microbiome similarity increased with both clustering and oral contact, leading to microbiome convergence among introduced bats. Our findings demonstrate that social interactions shape microbiome similarity even when controlling for past social history, kinship, environment and diet.

1. Introduction

The ‘social microbiome’—defined as the collective microbial community of an animal social network—can fundamentally shape the costs and benefits of group living [1]. A social microbiome is measured by sampling microbes across the social network that provides a reservoir of both pathogens and beneficial microbes [2–8]. To balance the costs and benefits of these various microbes, individuals can increase microbial transmission by performing behaviours such as mouth-to-mouth regurgitations or consuming faeces [1], or decrease microbial transmission through behaviours such as avoiding sick individuals [9].

Understanding the effects of social transmission on microbiome similarity in free-living animals is challenging, however, due to confounding effects of kinship and shared environments [1]: offspring might acquire microbes from parents, and individuals that are highly associated will often share the same spaces, food and water. Such influences are hard to disentangle in observational field studies. A more powerful approach is to control these confounding factors experimentally, rather than statistically.

Here, we introduce individuals from distant sites and track their social interaction rates to assess the role of social interactions in shaping gut microbiome composition. We used the common vampire bat, Desmodus rotundus, a highly social and highly gregarious species that is highly adapted to life in colonies [10].

© 2021 The Authors. Published by the Royal Society under the terms of the Creative Commons Attribution License http://creativecommons.org/licenses/by/4.0/, which permits unrestricted use, provided the original author and source are credited.
social species and obligate blood feeder. Due to this specialized diet, dietary variation plays a smaller role in explaining microbial diversity among vampire bats [10–12] compared to mammals with less specialized diets [13]. On the other hand, social transmission of microbes is likely a causal driver of microbial diversity in this species because female vampire bats hang in tight clusters and spend about 5% of their awake time grooming other individuals’ wings or fur with their mouths [14]. In addition, females regurgitate blood to their offspring and to other highly associated adults that failed to feed [14–17]. This oral contact (mouth-to-body allogrooming and mouth-to-mouth regurgitated food sharing) provides channels for microbial sharing between individuals.

To assess evidence for group-level convergence in the vampire-bat social microbiome, we sampled the faecal and gut microbiome of captive-born vampire bats from six zoos, 15 female vampire bats from a wild colony in Belize and an ‘experimentally merged’ colony composed of 26 wild-caught vampire bats and five captive-born offspring sourced from three distant sites in Panama, then housed together in captivity for four months. In the experimentally merged colony, social networks of rates of clustering and oral contact predicted gut microbiome similarity, and faecal samples showed evidence for microbiome convergence over time.

2. Material and methods

(a) Sample collection

To assess colony-level variation in faecal microbiomes, we obtained three to six faecal samples from vampire bats housed at six zoos: (i) North Carolina Zoological Park, Asheboro, North Carolina; (ii) Cincinnati Zoo and Botanical Garden, Cincinnati, Ohio; (iii) Dallas World Aquarium, Dallas, Texas; (iv) Memphis Zoological Garden and Aquarium, Memphis, Tennessee; (v) Aquarium and Rainforest at Moody Garden, Galveston, Texas; and (vi) Sedgwick County Zoo, Wichita, Kansas. In Belize, we collected faecal samples from 15 female bats (capture and fieldwork described previously [18]). In Panama, we individually sampled 26 wild-caught bats that were experimentally merged into one colony, as well as five captive-born offspring, for studies on social relationship formation (electronic supplementary material, table S2). We captured all bats from three distant wild roosts (120–340 km apart): six adult females, one juvenile female and two juvenile males from a cave at Lake Bayano, Panamá; 10 adult females from a hollow tree in Tolé, Panamá (including one bat that was not part of the merged colony) and eight adult females from a hollow tree in La Chorrera, Panamá. We then housed these bats together in an outdoor flight cage for four months as described previously [19]. We opportunistically took 85 faecal samples from isolated bats from 19 May 2019 to 16 October 2019. In all study colonies, faecal samples were smeared in duplicate on FTA cards (Whatman, GE Healthcare, sup. no. WB120055).

