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2	Thinking small: next-generation sensor networks close the size gap in vertebrate
3	biologging
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34 Abstract:

- 35 Recent advances in animal tracking technology have ushered in a new era in biologging.
- 36 However, the considerable size of many sophisticated biologging devices restricts their
- 37 application to larger animals, while old-fashioned techniques often still represent the state-of-
- 38 the-art for studying small vertebrates. In industrial applications, low-power wireless sensor
- 39 networks fulfill requirements similar to those needed to monitor animal behavior at high
- 40 resolution and at low tag weight. We developed a wireless biologging network (WBN), which
- 41 enables simultaneous direct proximity sensing, high-resolution tracking, and long-range
- 42 remote data download at tag weights of one to two grams. Deployments to study wild bats
- 43 created social networks and flight trajectories of unprecedented quality. Our developments
- highlight the vast capabilities of WBNs and their potential to close an important gap in
- biologging: fully automated tracking and proximity sensing of small animals, even in closed
- 46 habitats, at high spatial and temporal resolution.
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- 48
- 49 Keywords: wireless biologging network (WBN); ultra-low power; automated animal tracking;
- 50 proximity sensing; bats; terrestrial biologging

52 Introduction

Recent advances in animal tracking technology have ushered in a new era in biologging^{1,2}. 53 54 By collecting data of unprecedented quantity and quality, automated methods have revolutionized numerous fields including animal ecology³, collective behavior⁴, migration⁵, 55 and conservation biology⁶. For example, automated tracking of animals from space has 56 57 advanced considerably over the past decade, in particular for observing large-scale 58 movements¹. However, satellite communication for localization or data access requires a lot 59 of energy, and heavy transmitters greatly limit our ability to track smaller vertebrate species¹. 60 Efforts to further miniaturize increasingly powerful biologging devices culminated in the 61 launch of the ICARUS initiative in 2019, which aims to achieve global animal observation at a 62 small tag weight through a combination of GPS tracking, on-board sensing, energy 63 harvesting, and energy-efficient data access from low space orbit⁷. ICARUS promises a great 64 step forward in tracking large-scale movements such as migration. GPS tracking, however, is 65 often not ideal or feasible for field biologists studying behavior on smaller spatial scales. GPS 66 tracking of small vertebrate species is further limited by the considerable weight of GPS 67 devices¹. Satellite reception is hampered by complex habitats and impossible if animals go 68 inside trees, caves, or underground burrows. 69 In industrial applications or for civilian surveillance, low-power wireless sensor

70 networks (WSNs) fulfill requirements similar to those needed to track animal behavior at high resolution and at low tag weight⁸. Consistently, there have been numerous applications for 71 WSNs in wildlife monitoring ('biologging') since the early 2000s⁹. In the last decade, more 72 73 sophisticated approaches have created powerful monitoring systems, e.g., for high-resolution tracking¹⁰ and fully automated logging of social encounters^{11, 12}. The major challenge in 74 75 developing efficient wireless biologging networks (WBNs) is to design ultra-low power 76 communication networks in order to maximize performance, minimize energy consumption, 77 and reduce tag weight.

Here, we describe a system that takes WBNs to the next level: a multifunctional and
thus <u>B</u>roadly <u>A</u>pplicable <u>T</u>racking <u>S</u>ystem ('BATS', Figure 1). We first present a solution for

80 direct proximity sensing that enables the collection of proximity data at a temporal resolution 81 of seconds, at tag weights of one to two grams, and with runtimes of up to several weeks 82 depending on the sampling rate. Second, we describe an adaptive option for triangulating 83 spatial positions based on Received Signal Strength (RSS) by ground-borne localization 84 nodes. This adaptive option allows automated recording of robust movement trajectories 85 even in structurally complex habitats. Third, we explore a new, almost energy neutral solution 86 for remote data access over distances of several kilometers at low data rates. Finally, we 87 present an energy model that shows the effect of the parameter settings of software tasks on 88 the runtime of the animal-borne tag. First deployments of BATS have resulted in proximity 89 and tracking data of unprecedented guality and have demonstrated the high potential of 90 WBNs for studying (social) behavior. Our developments highlight the vast capabilities of 91 WBNs and their potential to close an important gap in biologging: fully automated tracking 92 and proximity sensing of small animals, even in closed habitats, at high spatial and temporal 93 resolution.

94

95 Results

96 The modular structure of BATS allows researchers to combine proximity sensing, long-range 97 telemetry, and high-resolution tracking (Figure 1) depending on the research question and 98 the behavior of the animals. We chose bats to test and validate the system since they are 99 small-bodied and move fast in dense vegetation, both challenges to the performance of the 100 WBN. Three recent field studies were conducted in temperate and tropical habitats on three 101 bat species: greater mouse-eared bats (*Myotis myotis*), common noctules (*Nyctalus noctula*) 102 and common vampire bats (Desmodus rotundus). Each study documented high-resolution 103 proximity data by direct proximity sensing among animals and automatically forwarding data 104 to ground nodes (Figure 1a) that were deployed at roosting or foraging sites. Bat-borne 105 mobile nodes that came within the reception range of the localization grid automatically 106 increased their sampling rate to enable high-resolution localization (Figure 1b). Data for the 107 synchronization of clocks was transmitted successfully over distances of more than 4 km by

108 long-range telemetry (Figure 1c). The following sections describe the empirical validation of

the system.

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112 Figure 1: BATS overview. (a) Animal-borne mobile nodes (MNs) document animal-animal 113 meetings, which are triggered by MN-beacons 24/7 and independently of ground 114 infrastructure. Each mobile node forwards its meeting data when it receives beacons from a 115 ground node (GN) that is dedicated to downloading and storing data. (b) When a tagged 116 animal enters a grid of localization nodes (depicted by an antenna with red/blue gain 117 patterns), a beacon of a tracking-dedicated GN triggers the transmission of localization 118 packets from the MN to the localization nodes. Received signal strength indicators (RSSIs) of 119 the impinging localization packets are then sent from the localization nodes to a work station 120 via a WLAN. (c) Long-range bursts, which contain encoded sensor data, are received by 121 long-range receivers. Long-range telemetry enables data transmission over distances of 122 several kilometers at a low data rate.

123

124 High-resolution social network data from direct proximity sensing

125 Fifty individuals of one large natural colony of common vampire bats (*Desmodus rotundus*)

126 were tagged simultaneously in Panama. Associations with other tagged bats are fluid and

127 highly dynamic both during day and night. For example, Figure 2a shows the course of the 128 meeting history and the dynamic range of degree centrality for a single bat (ID 56) over a 129 two-day period. The high temporal resolution of meetings (all mobile nodes in reach 130 communicate with each other every two seconds) also makes it possible to infer a behavior 131 such as departure from the roost or movement within the roost. For example, foraging bouts 132 can be identified by a sudden drop in meeting partners at night, which can be verified by 133 contacts to ground nodes outside the roost. Autonomous direct proximity sensing allows 134 monitoring changes in roosting associations, caused by moving among subgroups within the 135 roost (Figure 2b, c) and it also allows inferring 'social foraging networks' outside the roost 136 (Figure 2d). In addition, every meeting is labeled with a maximum signal strength intensity 137 indicator (RSSI). This makes it possible to subset the meeting dataset according to signal strength, an estimate for proximity¹³. RSSI values can distinguish close-contact associations 138 139 from associations based on merely occupying the same area.

