

1 **Proximity sensors reveal social information transfer in maternity colonies**
2 **of Greater noctule bats**

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26 **Summary**

- 27 1. Bats are a highly gregarious taxon suggesting that social information should be readily
28 available for making decision. Social information transfer in maternity colonies might
29 be a particularly efficient mechanism for naïve pups to acquire information on
30 resources from informed adults. However, such behaviour is difficult to study in the
31 wild, in particular in elusive and small-bodied animals such as bats.
- 32 2. The goal of this study was to investigate the role of social information in acquiring
33 access to two types of resources, which are crucial in the life of a juvenile bat: suitable
34 roosting sites and fruitful feeding grounds. We hypothesized that fledging offspring
35 will make use of social information by following informed members of the social
36 groups to unknown roosts or foraging sites.
- 37 3. In the present study we applied for the first time the newly developed miniaturized
38 proximity sensor system ‘BATS’, a fully automated system for documenting
39 associations among individual bats both while roosting and while on the wing. We
40 quantified associations among juveniles and other group member while switching
41 roosts and during foraging.
- 42 4. We found clear evidence for information transfer while switching roosts, mainly
43 among juveniles and their genetically identified mothers. Anecdotal observations
44 suggest intentional guidance behaviour by mothers, indicated by repeated commuting
45 flights among the pup and the target roost. Infrequent, short meetings with colony
46 members other than the mother indicate local enhancement at foraging sites, but no
47 intentional information transfer.
- 48 5. Our study illustrates how advances in technology enable researchers to solve long-
49 standing puzzles. Miniaturized proximity sensors facilitate the automated collection of
50 continuous data sets and represent an ideal tool to gain novel insights into the
51 sociobiology of elusive and small-bodied species.

52

53 **Key-words**

54 Evolved signals, foraging, information centre hypothesis, local enhancement, maternal care,
55 maternal guidance, *Nyctalus noctula*, roost switching

56

57 **Introduction**

58 The early development is a critical phase for an animal since it paves the way for later life by
59 affecting survival rate and overall fitness. It has been shown for several species that limited
60 access to food resources within the first weeks after birth has a negative impact on
61 reproductive success (Lindström 1999; Lummaa & Clutton-Brock 2002). However, a central
62 question is: how do offspring get access to resources in early life once they start to become
63 independent? Behaviours related to foraging might be genetically predefined, which is the
64 case in many invertebrates but also in vertebrate taxa (van Schaik *et al.* 2017). Over time,
65 ‘personal information’ which is acquired by direct interaction with the environment (Dall *et*
66 *al.* 2005) or individual learning by trial and error augment an individual’s capabilities (van
67 Schaik *et al.* 2017). If animals are born and raised in presence of their parents or other
68 conspecifics, information may be socially acquired (Galef Jr & Giraldeau 2001). Adopting
69 information from group members may be more efficient and less costly than individual
70 learning and contributes to an individual’s behavioural flexibility under changing conditions
71 (Dall *et al.* 2005; van Schaik *et al.* 2017).

72 Information obtained within colonies or groups of conspecifics enables better decisions in
73 various contexts such as predator avoidance, reduction of parasitism, habitat choice and
74 foraging (Evans, Votier & Dall 2016). The mechanisms of acquiring social information may
75 vary widely in complexity. Individuals may use ‘inadvertent social information’, which is
76 generated by social cues of conspecifics, i.e., eating may inform about the location of food or