In the experimentally merged colony, bats were fed with cattle or pig blood from a meat processing plant that was chemically defibrinated with 44 g of sodium citrate and 16 g of citric acid per 1 l container. The blood was either refrigerated for up to 6 days or stored frozen, then thawed immediately before being provided to the bats. Nine bats developed a Staphylococcus infection during the study, which required administration of enrofloxacin and isolation from the rest of the colony from 21 July to 5 August. However, no faecal samples were collected after 13 July, and we also failed to detect any clear effect of this antibiotic on the diversity of final gut microbiome sampled on 15 October (mean and 95% CI of Simpson diversity: 19 untreated bats = 0.881 [0.874, 0.887], nine treated bats = 0.876 [0.868, 0.883]; t-test: t = 0.92, d.f. = 19.3, p = 0.4). For the final gut sample, bats from the experimentally merged colony were sacrificed using isoflurane to anaesthetize them (inhaled ≥ 5%) prior to rapid decapitation. Gut samples were collected from the distal colon and smeared on FTA cards.

(b) Social network construction

In the merged colony, we recorded clustering and oral contact from video recorded by three infrared surveillance cameras (Foscam NVR Security System) for 6 h each day from 23 June 2019 to 4 August 2019, and from 11 August 2019 to 14 October 2019 (a total of 640 sampled hours), as described previously [19]. To measure clustering, all bats that were roosting in a contiguous group at the start of each half-hour were scored as associated. To measure rates of oral contact (which includes mouth-to-body or mouth-to-mouth contact), we measured the duration of any bout of licking that was at least 5 s in duration, noting the actor and receiver. Because mouth-to-mouth contacts were rare (never observed in 71% of pairs), we do not analyse them separately from mouth-to-body contacts.

We calculated undirected clustering networks using the simple ratio index in the R package asnipe [20], and undirected contact rates as the mean of the total duration of dyadic interaction bouts in both directions for each sample hour during which both bats were present in the flight cage. To reduce extreme skew in the edge weights for oral contact, we applied an inverse reciprocal transformation to (+ oral contact rates). We scaled network matrices to standardize units to standard deviations across variables.

(c) Microbiome sequencing

DNA was extracted from FTA cards in a designated pre-PCR BSL-2 laboratory using the Qiagen PowerSoil kit (Qiagen; cat. no. 47014). Every batch of 8–24 sample extractions included a negative control. Samples with discoloration after the wash buffer step in the protocol were eluted and re-bound to filter columns with binding buffer for one to three additional washes. Genomic libraries were constructed using the Illumina DNA Prep kit (Illumina, cat. no. 20018705). Duplicate samples were randomly selected or combined for separate library builds for the Belize colony, the aggregated zoo populations and the experimentally merged colony (electronic supplementary material, table S1). Extraction negatives had negligible quantities of DNA as quantified by Qubit readings (ThermoFisher Scientific, cat. no. Q32851), and were combined to make per-population negative libraries. A separate library negative was also constructed. Overall, 145 samples, including samples, duplicates and listed negative controls, were sequenced on a NovaSeq 6000 S4 lane (Illumina), resulting in approximately 1.75 billion 150 bp paired-end reads. Because we used DNA extraction without reverse transcription, our microbiome analyses do not include RNA viruses.

(d) Bioinformatics

Sequences from negative extraction and sequencing libraries were used to create population-specific filtering databases in addition to the human genome database provided by KneadData to filter all sample reads [21]. Paired-end reads were combined and taxonomically profiled using MetaPhlAn 3 [21]. MetaPhlAn 3 was run using default parameters, assigning taxonomy to genus/species based on unique nucleotide sequence markers and ignoring sequences that fail to match these markers [22]. We found high consistency in the duplicates from these initial profiles, varying less than 5% in read counts attributed to each
taxa. Once initial analyses were complete, duplicates (both paired sets of reads) were combined with their partner for further analyses.

MetaPhAn 3 identified 102 species-level taxa across all three populations [21]. Alignment data were analysed using the phyloseq R package [23–25]. To account for variable sequencing depth, we used a variance stabilized transformation, and assessed abundance in sample types and populations using DESeq2 [26]. Functional analysis of the filtered reads was done with HUMAnN3; hits were grouped by enzyme classes and split to taxonomic levels where possible [21]. We converted taxonomy-associated read data into Bray–Curtis distances, and defined ‘microbiome similarity’ as 1—Bray–Curtis distance.