140 The social networks created from direct proximity sensing are independent of the 141 whereabouts of the tagged bats and provide an adaptive temporal resolution of seconds. 142 Almost 400,000 individual meetings were recorded during the first eight days of our field test. 143 To take bats as an example, the typical approach for collecting social network data has been 144 to sample some unknown portion of co-roosting associations in a sample of identified roosts each day¹⁴. Our system allows complete networks of all bats every few seconds. This 145 146 temporal resolution makes changes in social gathering directly visible if time slices in highresolution data are small enough¹⁵. We believe this represents an extraordinary advance for 147 148 studying such small free-ranging animals, and it allows for an analytical depth which is so far 149 known predominantly from human social networks generated by communication among smart phones or social media¹⁵. 150

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Figure 2: High-resolution association data in wild vampire bats. (a) Meeting history of a single vampire bat (ID 56; 50 tagged bats in total) with other tagged bats. Red lines show meetings between bat 56 and other tagged bats (right-hand y-axis). The black line shows the degree centrality (number of associated tagged bats, left-hand y-axis) of bat 56 every two seconds. Date and time are on the x-axis. Shaded areas indicate night time. Vertical dashed lines show egocentric social networks at each snapshot of time during roosting (b,c) and foraging (d). Associations with the focal bat are indicated by red lines.

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162 RSSI-based localization from angle-of-arrival estimation:

Seventeen wireless localization nodes were used to track tagged 11 mouse-eared bats (*Myotis myotis*) over an area of approximately 1.5 ha in an old, natural deciduous forest in northern Bavaria (Germany, Forchheim). We were able to reconstruct flight trajectories from foraging mouse-eared bats. Figure 3b shows as an example two trajectories of one foraging mouse-eared bat during two different nights in early August.

168 We evaluated the spatial resolution of the tracking system by estimating a trajectory 169 from a defined reference path using unscented Kalman filters. The reference path and

170 estimated trajectories are shown in Figure 3a. The trajectories were calculated from angle-of-171 arrival estimates of signals impinging on localization nodes. Angles were estimated from 172 difference measurements of received signal strength (RSS) at two orthogonal antenna gain 173 patterns. This procedure in combination with a set of post-processing techniques for 174 probabilistic multipath mitigation makes the trajectories robust to multipath propagation. The 175 calculated trajectory is based on 4,912 data sets, while one set was composed of up to 2x17 176 RSS difference measurements (one per frequency band), if all 17 localization nodes were 177 within the reception range of the mobile node. For comparison, we also analyzed four tracks 178 recorded by a 15 g heavy-duty Ornitela GPS tracker, which is commonly used for tracking 179 large birds of up to 450 g body weight. The mean positioning error was 7.30 m for the 180 Ornitela GPS tracker and 5.65 m for the trajectory of the BATS system. 181 We calculated the positioning accuracy at lower densities of the localization grid. 182 Localization was less accurate with fewer localization nodes (Figure 4), but it was robust and 183 comparable to the full tracking grid (17 nodes) when using 15 - 16 nodes. With 12 - 14 184 nodes, we observed increasing variation in average error rates. With 11 nodes, the mean 185 error was similar to the results from GPS tracking. Variation increased steadily with lower 186 numbers of nodes and the mean error reached more than 10 m with a maximum error rate of 187 34 m at 6 nodes. At such low grid densities, the localization results tended to diverge, 188 resulting in increasing positioning errors. In addition, sparser grids lack robustness against 189 multi-path scattering. Consequently, the node density may only be reduced to a certain point. 190 while positioning errors remain quite stable (Figure 4). 191 These analyses show that 11 localization nodes over an area of 1.5 ha in a forested 192 habitat might be sufficient to construct high-resolution trajectories comparable in quality to a 193 heavy-duty GPS tracker, which would only last for a few hours using a 15 g device, or to reverse GPS in open desert habitats¹⁰. Only moderate resources and human effort are 194 195 needed to cover an area of a few hectares. For example, a setup as described above

196 consisting of 11 localization nodes is deployed and configured by two people in one to two

197 workdays.





Figure 3: Tracking bat movements in a forest. (a) Tracking grid in a deciduous forest of
Forchheim, Germany, consisting of 17 localization nodes (grey dots) covering an area of ca.
1.5 ha. Dashed black line: known reference path; blue line and blue shading: estimated path
and average localization error obtained by BATS; yellow lines: four individual GPS tracks. (b)
Estimated flight trajectories of a tagged mouse-eared bat during foraging on August 2nd and
5th.





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212 Distance verification of packet transmission by long-range telemetry:

213 Transmission distances of data packages were measured in an urban green area. 34 noctule 214 bats (Nyctalus noctula) were tagged in a forest within the city of Berlin and two long-range 215 telemetry receivers were placed at a distance of about 1 and 4 km from the forest. 216 Mobile nodes transmitted with each MN-beacon a burst for long-range transmission of 217 the mobile node's time stamp. During a period of two weeks, we were able to receive more 218 than 168,000 long-range bursts, which allowed us to successfully recover 9,511 complete 219 timestamps from 32 individual bats. To mitigate the impairment by interfering transmission, 220 one complete long-range telemetry packet is split over 24 single burst transmissions. At the 221 long-range receiver, 24 subsequent bursts are merged to one actual long-range packet 222 containing the ID and the bat's time reference. This transmit scheme assures that the mobile 223 node's transmit module is only activated for a short time period avoiding stress on the

batteries and hardware. In addition, it avoids interference of other channels by a timefrequency hopping pattern in transmission. Instead of a complete package loss, only a
fraction of the collection of bursts might be corrupted, which can be reconstructed by means
of error-correction codes at the receiver side. It is only due to this specialized telegramsplitting technique¹⁶ that a long-range transmission under extreme power-restrictions and
vastly occupied frequency channels becomes possible.

230 Reception of long-range data should perform best when the tagged bats move in 231 open airspace. However, we recovered a considerable number of these long-range bursts 232 while bats were inside their roosts during the day. 563 long-range bursts received during the 233 day were mapped to the known roosts of the bats, allowing us to measure the transmission 234 distance. Fifty-seven long-range bursts from four bats inside their roost were recovered over 235 distances of ca. 4.2 km (between roost 1 or 2 and the receiver at the cogeneration plant, 236 Supplementary Figure 1). 506 long-range bursts from five tagged bats were recovered at 237 distances between 667 and 819 m (between roost 1 or 3 and the receiver at the retirement 238 home, Supplementary Figure 1). Burst retrieval over distances of more than 4 km was 239 surprising. Theoretical calculations predicted transmission distances of about 5 km assuming 240 barrier-free transmission¹⁷. In the field, however, signals had to pass first through the wooden 241 wall of the tree roost and second the forest's vegetation, which should greatly reduce 242 transmission distance.

243 Data recovery is a major challenge in automated light-weight tracking-systems. Signal 244 transmissions inherently suffer from limited transmission power under heavy losses due to 245 distance, shadowing, and other interfering signals. Remote downlinks, e.g., per GSM (Global 246 System for Mobile Communications), add considerable weight in the form of circuitry and battery¹. Many light-weight trackers must therefore be retrieved, or energy harvesting must 247 be used to counter-balance the expenses for remote data download^{7, 18-20}, again adding 248 249 weight for the required hardware components. When tagged animals move on predictable 250 scales, energy-saving methods like transfer via VHF (Very High Frequency) or radio modems 251 may be an option to receive data over distances of hundreds of meters to few kilometers²¹.