77 fleeing about the presence of a predator (Dall *et al.* 2005). Such public information is created
78 non-deliberately and in group-living animals it may be difficult to hide certain information,
79 e.g., on foraging success. This might particularly apply for breeding colonies, where parents
80 must return to their young and may inadvertently inform others on foraging success via, e.g.,
81 time of arrival or fatness (Evans, Votier & Dall 2016). If information is provided deliberately,
82 ‘evolved signals’ are used to actively exchange information (Dall *et al.* 2005). Black-capped
83 chickadees, e.g., broadcast alarm calls which contain information on the presence and even
84 the size of a predator (Templeton, Greene & Davis 2005) and honey bees use the waggle
85 dance to inform conspecifics on the location of a food source (Leadbeater & Chittka 2007).
86 The ready availability of information at communal roosts gave rise to the Information Center
87 Hypothesis (ICH), which states that such assemblages primarily evolved for the efficient
88 exploitation of unevenly distributed food sources (Ward & Zahavi 1973). According to the
89 ICH colony members must assess the success of returning foragers, which are later followed
90 to food patches. However, information can also be generated right at the resource, a
91 mechanism termed ‘local enhancement’. Black-browed albatrosses, e.g., indirectly detect food
92 patches by approaching aggregations of foraging predators over sea (Grünbaum & Veit 2003).
93 Both advertent and inadvertent information can be used by juveniles to find food. Juvenile
94 rats prefer feeding sites where adults are present and scent marks and trails of adults cause
95 juveniles to explore such sites (reviewed by Galef Jr and Giraldeau (2001)). Juveniles, since
96 they are naïve, seem to particularly rely on acquiring social information from more
97 experienced individuals of the group like their parents (termed ‘vertical transmission’) or
98 other adults (‘oblique transmission’) (van Schaik *et al.* 2017).
99 Bats are an ideal taxon to study the mechanisms of social information use in groups since the
100 vast majority of species is gregarious and long-lived (Wilkinson & Boughman 1999; Kerth
101 2008; Smith, Lacey & Hayes 2017). However, there is surprisingly little known on whether
102 and how juveniles benefit from social information provided by group members. An interesting

103 case of information transfer across generations is reported for greater sac-winged bats. Here,
104 vocal development of pups is influenced by imitation of territorial songs of harem males and
105 leads to a group signature which is independent of relatedness (Knörnschild *et al.* 2010;
106 Eckenweber & Knörnschild 2013). When it comes to learning where to roost and where to
107 forage, knowledge on juveniles becomes scarce and existing literature focusses on horizontal
108 information transfer among adult peers. Empirical studies in the wild demonstrated that
109 several insectivorous species are attracted to feeding buzzes by conspecifics which may be
110 used as a signal of foraging success (Gillam 2007; Dechmann *et al.* 2009; Cvikel *et al.* 2015).
111 Female greater spear-nosed bats coordinate their foraging bouts at the day roost by screech
112 calls (Wilkinson & Boughman 1998). However, neither local enhancement nor recruitment at
113 the roost has been demonstrated in foraging juveniles, so far. Spatial association among home
114 ranges of mothers and offspring in at least three species and simultaneous feeding of mother-
115 pup pairs in vampire bats suggest that vertical information transfer, possibly in form of
116 following behaviour, might provide juveniles with insights on where to forage, but this
117 mechanism has yet has to be demonstrated (Wilkinson 1995; Schnitzler, Moss & Denzinger
118 2003).

119 Similarly little is known on how juveniles learn about the location of suitable roosts and the
120 few existing studies only involved adults. In Greater noctule bats local enhancement by
121 inadvertent acoustic cues significantly reduces the time required to locate a roost both in
122 captive and in wild experiments (Ruczyński, Kalko & Siemers 2007; Furmankiewicz *et al.*
123 2011). Kerth and Reckardt (2003) tracked nightly roost switching behaviour in Bechstein's
124 bats and assumed that recruitment of naïve by informed individuals already started at the day
125 roost, but could not unequivocally prove it. An exclusion experiment by Wilkinson (1992)
126 demonstrated that juvenile bats are able of relocating at a new roost with their mothers and the
127 author concluded that following behaviour is the only plausible explanation. One of the still
128 standing mysteries in bat ecology is how juveniles of temperate species locate swarming or

129 hibernation sites, which are often long distances from where they are born and reared. It has
130 been hypothesized that mothers guide their offspring (Sachteleben 1991), but so far nobody
131 was able to track such guidance behaviour. These examples emphasize that there are plenty of
132 indications on following and guidance behaviour in juvenile bats, but so far technological
133 limitations prevented the final proof.