(e) Statistical inference

To test the simultaneous effects of clustering and oral contact networks on gut microbial similarity in the experimentally merged colony, we used multiple regression quadratic assignment procedure with double semi-partialing (MRQAP-DSP) from the aspipe R package [20,27]. To create all 95% confidence intervals shown in square brackets, we used percentile bootstrapping in the boot R package [28].

To test for evidence of convergence in similarity of faecal samples, we compared the similarity of initial opportunistic pre-merge faecal samples from five Lake Bayano bats on 19 May 2019 to later samples from other Lake Bayano bats and to later samples from three Tolé bats that were also sampled before and after the merge on 14 June 2019. We then calculated the change in similarity for the 25 pairs where both bats were sampled before and after the merge (10 pairs captured at the same wild roost and 15 pairs introduced in captivity). To test the prediction that faecal microbiomes converged for introduced pairs and diverged for same-roost pairs, we fit a general linear mixed effects model (MCMCglm function and package using default priors) where fixed effects were time (days since initial sample, scaled), dyad type (same-roost versus introduced) and the interaction between time and dyad type. Both bats were entered as a multi-membership random effect. After an interaction was detected, we fit the same mixed model for both dyad types separately with time as the fixed effect. As an alternative approach, we also tested the interaction term using a permutation test; to get a permutation p-value, we fit the model with the same fixed effects (no random effects), then simulated the null hypothesis by randomizing the time differences within each dyad 1000 times to generate a distribution of expected values to compare with the observed.

3. Results

Bats from the same colony had more similar faecal microbiomes than bats from different colonies ($\beta = 0.55$, $n = 57$ bats, $p < 0.001$; figure 1). The rank order of faecal microbiome similarity from high to low was: (i) bats from the same colony, (ii) bats from different colonies merged into one colony and (iii) bats from different colonies, with clear differences in similarity among all cases (figure 1).

Over four months together, all of the introduced Panama bats from distant sites engaged in clustering, and most engaged in oral contact (78%, electronic supplementary material, figure S1). The final gut microbiome similarity was predicted by rates of both oral contact and clustering, each when controlling for the other (MRQAP: oral contact $\beta = 0.24$, $n = 27$, $p < 0.0001$; clustering $\beta = 0.28$, $p < 0.0001$). Each effect also remained when controlling for whether the bats shared their capture site (clustering: $\beta = 0.37$, $p < 0.001$, $n = 27$, capture site: $\beta = -0.30$, $p = 0.003$; oral contact: $\beta = 0.32$, $p < 0.001$; capture site: $\beta = -0.21$, $p = 0.07$). After four months together, bats sourced from the same wild roost did not have more similar gut microbiomes than introduced bats ($\beta = -0.17$, $p = 0.2$), and we did not detect that the five mothers had more similar gut microbiomes to their own pups (mean similarity = 0.974 [0.966, 0.981]) compared to other pups (0.972 [0.968, 0.975]).

All 25 pairs that were sampled both before and after the merge had faecal microbiome similarities that changed in the predicted direction (MCMCglm: posterior estimate of interaction with 95% credible interval = $-0.12 [-0.13, -0.09]$,

![Figure 1](image_url)
pMCMC < 0.001, permutation test p-value < 0.001); they increased in the 15 introduced pairs (+0.08 [0.06, 0.10], pMCMC < 0.001), and decreased in the 10 same-roost pairs (−0.05 [−0.07, −0.03], pMCMC < 0.001, figure 2).

4. Discussion

Three lines of evidence from both our broader sampling and controlled experiment suggest social transmission of microbes in common vampire bats leads to a ‘social microbiome’ [1]. First, vampire bats from the same colony had more similar faecal microbiomes than bats from different colonies, in both captivity and in the wild (figure 1). Second, after bats from three wild colonies were introduced in captivity and housed together for four months, the identity of their original wild colony did not predict gut microbiome similarity; instead, gut microbiome similarity in the experimentally merged colony was predicted by rates of clustering and oral contact (electronic supplementary material, figure S1). Third, analysis of microbial similarity in opportunistic faecal samples from eight bats in the experimentally merged colony found that all 15 introduced pairs converged while all 10 same-roost pairs diverged (figure 2).