252 Our scenario explores options to decrease the energy expense for downloading stored data 253 to a negligible proportion of the overall energy budget (compare Figure 5). For data 254 download over short distances of ca. 100m, we accumulate and pre-process data on-board 255 and use sophisticated communication protocols that maximize data-package reconstruction while minimizing energy demand^{22, 23}. The above described long-range telemetry mode 256 257 provides an option for robust transmission of small amounts of data at a low rate without the 258 expenditure of additional energy due to the hybrid modulation of the signal. In comparison, other long-range systems for biologging, such as LoRa¹², enable higher transmission rates. 259 260 However, the bi-directional communication between transmitter and receiver strongly 261 increases the energy demand no the mobile node. 262 263 Sensor node energy consumption and lifetime

264 A major strength of WBNs is the ease of adjusting parameters such as sampling rate and in 265 turn energy consumption. These adjustments can maximize runtime for a given battery 266 capacity, or alternatively maximize sampling rate to obtain higher resolution data. To 267 investigate the impact of the different software-task parameters on runtime, we derived a 268 model for energy consumption. We computed examples of runtimes of mobile nodes for two 269 battery capacities and different parameter settings (Table 1). For example, the increase in 270 energy consumption when tracking two to four hours per day can be compensated by 271 extending the MN-beacon intervals. We achieve runtimes of at least five days using a 12mAh 272 battery (corresponding to a 1g mobile node) even at the shortest beacon intervals of two 273 seconds (active mode) and with two hours of high-resolution tracking per day. Depending on 274 the parameter settings, we achieve runtimes of up to 13 days using the smaller battery and 275 25 days using 22mAh (Table 1).

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Table 1: Estimated runtimes of mobile nodes for two battery capacities of 12 or 22
mAh inferred by an energy model for MN-runtime. While the model comprises seven
energy consuming tasks, the shown runtimes are based only on varying MN-beacon intervals

- and localization time (i.e. animal is within the localization grid). For MN-beacon intervals two
- operation modes are possible, depending on whether an animal is within reception range of a
- ground node (inactive mode) or not (active mode).

MN-beaco	n interval [s]	Time inside tracking	Estimated runtime
if absent from	if near ground node	grid per day [h]	[h] for a battery
ground node	(inactive mode)		capacity of
(active mode)			12 / 22mAh
2	10	0	151 / 278
10	30	0	321 / 589
2	10	2	135 / 248
10	30	2	257 / 471
30	60	4	247 / 454

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284 Figure 5 illustrates the energy consumption of the different software tasks on the 285 mobile nodes of the six different scenarios described in Table 1. When localization is 286 disabled (i.e., only proximity sensing), sending out beacons to wake up other mobile nodes to 287 initiate meetings strongly drives the energy demand (Figure 5a, b). Therefore, modifying the 288 MN-beacon intervals has the highest impact on runtime. When localization is enabled, 289 tagged animals send localization packages whenever they enter the tracking grid. The high 290 duty-cycle of sending localization packages (8/s) strongly decreases the runtime (Figure 5c-291 e, Table 1). At active/inactive MN-beacon intervals of 2/10s, a daily localization period of two 292 hours decreases the overall runtime by 10.8% (Fig 5 a, c, Table 1). At four hours of 293 localization, the energy demand for localization dominates the overall energy consumption, in 294 particular at high MN-beacon intervals.





297 **battery.** Energy demand per software task depends on parameter settings for active/inactive

beacon interval [s] and amount of time an animal spends in the localization grid [h]. The

299 energy demand is shown for the seven major software tasks; MN = mobile node, GN =

300 ground node. Zero time in the localization grid (a, b) refers to a pure proximity sensing

301 scenario.

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303 Model-derived runtimes were compared with empirical runtimes from field tests on 304 noctule bats (Nyctalus noctula), where mobile nodes were either powered by a 12mAh 305 battery or a 22mAh battery, resulting in MN weights of 1.1g to 1.9g depending on housing. 306 The average runtime was 148h (max. 209h) for the small battery, while the model predicted 307 151h. For the larger battery, average runtime was 280h (max. 426h) with a predicted 308 average value of 277h. For both batteries, the predicted values were very close to the 309 observed (1.8% overestimation and 0.7% underestimation, respectively) indicating that the 310 model is a reliable tool for experimental design of a field study.

311

312 Discussion

In past years, developments in high-performance proximity sensing using significantly
 larger animal-borne tags²⁴ and in ground-based high-resolution tracking in low-clutter desert

environments¹⁰ have previously pushed the boundaries of what was technologically feasible. 315 316 BATS takes the next step by combining these functionalities while keeping the tag weight at 317 one to two gram. Adhering to the 5% rule²⁵, even animals weighing as little as 20g can be 318 tagged with this system. These smaller species make up a large proportion of birds and 319 mammals (see Figure 3 in¹) and WBNs will give researchers new capabilities to address a 320 wide range of questions in animal behavior and ecology. Our adaptive and scalable system 321 design provides great flexibility to tailor such a system, allowing adjustable use for any 322 species- and study-specific requirement. The design of the mobile node allows to add 323 multiple functionalities beyond the ones presented here, such as accelerometers, magnetometers, or even an on-board electrocardiogram (ECG) sensors²⁶. 324 325 An early example of automated tracking of small-bodied animals on a limited 326 geographic scale was ARTS, a system for automated VHF tracking, which was installed on Barro Colorado Island, Panama²⁷. This six-year endeavor in the 2000s already highlighted 327 328 the promising opportunities offered by WBNs: scalability, remote reconfiguration, full 329 automation, and low-cost tags. Yet, a rather low positioning accuracy (~50 m) and restricted coverage were limiting factors²⁷. Most of today's solutions for automated tracking of small 330 331 animals such as songbirds, bats, or rodents perform best at larger geographic scales or in 332 open habitats. For example, current versions of 1 g GPS loggers are suitable to explore seasonal large-scale movements^{18, 20}. However, they cannot reconstruct flight paths in a 333 334 complex environment, since they can only collect around 100 fixes. Furthermore, the 335 physical devices must be retrieved for data recovery, and satellite reception suffers within 336 vegetated areas. Alternatively, reverse GPS can track small animals much more energy-337 efficiently and at much higher temporal and spatial resolution by measuring time-of-flight at ground-based receiving stations¹⁰. However, time-of-flight measurements are inherently 338 339 affected by vegetation and perform best in open areas. Therefore, we combined signal 340 strength measurements (including angle of arrival (AoA) estimates) from two frequency 341 bands and probabilistic multipath mitigation²⁸ to create a system that is robust to multipath 342 propagation and thus performs well in complex environments. Common but costly measures

343 to resolve multipath propagation are large-aperture antenna arrays for AoA tracking or large 344 signal bandwidth for time-of-flight tracking. However, the future of animal tracking will most 345 certainly center on low cost, ultra-low power integrated circuits, which are currently 346 experiencing a noticeable push due to their broad applications in Industry 4.0 and 5G. This 347 technology has the potential to dramatically boost the capabilities of biologging devices. 348 Contact networks of small-bodied animals have received increased attention in past 349 years and are most commonly built from RFID- (radio-frequency identification) or PIT-350 (passive integrated transponder) tagged animals that were observed to be feeding or sleeping at the same site at the same time²⁹⁻³¹. Later developments for direct encounter 351 352 logging were able to log association independently of the locality. However, these sensors were either guite large and heavy¹¹ or had short runtimes of less than 24h³² due to the high 353 354 energy demand for the permanently active receiver — a major shortcoming for applications 355 in small-bodied species. We show that the use of wake-up receivers and adaptive operation 356 paired with novel wireless communication protocols dramatically reduce the energy demand 357 of such wireless sensor tags. We believe that direct encounter logging or more precisely 358 proximity sensing will enable diverse research in the future, as this approach creates large 359 datasets, with additional sensor data providing the behavioral context closing the gap 360 between social patterns and their underlying processes².