134 While emerging technologies have revolutionized the field of bio-logging and in turn our
135 understanding of behaviour of wild animals during the past decades, studies on small-bodied
136 vertebrates still lag behind due to the scarcity of fully automated lightweight devices (Kays *et*
137 *al.* 2015). Proximity loggers represent a powerful tool for the study of information transfer
138 (Rutz *et al.* 2015; St Clair *et al.* 2015), but studies making use of such devices are generally
139 rare and the loggers used in the aforementioned studies are by far too heavy for tagging
140 medium-sized bats. Smaller tag versions of acceptable weight, however, show dramatically
141 reduced runtimes of less than 24 h (Levin *et al.* 2015). In the present study we used the newly
142 developed miniaturized proximity sensor system ‘BATS’, a fully automated system for
143 documenting associations among individuals at a tag weight of one to two gram and runtimes
144 of at least one to two weeks (Duda, Weigel & Koelpin 2018). Our developments enable us to
145 study interactions among tagged bats both while roosting and while on the wing. Here we
146 report on the first extensive study to apply our system and proximity sensors to free-ranging
147 bats, in general.

148 The goal of this study was to investigate the use of social information in acquiring access to
149 two types of resources, which are crucial in the life of a juvenile bat: suitable roosting sites
150 and fruitful feeding grounds. We hypothesized that fledging offspring will make use of social
151 information by following either the mother or other informed members of the social groups to
152 unknown roosts or foraging sites. If juveniles use social information when switching roosts,
153 we expect that the successfully switching juvenile will be associated with at least one
154 individual of the group shortly before and shortly after leaving the current roost and shortly

155 before and shortly after arriving at the new roost. If social information is used for finding
156 foraging grounds, we would expect juveniles to be associated with at least one roosting
157 partner shortly before and shortly after starting the bout, during several minutes after starting
158 while commuting to the foraging ground, and possibly, but not necessarily when returning to
159 the roost. The BATS-tracking system enabled us to classify and quantify the aforementioned
160 events.

161

162 **2. Materials and methods**

163 2.1 Field site and study species

164 This study was conducted in “Königsheide Forst”, a mixed forest in Berlin, Germany, from
165 June to August 2016 and 2017, respectively. The study site comprises ample of roosting
166 opportunities for bats such as natural tree holes and roughly 130 bat boxes. During this time
167 of the year females of the common noctule bat (*Nyctalus noctula*) form temporary groups, so
168 called maternity colonies, to jointly give birth and rear their young. Mothers give birth to one
169 or two offspring and individuals of a maternity colony frequently switch roosts, but usually
170 stay within the area of the nursing colony. Moving among roosts may involve a change in
171 group composition. However, strong, non-random inter-individual bonds have been observed
172 in captive studies as well as a certain degree of maternal care such as allogrooming of
173 offspring (Kleiman 1969; Kozhurina 1993).

174 The ideal opportunity to observe information transfer in maternity colonies should be the
175 moment when the offspring start to fledge in order to track their behaviour during the first
176 nights of independent flight. Therefore, we daily monitored the bat boxes, including checks
177 after sunset when adults and already flying juvenile had emerged from the roost. We aimed at
178 tagging the majority of a social group including juveniles, which have started fledging only
179 recently or which not fledged at all, yet. We therefore prepared to capture on the following

180 day when around a third of the offspring were still inside the roost while the rest of colony
181 (including already fledged youngsters) was foraging.

182

183 2.2 Sample collection, molecular analysis and identification of mother pup pairs

184 In 2016 we captured a social group from a single bat box while in 2017 bats were caught from
185 two different bat boxes which were roughly 300m apart. Bats were kept in cotton cloth bags
186 until they were weighted, sexed and the forearm was measured using a calliper. If the
187 epiphyseal gaps were closed and the phalangeal–metacarpal joints were knobby, individuals
188 were considered adult (Brunet-Rossinni & Wilkinson 2009). We collected tissue samples with
189 a biopsy punch (Ø 4 mm, Stiefel Laboratorium GmbH, Offenbach, Germany) and preserved
190 them in 80% ethanol. In the lab we used the salt–chloroform procedure (Miller, Dykes &
191 Polesky 1988) modified by Heckel *et al.* (1999) for DNA isolation.