These findings corroborate previous studies of primates and rodents showing that social networks predict microbiome similarity after statistically controlling for environment and diet [6,29–41]. For example, laboratory mice housed together show convergence in their microbiomes [42,43]. A key advantage of our study is that we combined a controlled diet and environment with high-resolution interaction rates (sampling 6 h d⁻¹ for four months) among both familiar individuals and individuals with no previous contact. Our findings confirm that direct horizontal social transmission of microbes is an important component of microbiome similarity [1]. While mammalian gut microbiomes can be seeded through vertical transmission at birth [44], these microbiomes are highly mutable [34–39,45]. Even in highly constrained communities, like the gut microbiomes of the common vampire bat, we still see identifiable variation across populations and over time.

A common challenge in microbiome studies, especially in novel host animals, is the inability to identify significant portions of the microbial community. In studies of social transmission of microbes, strain-level identification appears to present the most robust evidence for social behaviours transmitting microbes, yet this method is rare [46,47]. Increasing the depth and breadth of sequencing of a microbiome, as done here, is a useful step in providing sequence data for novel and less-characterized microbes, which can aid attempts to better track specific taxa that are socially transmitted. The high consistency of identified species in the microbiomes we observed within and across vampire bat colonies from different geographical locations and states of captivity might be a result of their obligate and specialized diet, but many of our reads (approx. 76%) could not be assigned to any known taxa, showing yet unknown complexities in the common vampire bat’s microbiome.

Acknowledgements. We thank the participating zoos and staff for their aid in sample collection for this study. We also appreciate the time and aid provided by Alvaro Hernandez and Chris Wright for the sequencing on this project. We thank Aura Ruolo for important guidance on the analysis and prior literature. We thank three anonymous reviewers who provided comments that improved the manuscript.

Figure 2. Evidence for convergence from opportunistic faecal samples from eight bats. Each regression line shows the change in microbiome similarity for one of 25 selected pairs of bats from different roosts (top) or the same roost (bottom). For each pair, the first bat was sampled soon after capture and prior to the colony merge (dashed line), while the second bat was sampled both before and after the colonies were merged. Bats from different roosts were captured 340 km apart. Regression lines are labelled by dyad in electronic supplementary material, figure S2.

Ethics. This work was approved by the Smithsonian Tropical Research Institute Animal Care and Use Committee (no. 2015-0501-2022) and the Panamanian Ministry of the Environment (no. SEX/A-67-2019).

Data accessibility. The datasets and R code supporting this article have been uploaded to Figshare [48]. Sequence data are available through the NCBI SRA under BioProject PRJNA739024.

Authors’ contributions. K.Y. carried out the molecular laboratory work and sequence alignments, participated in data analysis and study design and drafted the manuscript; I.R. collected the social network data and critically revised the manuscript; R.S.M. supervised the molecular laboratory work and sequence alignments and critically revised the manuscript; G.C. supervised the collection of social data, participated in data analysis and study design and helped draft the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

Funding. Work by K.Y. was supported by the National Science Foundation Integrative Graduate Education and Research Traineeship Program Vertically Integrated Training with Genomics at the University of Illinois Urbana-Champaign. Work by I.R. was supported by a short-term fellowship from the Smithsonian Tropical Research Institute, a student research grant from the Animal Behavior Society and a graduate enrichment fellowship from the Ohio State University. Work by G.C. is supported by a grant from the National Science Foundation (Integrative Organismal Systems no. 2015928).

We thank the participating zoos and staff for their aid in sample collection for this study. We also appreciate the time and aid provided by Alvaro Hernandez and Chris Wright for the sequencing on this project. We thank Aura Ruolo for important guidance on the analysis and prior literature. We thank three anonymous reviewers who provided comments that improved the manuscript.
References

1. Sarkar A et al. 2020 Microbial transmission in animal social networks and the social microbiome. *Nat. Ecol. Evol.* 4, 1020–1035. (doi:10.1038/s41559-020-1220-8)

2. Gilbert JA. 2015 Social behavior and the microbiome. *Elife* 4, e07322. (doi:10.7554/elife.07322)

3. Archie EA, Tung J. 2015 Social behavior and the microbiome. *Curr. Opin. Behav. Sci.* 6, 28–34. (doi:10.1016/j.cobeha.2015.07.008)