361 Ongoing work on ultra-low power sensor networks not only targets animal tracking 362 systems but a variety of "Internet of Things"-solutions in general. Energy efficiency is not only 363 a question of hardware circuit design but also of how to interact across all relevant layers in 364 the node's software stack (i.e., application, and operating system). On the mobile node, the 365 interaction aspect between communication layers (e.g., application and MAC layer) concerns 366 the placement of certain functions (e.g., retransmissions) within the entire software 367 hierarchy³³ such that energy-efficient operation is not affected by unnecessary functional redundancies. Besides, cross-layer designs that optimize the timing of communication 368 369 processes and make them deterministic at least within limits³⁴ form the software-engineering 370 basis for an overall energy-aware systems approach. In our scenario, energy-efficient and

371 reliable communication between nodes are cross-cutting concerns, since failed 372 communication attempts lead to additional overhead for retransmissions. Very promising 373 examples for low-power communication initiation are novel selective wake-up receivers³⁵, 374 which allow the small tags to enter sleep modes in the nano-ampere range rather than 375 constantly operating in the micro- or milli-ampere range. Selective wake-up concepts allow 376 waking up dedicated recipients of a message (or a selected subset thereof) instead of 377 waking up all systems in communication range. Integrated into the animal tracking nodes, 378 this could enable the next quantum leap on low-power operation. The alternative to making 379 the receiver operate on a lower energy budget is to make the communication more reliable. 380 Recent advances in integrating coding for forward error correction into such lightweight systems show very promising results, e.g., using erasure codes²². Ultra-reliable 381 382 communication protocols currently used in 5G networks can also be applied to localization 383 nodes, which are used for quasi-live tracking in the bat tracking scenario. For example, the 384 ground network can be used as a distributed antenna array, which allows the use of smart 385 decoding algorithms for very weak communication signals to further optimize data recovery³⁶.

386

387 Conclusions

388 There is no single best method for tracking animal behavior. RFID- and PIT-tags allow 389 monitoring presence of animals at known sites at low cost. Satellite-based localization will 390 remain the method of choice to monitor large-scale movements such as migration or to explore unpredictable events such as nomadism^{1, 37}. However, we believe that WBNs like 391 392 BATS will greatly benefit biologging of small animal species that move over smaller and more 393 predictable spatial scales, especially inside of habitats where signal transmission is 394 constrained. The homologies of applications between mobile communications and biologging (e.g., Bluetooth low energy for communication among mobile nodes¹²) will boost the 395 396 development of WBNs. Experimental setups including automated triggers (e.g., acoustic 397 playbacks or other sensory cues) might easily be integrated and direct proximity sensing will 398 bring exciting research opportunities. Such setups will allow to study the effect of social

399	network dynamics on phenomena such as transmission of social information ³⁰ and
400	pathogens ³⁸ , and key ecosystem functions such as pollination and seed dispersal ³⁹ .
401	
402	4. Methods
403	The WBN hardware, software, and functionality:
404	Figure 1 is a schematic overview of BATS. In order to study its performance, we empirically
405	evaluated the three major functions of the system: proximity sensing (Figure 1a), high-
406	resolution tracking at local scales (Figure 1b), and long-range telemetry (Figure 1c). See
407	Glossary (Supplementary Table 1) for definitions of terms.
408	
409	Proximity sensing:
410	Any given mobile node (MN) dyad generates meetings whenever it comes within reception
411	range (5 - 10 m depending on the environment). The animal-borne MN consists of a 22mm x
412	14mm Flex PCB circuit board, which is populated with a central System-on-Chip (EFR32,
413	Silicon Labs) containing an ARM Cortex-M4 core and two radio frontends for 868/915MHz
414	and 2.4GHz (Supplementary Figure 2). The transmitter in the sub-GHz frontend periodically
415	sends MN-beacons, a signal that contains a wake-up sequence. The rate of beacons is
416	configurable (see below). A low-power wake-up receiver on the MN triggers the conventional
417	receiver to receive incoming information on the ID whenever a MN-beacon is received from
418	another MN. Subsequently, a meeting is created between the communicating MN-dyad

419 (Figure 1a left). While a conventional receiver draws a relatively high current in receiving

420 mode waiting for incoming packages, a wake-up receiver achieves this functionality with a

421 low current (yet, at cost of sensitivity and performance). When no further MN-beacons are

received from the meeting partners for 5 MN-beacon intervals, the meeting is closed and

423 stored to memory along with the ID of the meeting partner, meeting duration, maximum RSSI

424 and a relative timestamp. The mobile node contains both persistent and volatile random-

425 access memory for data storage.

426 The conventional receiver of the sub-GHz frontend is periodically activated to observe 427 the presence of a ground node (at a fixed interval of every two seconds), which is indicated 428 by a ground node beacon (GN-beacon), periodically broadcast by the transmitter of each 429 ground node (Figure 1a right). The transmitter supports several configurations defining the 430 main purpose of the ground node (GN) and enabling location-dependent adaptive operation 431 of the WBN. (i) A download-dedicated GN broadcasts a signal that enables transmitting MN 432 data based on a customizable RSSI threshold received at the mobile node. (ii) A tracking-433 dedicated ground node positioned within the grid of localization nodes for high-resolution 434 tracking broadcasts a signal that activates the 2.4GHz frontend in addition to the sub-GHz 435 front end on the MN, transmitting 'localization packets' at a rate of 8 packets per second. (iii) 436 A presence-detection-dedicated GN triggers the transmission of 'presence signals' by an MN 437 and stores incoming signals which can be used to determine presence/absence of tagged 438 individuals (presence at resources or at sleeping sites). Combinations of functionalities (i-iii) 439 may be used in a single GN if desired (e.g., a tracking-dedicated GN can also trigger data 440 download). Incoming MN data is received by the GN and stored by a Raspberry Pi 441 (Raspberry PI Foundation, Cambridge, UK) to a SD card along with the ID of the transmitting 442 MN and the receiving GN, respectively, and a timestamp, which is provided by a GPS unit. 443 The Raspberry Pi also hosts a WiFi allowing the user remote data access. 444 Visualization of proximity sensing data is facilitated by the custom-made software

'meeting splitter' (see Figure 2). For each specified mobile node ID, the current meeting 445 446 partners are projected onto a discrete time axis (one second resolution). We specified a 447 configurable time window around each point on the time axis (five seconds in case of Figure 448 2). All ongoing meetings, which overlap with the window around the respective point in time, 449 are included in the set of associated bats at this particular point in time. The result per bat is 450 a set of associated bats per each second in the dataset. A subsequent automated analysis 451 classifies each meeting as inside or outside the roost, depending on the number of 452 simultaneous meeting partners (not applied in this manuscript).

453

454 RSSI-based high-resolution tracking:

455 Localization nodes (LN) perform field strength measurements, which are collected by WLAN 456 and are processed by a PC including a file system whenever animal-borne mobile nodes 457 enter the localization grid (Figure 1b; localization nodes collect localization packets from 458 mobile nodes; the transmission is triggered by a ground node). Each localization node 459 comprises a software-defined radio (consisting of a radio-frequency frontend, a highly 460 integrated analog-to-digital converter, a field-programmable gate array and a microcontroller) 461 and two receiving antenna gain patterns each with two main lobes (Figure 1b, red and blue 462 pattern, respectively). The bi-lobed shape indicates the directional sensitivity of the antenna, 463 while the direction of each lobe represents its maximum in sensitivity. The red pattern is 464 rotated by 90° compared to the blue pattern, and both are simultaneously used to estimate 465 the angles of arrival (AoA) of the localization packages transmitted by the animal-borne MNs. 466 The difference in received signal strength (RSS) of the two patterns relates to AoA: If the 467 difference – RSS of the blue pattern minus RSS of the red pattern – is maximum, the wave 468 front impinges on the localization node either from east or west; if the RSS difference is 469 minimum, the direction of arrival is N or S. Accordingly, there are four options for the AoA if 470 the difference is zero: NE, NW, SE or SW. These ambiguities are resolved by fusing 471 measurements of several localization nodes.