192 We used the DNA Analyser 4300 and the SAGA^{GT} allele scoring software (both: LI-COR
193 Biosciences, Lincoln, NE, USA) to genotype a total of 75 individuals (n_f= 33 adult
194 females, n_j=42 juveniles) at 9 polymorphic microsatellite loci. We used the loci P11, P217,
195 P219 and P223 which were isolated from the focus species *Nyctalus noctula* (Mayer,
196 Schlötterer & Tautz 2000). Nleis3 and Nleis4 were isolated from the closely related *Nyctalus*
197 *leisleri* (Boston, Montgomery & Prodöhl 2009) and G6-Mluc, G31-Mluc, H23-Mluc and
198 H29-Mluc have originally been isolated from *Myotis myotis* (Castella & Ruedi 2000), but
199 were subsequently modified for cross-species utility in vespertilionid species (Jan *et al.* 2012).
200 To calculate allele frequencies all adult individuals from both years (n=33) were used. All
201 individuals were genotyped at least at eight loci, and genotypes were 99.7% complete. See
202 Table S1 in supporting information for allele numbers per locus, results of Hardy–Weinberg
203 tests, null allele frequencies, and non-exclusion probabilities for the nine microsatellite
204 markers.

205 Parentage analyses were performed with CERVUS v. 3.0 (Kalinowski, Taper & Marshall
206 2007) separately for the social groups caught in 2016 and 2017, respectively, since our
207 objective was to identify mother-pup pairs within year, not across years. The 2016 data set
208 comprised 20 juveniles and 13 adult females (candidate mothers), while 22 juveniles and 24
209 candidate mothers were used for 2017. Four of the 24 adult females in 2017 were recaptures
210 that were already caught in 2016 as juvenile (n=1) and adults (n=3).

211 Simulations were run with 100 000 cycles, a proportion of 80% sampled candidate mothers,
212 an estimated genotyping error of 2%, and for two confidence levels (80% and 95%). One
213 mismatch per mother-offspring dyad was accepted to account for genotyping errors or
214 mutations. A mother could be assigned to 40 (2016: n=18; 2017: n=22) of the 42 analysed
215 juveniles. Thirty-three mother-pup pairs were assigned at 95 % confidence with no mismatch,
216 six at 95 % confidence with one mismatch and only one with 80 % confidence and one
217 mismatch.

218

219 2.3 Automated encounter detection among tagged bats

220 Our team developed a tracking system for direct encounter detection, which bases on wireless
221 sensor network technology for field strength related distance estimation between individuals.
222 The system is fully automated including remote data download and does not require
223 recapturing tagged animals thus reducing disturbance of the animals to a minimum. The
224 centrepiece of the tracking hardware is the animal-borne mobile node, in the following
225 referred to as 'proximity sensor'. Once deployed, a wake-up receiver on the proximity sensor
226 permanently scans its surroundings for signals of other proximity sensors, which are
227 constantly broadcasted every two seconds. This operation mode is independent of any further
228 infrastructure. Whenever one or more tracking sensors are within reception range of ca. 10 m
229 maximum distance (Ripperger *et al.* 2016), a so called 'meeting' is created. As soon as no
230 signal has been received by the respective meeting partner for five sending intervals

231 (corresponding to 10 seconds), the meeting is closed and stored to on-board memory along
232 with the ID of the meeting partner, a timestamp, total meeting duration, and a maximum
233 signal strength indicator (RSSI) of the meeting. The signal, which is broadcasted every 2 s, is
234 simultaneously used as an indicator of presence at a site of interest, e.g. a roost, when the
235 signal is received by a stationary node, in the following referred to as ‘base stations’. We
236 positioned base stations near potential roosts to detect presence of individual tagged bats
237 inside a particular bat box or tree hole and we therefore termed a bat signal which are picked
238 up by base stations ‘presence signal’. Base stations also provide remote data download, while
239 all downloaded data is locally stored and can be accessed by the user. In 2016 the system
240 could operate a maximum of 30 IDs at a time, while in 2017 the maximum number of
241 observable individuals has been increased to 60. In the following we give a brief overview of
242 the hardware components and the functionality of the system. For an elaborate, in-depth
243 description of the software see Cassens *et al.* (2017) and for hardware see Duda, Weigel and
244 Koelpin (2018).