4. Lombardo MP. 2008 Access to mutualistic endosymbiotic microbes: an underappreciated benefit of group living. *Behav. Ecol. Sociobiol.* 62, 18. (doi:10.1007/s00265-007-0428-9)

5. Vuong HE, Yano JM, Fung TC, Hsiao EY. 2017 The adaptations underlying the evolution of sanguivory in bats describes influences of host phylogeny, life history, physiology and geography. *Mol. Ecol. Resour.* 20, 204–215. (doi:10.1111/1755-0998.13101)

6. Kuthyar S, Manus MB, Amato KR. 2019 Leveraging non-human primates for exploring the social transmission of microbes. *Curr. Opin Microbiol.* 50, 8–14. (doi:10.1016/j.mib.2019.09.001)

7. Gogarten JF et al. 2020 Metabarcoding of eukaryotic parasite communities describes diverse parasite assemblages spanning the primate phylogeny. *Mol. Ecol. Resour.* 20, 204–215. (doi:10.1111/1755-0998.13101)

8. Xavier JB. 2016 Sociomicrobiology and pathogenic bacteria. *Microbiol. Spectr.* 4, 4. (doi:10.1128/microbiolspec.VMBF-0019-2015)

9. Stockmaier S, Stroeymeyt N, Shattuck EC, Hawley DM, Meyers LA, Bolnick DI. 2021 Infectious diseases and social distancing in nature. *Science* 371, eabc8881. (doi:10.1126/science.abc8881)

10. Phillips CD et al. 2012 Microbiome analysis among bats describes influences of host phylogeny, life history, physiology and geography. *Mol. Ecol. Resour.* 21, 2617–2627. (doi:10.1111/j.1365-294X.2012.05568.x)

11. Zepeda Mendoza M, et al. 2018 Hologenic adaptations underlying the evolution of sanguivory in the common vampire bat. *Nat. Ecol. Evol.* 2, 659–668. (doi:10.1038/s41559-018-0476-8)

12. Ingala MR, Becker DJ, Bak Holm J, Kristiansen K, Simmons NB. 2019 Habitat fragmentation is associated with dietary shifts and microbiota variability in common vampire bats. *Ecol. Evol.* 9, 6508–6523. (doi:10.1002/eev.32228)

13. Mueggde BD, Kuczyński J, Knights D, Clemente JC, Gonzalez A, Fontana L, Henriët K, Boyd R, Gordon JL. 2011 Diet drives convergence in gut microbiome functions across mammalian phylogeny and within humans. *Science* 332, 970–974. (doi:10.1126/science.1198719)

14. Carter G, Leffler L. 2015 Social grooming in bats: are vampire bats exceptional? *PLoS ONE* 10, e0138430. (doi:10.1371/journal.pone.0138430)

15. Wilkinson G. 1985 The social organization of the common vampire bat. *Behav. Ecol. Soc. Biol.* 17, 123–134.

16. Carter GG, Wilkinson GS. 2013 Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. *Proc. Biol. Sci.* 280, 20122573. (doi:10.1098/rspb.2012.2573)

17. Carter GG, Farine DR, Crisp RJ, Vrtilek JK, Ripperger SP, Page RA. 2020 Development of new food-sharing relationships in vampire bats. *Curr. Biol.* 30, 1275–9 e3. (doi:10.1016/j.cub.2020.01.055)

18. Ripperger SP, Stockmaier S, Carter GG. 2020 Tracking sickness effects on social encounters via continuous proximity-sensing in wild vampire bats. *Behav. Ecol.* 31, 1296–1302. (doi:10.1093/beheco/araa111)

19. Razik I, Brown BKG, Page RA, Carter GG. 2021 Nonkin adoption in the common vampire bat. *R. Soc Open Sci.* 8, 201927. (doi:10.1098/rsos.201927)

20. Farine DR. 2013 Animal social network inference and permutations for ecologists in R using asapine. *Methods Ecol. Evol.* 4, 1187–1194. (doi:10.1111/2041-210X.12121)