472 This design allows us to exploit not only error-prone absolute field strength measurements⁴⁰, but also fail-safe angles of arrival. These are not affected by faulty 473 474 propagation laws or shadowing effects, because both error sources disappear when forming 475 the RSS differences. The angular resolution of the AoA estimates improves with increasing 476 ambiguity of the antenna pattern designs. However, more localization nodes have to be in reach to resolve the ambiguity⁴¹. During the Forchheim field trial, we collected up to 272 477 478 angle estimates per second when all 17 localization nodes were in reception range. 479 To further improve localization accuracy, we exploited three sources of information 480 ((a) model-based Bayesian positioning, (b) frequency diversity, (c) retrodiction), which 481 increase robustness against multipath propagation. This effect complicates the positioning

process, in particular in structurally complex environments since wave fronts impinge a
localization node out of the different directions of multiple reflectors (e.g., surrounding
vegetation). The information sources to counteract multipath-related adverse effects are
described in the following:

486 (a) Model-based Bayesian positioning: Due to the nature of multipath propagation, a stochastic model can be devised to characterize the resulting spread in the AoA estimates²⁸. 487 488 This AoA measurement model can be incorporated into the likelihood function of the 489 recursive Bayesian positioning process, e.g., based on a Kalman filter or a related grid-based estimation filter⁴². The recursive estimation process yields a probability distribution 490 491 characterizing where the bat may be, considering propagation characteristics from a local 492 channel model⁴³. All measurements are fused during the recursive process taking into 493 account a movement model reflecting the flight characteristics of a bat (e.g., max. flight 494 speed). The better the agreement of the various AoA estimates, the more pronounced the 495 positioning probability distribution.

496 (b) Frequency diversity: Multipath propagation leads to frequency-dependent fading. 497 We therefore measured field strength not only on the primary far-reaching carrier frequency 498 at 868 MHz, but also on a secondary carrier frequency at 2.4 GHz. On both carrier 499 frequencies, wave forms comprising several subcarriers are employed to enhance the field-500 strength based AoA estimation process. Due to the large carrier frequency separation (> 501 1.4GHz), frequency-dependent fading effects are de-correlated even if multipath time-of-flight 502 differences are minor, i.e., in the range of a few meters, which corresponds to our accuracy 503 level.

(c) Retrodiction. If we do not have to estimate the position of a particular bat in realtime, we can exploit all measurements of a bat to estimate a complete trajectory. Forwardbackward filtering enhances estimation quality considerably, yielding a positioning quality in the range of 4 m (1 - σ). Performance limits of field-strength based positioning have been discussed in depth^{41, 44}.

509

510 We evaluated the trade-off between tracking grid density and localization guality for the 511 Forchheim setup, which comprised 17 localization nodes. In particular, we asked: how many 512 localization nodes are required to obtain localization quality comparable to heavy-duty GPS 513 tracking? We selected subsets of 6 to 16 out of the 17 localization nodes in order to observe 514 the decrease in positioning accuracy with decreasing grid density. Trajectories including 515 standard deviation were estimated for each subset of localization nodes. 17 configurations 516 were calculated for the grid consisting of 16 nodes (all possible subsets of the full grid) and 517 25 unique, randomly chosen subsets for all remaining grid configurations (6 to 15 nodes, 518 respectively) to obtain average errors for the given number of nodes (see Figure 4). 519

520 Long-range telemetry

521 Our long-range telemetry approach aimed at transmitting long-range bursts from mobile 522 nodes over distances of up to several kilometers – much longer distances than our 523 download-dedicated ground nodes would allow for – within the city of Berlin, under harsh 524 shadowing by obstacles (vegetation, buildings, etc.) or in presence of numerous interferes. 525 We periodically transmitted 'long-range bursts', i.e., relative timestamps in form of seconds 526 since mobile node start-up generated by a simple clock counter. These timestamps are 527 crucial for post-processing of meeting because they allow accounting for clock drift on the 528 mobile node. We embedded the long-range functionality into the existing modulation scheme 529 using a hybrid phase-alternating modulation on top of the pure amplitude-modulated wake-up sequences of the MN-beacon⁴⁵. As a consequence of the extreme energy limitation of the 530 531 MN, we ensured the required Signal-to-Noise-Ratio (SNR) by counterbalancing the rate and 532 the desired transmission distance. The combination of the hybrid modulation, the channel encoding procedure^{17, 45} and the 'Telegram-splitting' technique¹⁶ enables an ultra-low power 533 534 long-range transmission without additional expenditure of energy. The long-range bursts 535 were received at two long-range receivers, which were deployed on exposed sites (rooftops) 536 at distances of ca. 200 - 1,800m (retirement home) and 3,300 - 4,500m (cogeneration plant;

see Figure S1) to the proximate respectively ultimate border of the urban forest where theroosts of the tracked bats were located.

539 We quantified communication distances in the field, which was possible when a 540 tagged bat occupied a known roost and was simultaneously received by the long-range 541 receiver. We therefore matched timestamps of signals received simultaneously by GNs at 542 roosting sites and at long-range receivers. In case of a match, we quantified the distances 543 between roosts and long-range receivers in the R package geosphere using the Haversine 544 function⁴⁶. The empirically assessed communication distances have then been compared to a theoretical model of long-range transmission distances⁴⁷. This model evaluates achievable 545 546 rate and distance of transmission based on the energy relation of the SNR, presuming the 547 transmission power given by the MN's hardware configuration and a desired target payload 548 rate. For simulating the channel characteristics faced by the MN, the model comprises 549 parameters like the path loss in dependence of the signal-center frequency, the transmission 550 distance and receiver and transmitter heights. Environmental influences like attenuation by 551 obstacles, multi-path propagation or unpredictable rotation of the MN's rod antenna are 552 incorporated by means of a random variable, stating the superimposed attenuation effects. 553 Based on these assumptions we were capable of overcoming path losses of over 150dB for a distance of 5 km and more, under reasonable rates of packet loss¹⁷, thus accomplishing an 554 555 ultra-robust implementation supporting payload data rates of a few bits per second.

556

557 Sensor node energy consumption and runtime

A crucial aspect for biologging is knowledge on the runtime of the sensor nodes. Static program-code analysis methods of the mobile node are able to determine upper bounds on the nodes' runtime⁴⁸. However, in the context of the BATS tracking system, precise estimates for the average uptimes of the system proved to be more beneficial for the empirical studies than upper bounds for the lifetime. Consequently, we focused on an energy model to determine the average runtime of the mobile nodes, which is strongly dependent on the tasks executed by the software. Our models are based on measurements of each executed task in

combination with empirically determined activity parameter of each task. That way, we
ensure highest accuracy for our model. In our setting, seven different tasks are implemented:
(i) Standby, (ii) sending MN-beacons, (iii) receiving MN-beacons, (iv) observing ground node
availability, (v) transmitting data to a ground node, (vi) sending localization packets, and (vii)
sending presence signals (see Table S Glossary for definition of terms).

570

571 We determined the runtime by using the specific energy demand for a task and by translating

it to an average current draw. With the average current draw and a given battery capacity,

573 the runtime can be computed as follows:

$$T_{runtimeavg} = \frac{E_{battery} \cdot \eta_{DCDC}}{\sum I_{tasks}}$$

574

575 ŋDCDC represents the efficiency of the DCDC-converter, which is permanently active and 576 consumes energy. Determining ŋDCDC is impractical, because it highly depends on the 577 actual current drain of the application for the entire runtime. For this reason, we assume a 578 fixed efficiency of 0.95, which translates to only 95% of the battery capacity being available 579 for software tasks. This way, losses caused by the DCDC and parasitic discharges of the 580 battery are modeled in a coarse-grained manner.