245

246 2.3.1 Proximity sensors: We used a refined version of miniaturized proximity sensors, which
247 has been described and tested in free-ranging bats first in Ripperger *et al.* (2016). The
248 proximity sensor comprises a System-on-Chip (SoC) for communication control and on-board
249 data processing, a transceiver which enables communication in the 868MHz frequency band
250 with other proximity sensors or base stations and a wake-up-receiver which activates full
251 system functionality from an energy-saving low-power mode whenever communication
252 partners are in range. A lithium-polymer battery powers the mobile node. We built two
253 versions of the proximity sensor that differ in weight since adult females and offspring of
254 noctule bats varied considerably in body weight. The low-weight version for tagging offspring
255 was equipped with a 15 mAh battery and was housed in the fingertip of a nitrile lab glove.
256 The heavier version for adult females was equipped with either two 15 mAh battery of a

257 single 24mAh batteries and housed in a 3D-printed plastic case ensuring longer runtime. The
258 different proximity sensor versions resulted in a total weight of 1.1 to 1.9 g including battery
259 and housing.

260

261 2.3.2 Base stations and data access

262 The base station contains a receiver for the reception of presence signals and transmitted data.
263 Presence signals and downloaded data are stored by a Raspberry Pi (Raspberry Pi Foundation,
264 Cambridge, UK) to a SD card along with the ID of the transmitting proximity sensor and the
265 receiving base station, respectively, and a timestamp which is provided by a GPS unit. At the
266 same time the Raspberry Pi hosts a WiFi hotspot allowing the user remote data access. The
267 data is then stored in a MySQL database.

268

269 2.4 Tagging and data collection

270 On July 15th 2016 we tagged in total 26 individuals, 10 juveniles and 16 adult females, from a
271 single bat box. On July 18th 2017 we tagged in total 34 individuals, 19 juveniles and 15 adult
272 females from two bat boxes. This adds up to a total of 60 tracked bats, 29 of which were
273 juveniles and 31 were adult females. According to individual body weight we used different
274 versions of the proximity sensors. Bodyweight ranged from 17g to 25g for juveniles and
275 averaged at 21.26g +/- 2.04, while adult body weight ranged from 23.5g to 35g at an average
276 of 27.73g +/- 2.27. Individual tag-to-body weight ratios ranged from 4.4% to 7% for juveniles
277 and from 4.2% to 8% in adults, which is well within the recommendations for short-term
278 biologging studies in bats (Amelon *et al.* 2009; O'Mara, Wikelski & Dechmann 2014).
279 Proximity sensors were glued to the fur on the back of the bats using surgical cement (Perma-
280 Type, Plainville, CT, USA) and drops off when the cement loses its tackiness.

281 Data collected during the first night after the tagging event was discarded to account for
282 potential behavioural changes right after tagging and actual data collection started the night

283 after in order to allow the bats to get used to the tag. In 2016 data collection lasted until July
284 28th (12 days) and in 2017 until August 8th (20 days). We installed three respectively five base
285 stations in 2016 and 2017 at day roosts to download data and to receive presence signals for
286 individual bats. Whenever bats switched to unknown roosts we used a handheld 868 MHz
287 panel antenna (HSP-868C, WiMo, Herxheim, Germany) connected to a base station to
288 localize the unknown roost and relocate base station.