21. McVier LJ, Abu-Ali G, Franzosza EA, Schwager R, Morgan XC, Waldron L, Segata N, Huttenhower C. 2018 Biobakery: a metacomic analysis environment. *Bioinformatics* 34, 1235–1237. (doi:10.1093/bioinformatics/btx754)

22. Beghini F et al. 2021 Integrating taxonomic, functional, and strain-level profiling of diverse microbial communities with bioBakery 3. *Elife* 10, e65088. (doi:10.7554/elif/e65088)

23. McMurdie PJ, Holmes S. 2015 Shiny-phyloseq: web application for interactive microbiome analysis with provenance tracking. *Bioinformatics* 31, 282–283. (doi:10.1093/bioinformatics/btu616)

24. Wickham H. 2016 *Ggplot2: elegant graphics for data analysis*. Cham, Switzerland: Springer International Publishing. Imprint: Springer.

25. RStudio Team. 2016 *RStudio: integrated development for R*. Boston, MA: Rstudio, Inc.

26. Love MI, Huber W, Anders S. 2014 Moderated statistical tests for designing, and interpreting microbiome functional, and strain-level profiling of diverse microbial communities with bioBakery 3. *Elife* 10, e65088. (doi:10.7554/elif/e65088)

27. Dekker D, Knackhert D, Snijders TA. 2007 Sensitivity of MRQAP tests to collinearity and autocorrelation in metagenomic data. *Environ. Microbiol.* 9, 251–262. (doi:10.1111/j.1462-2920.2007.01069.x)

28. Cytney A, Ripley B. 2015 boot: Bootstrap R (S-Plus) Functions. *R package version 1.3-28.*

29. Balasubramaniam KN, Beisner BA, Hubbard JA, Vandeelst JJ, Atwell ER, McGowan B. 2019 Affiliation and disease risk: social networks mediate gut microbial transmission among rhesus macaques. *Anim. Behav.* 151, 131–143. (doi:10.1016/j.anbehav.2019.03.009)

30. Grineisen LE, Livemore J, Alberts S, Tung J, Archie EA. 2017 Gut microbial transmission among rhesus macaques. *Appl. Microbiol. Biotechnol.* 96, 5337–5352. (doi:10.1007/s00253-016-6797-9)

31. Sharma A et al. 2019 Longitudinal homogenization of the microbiome between both occupants and the built environment in a cohort of United States Air Force Cadets. *Microbiome* 7, 50. (doi:10.1186/s40168-019-0686-6)

32. Limbick B, Brinkman B, yacht RN, Cauwe B, Vandenabeele P, Liston A, Raes J. 2013 Inflammation-associated enterotypes, host genotype, and inter-individual effects drive gut microbiota variation in common laboratory mice. *Genome Biol.* 14, R4. (doi:10.1186/gb-2013-14-1-r4)
43. Hufeldt MR, Nielsen DS, Vogensen FK, Midtvedt T, Hansen AK. 2010 Variation in the gut microbiota of laboratory mice is related to both genetic and environmental factors. Comp. Med. 60, 336–347.

44. Dominguez-Bello MG, Costello EK, Contreras M, Magris M, Hidalgo G, Fierer N, Knight R. 2010 Delivery mode shapes the acquisition and structure of the initial microbiota across multiple body habitats in newborns. Proc. Natl Acad. Sci. USA 107, 11 971–11 975. (doi:10.1073/pnas.1002601107)

45. Kolodny O, Weinberg M, Reshef L, Harten L, Hefetz A, Gophna U, Feldman MW, Yovel Y. 2019 Coordinated change at the colony level in fruit bat fur microbiomes through time. Nat. Ecol. Evol. 3, 116–124. (doi:10.1038/s41559-018-0731-z)

46. Springer A, Mellmann A, Fichtel C, Kappeler PM. 2016 Social structure and Escherichia coli sharing in a group-living wild primate, Verreaux’s sifaka. BMC Ecol. 16, 6. (doi:10.1186/s12898-016-0059-y)

47. Brito IL et al. 2019 Transmission of human-associated microbiota along family and social networks. Nat. Microbiol. 4, 964–971. (doi:10.1038/s41564-019-0409-6)

48. Yarlagadda K, Carter G. 2021 Data and R code for ‘Social convergence of gut microbiomes in vampire bats’. Figshare. (doi:10.6084/m9.figshare.14992440.v3)