The idle current during standby is given in a current draw, which does not require any further calculations. The other tasks (e.g., observing GN availability, sending localization packets) are executed in predefined cycle times (duty cycle). Based on the measured energy demand and the duty cycle, we calculated an average current draw for each task. The energy demand for each task was measured in the lab with an Agilent DC power analyzer precise source meter. In the case of a localization packet, which is sent every 128ms, the average current draw can be expressed as follows:

588
$$I_{localization} = \frac{E_{localizationpacket}}{T_{dutycycle} \cdot V_{supply}} \cdot \frac{T_{localization}}{T_{day}}.$$

The average time spent inside the localization grid ($T_{localization}$) per day is strongly dependent on the species-specific animal behavior and the experimental design. For the calculations presented here, we set the daily localization period to 2 or 4 hours, respectively. Observing a ground node in receiving range is carried out at a fixed duty cycle of 2 seconds. Here, the task is independent of the behavior of the tracked animal and the energy demand is calculated as follows:

$$I_{basestationRX} = \frac{E_{basestationRX}}{T_{dutycycle} \cdot V_{supply}}$$

595 The transmission rate of MN-beacons and presence signals is adaptive based on the contact 596 to a ground node (i.e., a mobile node near a GN at a roost will decrease the duty cycle in 597 comparison to a MN on a foraging animal which is not in reception range of a GN). In turn, 598 the energy demand for sending beacons and presence signals highly depends on the 599 behavior of the tracked study species and the individual animal (e.g., time spent near GNs at 600 roosting sites). We therefore used empirical data obtained in the Berlin field test to inform our 601 energy model with realistic averaged parameter values for duty cycles of each task and the 602 amount of transmitted data. We quantified the average time-tagged bats spent in reception 603 range of a GN (inactive mode, decreased duty cycle) versus the time bats spent outside the 604 reception range of any GN (active mode, increased duty cycle). The common noctule bats in 605 the Berlin field test spent on average 47% of the observation time in the inactive mode and 606 the energy demand for transmitting beacons and presence signals calculates as follows:

$$I_{beaconTX} = \frac{E_{beaconTX}}{V_{supply}} \cdot \left(\frac{r_{\underline{inactive}}}{T_{inactive}} + \frac{1 - r_{\underline{inactive}}}{T_{active}}\right)$$

607

$$I_{presenceTX} = \frac{E_{presenceTX}}{V_{supply}} \cdot \frac{\frac{r_{inactive}}{active}}{r_{inactive}}$$

608

Receiving a MN-beacon depends on the duty cycle at which beacons are transmitted and on the number of mobile nodes in receiving range. During the Berlin field test, we calculated the average number of 2.05 maximum parallel meetings.

$$I_{beaconRX} = \frac{E_{beaconRX} \cdot N_{avgEncounter}}{V_{supply}} \cdot \left(\frac{r_{\underline{inactive}}}{active}}{T_{inactive}} + \frac{1 - r_{\underline{inactive}}}{active}}{T_{active}}\right)$$

612

For data download to a GN, we assumed static energy consumption (the energy demand for sending a data packet highly depends on the size of the packet to be transmitted²³. The number of data packets to be transmitted is again dependent on the behavior of the tracked animal (depending on how many meetings an individual accumulates). Mobile nodes on common noctule bats sent on average 23.7 packages per hour to a ground node. Thus the current draw can be denoted as:

$$I_{download} = \frac{E_{packet} \cdot N_{packetsperhour}}{3600s \cdot V_{supply}}$$

Based on these calculations, we matched the estimated average runtimes to the observed
runtimes during the Berlin field test (based on the last beacon or packet received from each
individual tagged bat).

622

623 Adaptive operation, scalability, and reconfiguration:

624 The adaptive operation contributes to the energy efficiency of BATS. We define location-625 specific communication schemes on the mobile nodes which are initiated by ground nodes. 626 At a noctule bat day roost, for example, GNs activated the inactive beacon interval where 627 MN-beacons for meeting generation were only sent every 10 seconds. When tagged bats 628 leave their roost and move beyond the reception range of the GN, the MN switches to the 629 active interval, sending a MN-beacon every two seconds, which increases the probability to 630 detect also very short meetings in comparison to the inactive rate. Similarly, localization 631 packets, which strongly increase the energy demand, should only be sent when the tagged 632 animal moves within the tracking grid and are therefore triggered by a GN within the grid. 633 BATS tracks multiple individuals simultaneously. Our current design allows for the 634 observation of up to a theoretical maximum of 60 individuals. Field deployments containing 635 11 to 50 tagged bats empirically validated this targeted scalability. The scale of the

localization grid can be adapted to the ranges required for experimental setups. While we
tracked mouse-eared bats on 1.5ha, smaller areas might be sufficient to track, e.g., rodents
(bank voles, which showed a density of 40 - 162 individuals per hectare, have been tracked
on less than 0.5ha using automated VHF telemetry⁴⁹). Tracking grids larger than 1.5ha are
certainly possible from a technological point of view. Yet, one has to keep in mind that effort
for maintenance (e.g., replacing power sources for localization nodes) scales with the size of
the tracking grid.

Since settings for communication schemes are sometimes difficult to pick a priori, we built an option for reconfiguration of so-called 'soft-settings' (active/inactive rate of MNbeacons, RSSI-thresholds for data download, localization interval, or timeout duration after which a running meeting is terminated, etc.). Four values for every soft-setting (e.g., active rate 2s, 4s, 10s, 30s) can be defined a priori and during operation ground nodes can be used to trigger a switch between these pre-defined values at the mobile node.

649

650 Field deployments:

BATS functions as a modular system and hardware setup and software configurations are easily tailored to a specific use case. We evaluated BATS during three major field studies by applying mobile nodes to vampire bats, noctule bats, and mouse-eared bats with body weights of 27 - 48g, 18 - 35g, and 22 - 28g respectively. While at least two of the three major functionalities (proximity sensing, high-resolution tracking, long-range telemetry) have been used in all three field studies, we focus on one specific functionality per deployment.

657

658 Proximity sensing in vampire bats:

659 We tagged 50 common vampire bats (*Desmodus rotundus*; 44 adult females, 6 subadults)

660 from a colony roosting in a cave tree near Tolé, Panama, to document social networks with

high resolution. Field work was conducted during September and October 2017. Mobile

nodes were powered by a 22mAh LiPo battery and housed in a 3D-printed plastic case,

resulting in a total weight of 1.8g. One download-dedicated ground node was positioned

664 inside the roost and five ground nodes were placed on surrounding cattle pastures to detect665 the presence of foraging or commuting bats.

666

667 Long-range telemetry in noctule bats:

668 We captured and tagged 34 common noctule bats (*Nyctalus noctula*; 19 adult females and

15 juveniles) from two bat boxes in a nursing colony an urban forest in the city of Berlin,

670 Germany ('Königsheide Forst')⁵⁰. Mobile nodes were powered by either a 12mAh or a 22mAh

battery and were housed either in a 3D-printed plastic case or in a fingertip of a nitrile lab

672 glove that was sealed with glue. Total weight varied between 1.1 - 1.9g depending on

673 housing and battery. We positioned 5 ground nodes underneath known roosts to document

the presence of individual bats and to remotely download data. In addition, we set up two

675 long-range receivers to evaluate model-based predicted data retrieval over distances of up to

4-5km¹⁷. This opportunity is particularly valuable to retrieve data of tagged individuals that

677 moved to an unknown roost.