289

290 2.5 Analysis of tracking data

291 We used the library RMySQL in R (James & DebRoy 2012) to access the data, which were
292 managed in HeidiSQL, a Windows client for MariaDB. In a first step we plotted and visually
293 explored presence signals and meetings received at base stations to define foraging bouts and
294 roost switching events, respectively, for all individual juveniles (see Fig. 2a-c for examples).
295 To evaluate potential information transfer we queried the meeting database for events, which
296 matched the timestamp of foraging bouts or roost switches, respectively. If information
297 transfer would play a role during foraging or roost switching, we would expect to find
298 meetings among offspring and other group members associated with these events. In detail,
299 we proceeded as follows.

300

301 2.5.1 Evaluation of information transfer during roost switching

302 We defined a roost switch as an event during which an individual changes its roost and
303 potentially its roosting partners without prolonged absence times which may indicate
304 foraging. A roost switch can be detected if a bat switches between two roosts which are both
305 equipped with a base station receiving presence signals (Fig. 2b). If at least one roost is
306 equipped with a base station, presence signals can be used to determine departure time or
307 arrival, respectively. If the unmonitored roost is occupied by other tagged bats (indicated by
308 reciprocal, stable meetings) we can at least unequivocally classify this event as a roost switch

309 (Fig. 2c). However, we cannot determine the time of arrival respectively departure at the
310 unmonitored roost because bats may leave jointly. If juveniles use social information when
311 switching roosts, we expect that the switching juvenile will be associated with at least one
312 individual of the group shortly before and shortly after leaving the current roost or arriving at
313 the new roost. To this end we define the moment of departing from or arriving at a monitored
314 roost, respectively, when the steady reception of signal beacons at a base station gets cut off
315 or starts. We subsequently queried the meeting database for meetings which are active or
316 which started within 60s before and within 60s after the moment of leaving or arriving at a
317 roost.

318

319 2.5.2 Evaluation of information transfer during foraging bouts

320 We defined a foraging bout as an event where an individual starts from a known roost, returns
321 to the same roost and does not visit other monitored roosts or roosts with tagged bats
322 (indicated by stable, lasting meetings) in between (Fig. 2a). We chose these strict rules to
323 ensure that the events we are looking at relate to foraging and do not overlap with roost
324 switching events. If social information would play a role in locating foraging grounds we
325 would expect a juvenile to associate with at least one roosting partner upon starting the bout,
326 during several minutes after departure while commuting to the foraging ground, and possibly,
327 but not necessarily when returning to the roost. As described above we equally defined the
328 start and the end of the foraging bout as the end and the start of the steady reception of the
329 presence signal, respectively. We then queried all meetings which were ongoing or started
330 within 60s before and within 60s after starting a foraging bout and returning, respectively. In
331 addition, we queried all meetings which originated during the entire foraging bout.

332

333 2.5.3 Statistical testing

334 We used a Mantel-Test to test whether social information used by juveniles is obtained by
335 their mothers in the first place or by any roosting partner. To this end we created a binary
336 matrix containing “1” for dyads which have been associated while roost switching and “0” for
337 dyads which have never been observed switching communally. Accordingly, foraging
338 associations were transformed into a binary matrix. For testing the effect of maternity we
339 created a second binary correlation matrix which listed the genetically determined identity of
340 mother-pup pairs as “1”, while all other dyads were marked “0”. We tested the years 2016 and
341 2017 separately and ran Mantel tests in the library “ade4” version 1.7-11 in RStudio 1.1.453
342 using Monte-Carlo permutation tests with 9999 replicates (Dray & Dufour 2007; R
343 Developing Core Team 2015).

344

345 **3. Results**

346 3.1 Genetic analyses

347 Mother and juvenile bats were caught in day roosts at the time of weaning. In 24 determined
348 mother-pup pairs, both individuals were tagged with proximity sensors (2016: n=9, all
349 assigned at 95 % confidence with no mismatch; 2017: n=15, 12 pairs assigned at 95 %
350 confidence with no and three pairs at 95 % confidence with one mismatch). These 24 mother-
351 pup pairs generated the data for the following section.