678

679 High-resolution tracking of mouse-eared bats

680 We captured 11 mouse-eared bats (*Myotis myotis*) using mist-nets set up at ground level in a 681 mature deciduous forest near Forchheim, Germany. When hunting for ground beetles, 682 mouse-eared bats are faithful to their foraging sites for consecutive days. We therefore mist-683 netted bats at an attractive foraging site rather than catching them from a roost in order to 684 track repeated bouts by returning individuals over the course of several days. Mobile nodes 685 were powered by 22mAh batteries and housed in fingertips of nitrile lab gloves (total weight 686 1.4g). At the capture site we installed a tracking grid consisting of 17 localization nodes 687 covering roughly an area of 1.5ha (see Figure 3). Distance between tracking stations varied 688 between ca. 25 - 40m. The irregular configuration was due to the presence of thick trees. We 689 aimed at positioning tracking stations at least 3 - 5m away from trees to reduce shielding of 690 the signal. We set up a polygon-shaped reference path for estimating localization errors and 691 determined the true position of the corners using a Leica Robotic Total Station TS16

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sensor node (once) or a GPS tracker (four times) (Ornitela OrniTrack-15; a 15g solar

694 powered GPS-GSM/GPRS tracker; maximum logging rate 1 fix per second at a lifetime of ca.

4h without solar harvesting) along the calibration path and calculated the average localization

- 696 error based on the obtained tracks.
- 697
- 698 Ethics
- 699 Work on vampire bats: All experiments were approved by the Smithsonian Tropical Research

700 Institute Animal Care and Use Committee (#2015-0915-2018-A9 and #2017-0102-2020) and

by the Panamanian Ministry of the Environment (#SE/A-76-16 and #SE/AH-2-17).

702 Work on noctule bats: All necessary permits were obtained from SenStadtUm (I E 222/OA-

703 AS/G_1203) and LaGeSo (I C 113-G0008/16).

704 Work on mouse-eared bats: All experiments were approved by the government of Upper

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707

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- 721

722 Author contributions

- 723 SPR and FM conceived the ideas and designed the biologging studies; ND, BC, MH, TN,
- PW, and MS developed and tested the tracking technology; SPR, GGC, ND, BC, MH, TN,
- and MS collected the data; MH, TN, MS, SH, BC, PW and SPR analyzed the data; SPR led
- the writing of the manuscript. SPR, GGC, RAP, AK, RW, JT, JR, KMW, WSP, RK, FD, and
- 727 FM contributed to acquiring funds. All authors contributed critically to the drafts, gave final
- approval for publication and agree to be held accountable for the work performed therein.
- 729

730 References

- Kays, R., Crofoot, M.C., Jetz, W. & Wikelski, M. Terrestrial animal tracking as an eye on life
 and planet. *Science* 348, aaa2478 (2015).
- 733 2. Krause, J. et al. Reality mining of animal social systems. *Trends Ecol. Evol.* 28, 541-551
 734 (2013).
- Wilmers, C.C. et al. The golden age of bio-logging: how animal-borne sensors are advancing
 the frontiers of ecology. *Ecology* 96, 1741-1753 (2015).
- Hughey, L.F., Hein, A.M., Strandburg-Peshkin, A. & Jensen, F.H. Challenges and solutions for
 studying collective animal behaviour in the wild. *Philosophical Transactions of the Royal Society B: Biological Sciences* 373, 20170005 (2018).
- McKinnon, E.A. & Love, O.P. Ten years tracking the migrations of small landbirds: Lessons
 learned in the golden age of bio-logging. *The Auk* 135, 834-856 (2018).
- Fraser, K.C. et al. Tracking the conservation promise of movement ecology. *Frontiers in Ecology and Evolution* 6, 150 (2018).
- 7. Curry, A. The internet of animals that could help to save vanishing wildlife. *Nature* 562, 322
 (2018).
- 746 8. Oppermann, F.J., Boano, C.A. & Römer, K. in The Art of Wireless Sensor Networks 11-50
 747 (Springer, 2014).

748	9.	Juang, P. et al. Energy-efficient computing for wildlife tracking: design tradeoffs and early
749		experiences with ZebraNet. SIGPLAN Not. 37, 96-107 (2002).
750	10.	Toledo, S., Kishon, O., Orchan, Y., Shohat, A. & Nathan, R. in Software Science, Technology
751		and Engineering (SWSTE), 2016 IEEE International Conference on 51-60 (IEEE, 2016).
752	11.	Rutz, C. et al. Automated mapping of social networks in wild birds. Curr. Biol. 22, R669-R671
753		(2012).
754	12.	Ayele, E.D., Meratnia, N. & Havinga, P.J. in New Technologies, Mobility and Security (NTMS),
755		2018 9th IFIP International Conference on 1-5 (IEEE, 2018).
756	13.	Ripperger, S. et al. Automated proximity sensing in small vertebrates: design of miniaturized
757		sensor nodes and first field tests in bats. Ecology and Evolution 6, 2179-2189 (2016).
758	14.	Wilkinson, G.S. et al. Kinship, association, and social complexity in bats. Behav. Ecol.
759		Sociobiol. 73 , 7 (2019).
760	15.	Sekara, V., Stopczynski, A. & Lehmann, S. Fundamental structures of dynamic social
761		networks. Proceedings of the national academy of sciences 113, 9977-9982 (2016).
762	16.	Kilian, G. et al. Increasing Transmission Reliability for Telemetry Systems Using Telegram
763		Splitting. IEEE Transactions on Communications 63, 949-961 (2015).
764	17.	Schadhauser, M., Robert, J. & Heuberger, A. in Smart SysTech 2017; European Conference
765		on Smart Objects, Systems and Technologies 1-8 (VDE, 2017).
766	18.	Hallworth, M.T. & Marra, P.P. Miniaturized GPS tags identify non-breeding territories of a
767		small breeding migratory songbird. Scientific reports 5, 11069 (2015).
768	19.	Cvikel, N. et al. Bats Aggregate to Improve Prey Search but Might Be Impaired when Their
769		Density Becomes Too High. Curr. Biol. 25, 206-211 (2015).
770	20.	Conenna, I., López-Baucells, A., Rocha, R., Ripperger, S. & Cabeza, M. Movement
771		seasonality in a desert-dwelling bat revealed by miniature GPS loggers. Movement ecology 7,
772		1-10 (2019).
773	21.	Tomkiewicz, S.M., Fuller, M.R., Kie, J.G. & Bates, K.K. Global positioning system and
774		associated technologies in animal behaviour and ecological research. Philosophical
775		Transactions of the Royal Society B: Biological Sciences 365, 2163-2176 (2010).
776	22.	Dressler, F. et al. Monitoring Bats in the Wild: On Using Erasure Codes for Energy-Efficient
777		Wireless Sensor Networks. ACM Transactions on Sensor Networks (TOSN) 12, 1-29 (2016).

778	23.	Cassens, B. et al. in Proceedings of the 2019 International Conference on Embedded
779		Wireless Systems and Networks 59-70 (Junction Publishing, 2019).
780	24.	St Clair, J. et al. Experimental resource pulses influence social-network dynamics and the
781		potential for information flow in tool-using crows. Nature Communications 6, 7197 (2015).
782	25.	O'Mara, M.T., Wikelski, M. & Dechmann, D.K. 50 years of bat tracking: device attachment and
783		future directions. Methods in Ecology and Evolution 5, 311-319 (2014).
784	26.	Duda, N. et al. in 2019 IEEE Topical Conference on Wireless Sensors and Sensor Networks
785		(WiSNet) 1-4 (IEEE, 2019).
786	27.	Kays, R. et al. Tracking Animal Location and Activity with an Automated Radio Telemetry
787		System in a Tropical Rainforest. The Computer Journal (2011).
788	28.	Nowak, T., Hartmann, M., Tröger, HM., Patino-Studencki, L. & Thielecke, J. in 2017 IEEE
789		International Conference on Communications Workshops (ICC Workshops) 1024-1029 (IEEE,
790		2017).
791	29.	Kerth, G., Perony, N. & Schweitzer, F. Bats are able to maintain long-term social relationships
792		despite the high fission-fusion dynamics of their groups. Proceedings of the Royal Society B:
793		Biological Sciences 278, 2761-2767 (2011).
794	30.	Aplin, L.M. et al. Experimentally induced innovations lead to persistent culture via conformity
795		in wild birds. <i>Nature</i> 518 , 538-541 (2015).
796	31.	Lopes, P.C., Block, P. & König, B. Infection-induced behavioural changes reduce connectivity
797		and the potential for disease spread in wild mice contact networks. Scientific reports 6, 31790
798		(2016).
799	32.	Levin, I.I. et al. Stress response, gut microbial diversity and sexual signals correlate with social
800		interactions. <i>Biol. Lett.</i> 12 , 20160352 (2016).
801	33.	Saltzer, J.H., Reed, D.P. & Clark, D.D. End-to-end arguments in system design. ACM
802		Transactions on Computer Systems 100, 277-288 (1984).
803	34.	Schmidt, A. et al. Cross-Layer Pacing for Predictably Low Latency. Proc. 6th Intl. Worksh. on
804		Ultra-Low Latency in Wireless Networks (Infocom ULLWN). IEEE (2019).
805	35.	Blobel, J. & Dressler, F. in 2017 IEEE Conference on Computer Communications Workshops
806		(INFOCOM WKSHPS) 984-985 (IEEE, 2017).
807	36.	Nabeel, M., Amjad, M.S. & Dressler, F. in 2018 IEEE Global Communications Conference
808		(GLOBECOM) 1-6 (IEEE, 2018).

- 809 37. Teitelbaum, C.S. & Mueller, T. Beyond Migration: Causes and Consequences of Nomadic
 810 Animal Movements. *Trends Ecol. Evol.* (2019).
- 811 38. Stroeymeyt, N. et al. Social network plasticity decreases disease transmission in a eusocial
 812 insect. Science 362, 941-945 (2018).
- 813 39. Consortium, T.Q. Networking Our Way to Better Ecosystem Service Provision. *Trends Ecol.*814 *Evol.* 31, 105-115 (2016).
- Nowak, T., Hartmann, M., Zech, T. & Thielecke, J. in 2016 IEEE-APS Topical Conference on
 Antennas and Propagation in Wireless Communications (APWC) 110-113 (IEEE, 2016).
- 817 41. Nowak, T., Hartmann, M. & Thielecke, J. Unified performance measures in network
 818 localization. *EURASIP Journal on Advances in Signal Processing* 2018, 48 (2018).
- 42. Hartmann, M., Nowak, T., Pfandenhauer, O., Thielecke, J. & Heuberger, A. in 2016 12th
- Annual Conference on Wireless On-demand Network Systems and Services (WONS) 1-8
 (IEEE, 2016).
- 43. Nowak, T., Hartmann, M. & Thielecke, J. in 2018 11th German Microwave Conference
 (GeMiC) 115-118 (IEEE, 2018).
- 44. Nowak, T., Hartmann, M., Patino-Studencki, L. & Thielecke, J. in 2016 13th Workshop on
 Positioning, Navigation and Communications (WPNC) 1-6 (IEEE, 2016).
- 45. Duda, N. et al. BATS: Adaptive Ultra Low Power Sensor Network for Animal Tracking.
 827 Sensors 18, 3343 (2018).
- 46. Hijmans, R.J., Williams, E., Vennes, C. & Hijmans, M.R.J. in Spherical trigonometryv 1.5-7
 (2019).
- 830 47. Schadhauser, M., Robert, J. & Heuberger, A. in Smart SysTech 2016; European Conference
 831 on Smart Objects, Systems and Technologies 1-9 (VDE, 2016).
- Wägemann, P., Dietrich, C., Distler, T., Ulbrich, P. & Schröder-Preikschat, W. Whole-system
 worst-case energy-consumption analysis for energy-constrained real-time systems. *Leibniz*
- 834 International Proceedings in Informatics, LIPIcs 106 (2018) **106**, 24 (2018).
- 835 49. Schirmer, A., Herde, A., Eccard, J.A. & Dammhahn, M. Individuals in space: personality836 dependent space use, movement and microhabitat use facilitate individual spatial niche
- 837 specialization. *Oecologia* **189**, 647-660 (2019).
- 838 50. Ripperger, S. et al. Proximity sensors on common noctule bats reveal evidence that mothers
 839 guide juveniles to roosts but not food. *Biol. Lett.* **15**, 20180884 (2019).



Supplementary Figure 1: Experimental setup for long-range telemetry in the city of
Berlin, Germany. Yellow symbols mark the positions of two long-range telemetry receivers
(asterix = retirement home, circle = cogeneration plant). Red symbols show the locations of
bat day roosts 1 to 3 (tree holes). Map data ©2019 GeoBasis-DE/BKG (©2009), Google.



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847 Supplementary Figure 2: animal-borne mobile node for proximity sensing. (a) Common

vampire bat (*Desmodus rotundus*) carrying a mobile node housed in a plastic case; (b) bare

849 mobile node on a quarter US dollar coin for comparison of size .

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852 **Supplementary Table 1: Glossary.** Description of hardware components, communication

and data types and software tasks considered for the energy model.

Keyword	Description
Hardware	
Mobile node (MN)	Animal-borne sensor node.
Ground node (GN)	Multifunctional ground-based sensor nodes. Depending on the GN-
	configuration, it receives data from MNs, triggers transmission of
	localization packets at the MN, or triggers the transmission of presence
	signals at the MN.
Localization node	Sensor node containing a dual-band antenna for high-resolution
	positioning of MNs. Arranged in a tracking grid.
Long-range receiver	Long-range telemetry-dedicated sensor node for receiving long-range
	bursts.

Communication and data types		
Ground node beacon	A packet sent by a ground node that triggers action on the MN (e.g.,	
(GN-beacon)	data download).	
Mobile node beacon	A packet sent by a mobile node. It contains a wakeup sequence which	
(MN-beacon)	wakes other MNs from standby.	
Long-range burst	A packet embedded in the wakeup sequence of the MN-beacon for	
	data transmission to a long-range receiver.	
Localization packet	A packet sent by a MN to localization nodes for high-resolution	
	tracking. Transmission is initiated by a GN-beacon.	
Presence Signal	A packet sent by a MN to indicate the presence of a bat in range of a	
	GN. Transmission is initiated by a GN-beacon.	
Software task on the mo	bile node	
(i) standby	An idle state where only mandatory devices are active (e.g., wakeup	
	receiver). The idle state is terminated by the reception of a wakeup.	
(ii) sending beacons	Sending a MN-beacon to wake nearby MNs from standby. Nearby MNs	
	immediately send their IDs in return.	
(iii) receiving beacons	If the wakeup receiver receives a wakeup sequence, the conventional	
	receiver is activated to receive the IDs of nearby MNs (encoded in the	
	MN-beacons).	
(iv) observing ground	Every 2 s the receiver is activated to check whether GN-beacons are	
node availability	received.	
(v) transmitting data to a	If beacons of a download-dedicated GN are received, the transmitter is	
ground node	activated and data download is initiated.	
(vi) sending localization	If beacons of a tracking-dedicated GN are received, localization	
packets	packets are sent (duty cycle 8/s; 868MHz & 2.4GHz)	
(vii) sending presence	If beacons of a GN are received, a presence signals is send	
signals		

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