352 3.2 Tracking results

353 In 2016 we received a total of 561,795 presence signals and 13,292 meetings from 23
354 individual bats and in 2017 we received 2,667,409 localization signals and 53,391 meetings
355 from 33 individual bats. One individual in 2016 and three individuals in 2017 did not get in
356 contact with base stations. These four individuals may have left the study area between
357 tagging and the following night.

358 3.2.1 Evaluation of joint roost switching events

359 To evaluate information transfer on roosts we screened the data set for joint departures from
360 and joint arrivals at roosts for all tagged juveniles. In 2016 we observed ten events of seven
361 individual juveniles being associated with another individual while switching among two
362 roosts. In all except one event the associated bats arrived together at a new roost, even though
363 successful switching took several approaches in two cases and temporary roosts may be used
364 in between (Table 1, Fig. 3). In six cases both roosts have been monitored by a base station, in
365 two cases the juveniles left a monitored roost and switched to a roost where other tagged bats
366 have been roosting and in the remaining two cases the juveniles switched from a monitored
367 roost to an unknown roost where no other tagged bats were present, except the one which
368 accompanied the juvenile during switching. In all 10 cases the juvenile was in company of its
369 identified mother and no other tagged bat.

370 In 2017 we observed six events where 5 individual juveniles switched roosts in company.
371 Twice, the juvenile switched among two monitored roosts and four times among one
372 monitored and an unmonitored site. Twice, the juvenile was associated with its identified
373 mother, in four cases with another adult female.

374 Some juveniles switched directly among roosts. Such events took only seconds to minutes
375 (see table xx). During other events stopover sites were used and several attempts of mothers
376 re-associating with their young were necessary before both arrived at the new roost. Such
377 unsuccessful tandem flights underline that the offspring was actively flying and not carried by
378 the mother.

379 In both years significantly more mother-pup dyad have been observed switching roosts
380 communally than expected by chance (Mantel tests, 9999 replicates; 2016: $r = 0.88$, $p <$
381 0.001 ; 2017: $r = 0.21$, $p < 0.01$).

382

383 3.2.2 Associations during foraging bouts

384 In total we detected 42 foraging bouts of juveniles, which matched our definition above,
385 conducted by 13 individuals (2016: four juveniles, eight bouts; 2017: nine juveniles, 34
386 bouts). Foraging bouts lasted on average 1:14:53 h with a standard deviation of 36:19 min.
387 During 6 of these 42 foraging bouts (14 %, n = 7 individual juveniles, all 2017) we detected in
388 total 28 short meetings, which lasted between 1 and 30 seconds (average: 7.4 s +/- 8.6). Two
389 of these meetings occurred within less than 90 s after two co-roosting individuals left a roost;
390 however, no further meetings have been documented during these foraging bouts. All
391 remaining meetings originated at least several minutes after emergence from the roost. Eight
392 times the meeting partner was another juvenile and twice an adult female. Only in one case
393 the meeting partner was the identified mother. Accordingly, meetings among mother-pup
394 dyads have not been observed more often than expected by chance (Mantel tests, 9999
395 replicates, $r = 0.08$, $p > 0.05$).

396 In 13 out of the 42 foraging bouts of juveniles (2016: n = two individuals; 2017: n = seven
397 individuals) the identified mother was co-roosting before both started a bout. In all 13 cases
398 the mother started its foraging bout considerably earlier than the juvenile (between 4:31 min
399 and 1:26:02 h, average: 36:45 min (+/- 24:57)).

400

401 **Discussion**

402 The study of information transfer in free-ranging bats is particularly challenging due to their
403 small body size and their elusive, nocturnal life. We tracked bats using novel, miniaturized
404 proximity sensors and demonstrated that juveniles use social information of group members
405 and for finding roosts mothers seem to intentionally guide their young. However, during
406 foraging mothers did not guide their offspring, but meetings with other colony members may
407 reflect local enhancement at feeding grounds.

408 To the best of our knowledge our study shows for the first time that recruitment to a new roost
409 starts already at the occupied roost. Furthermore, the repeated commuting flights we observed

410 in at least two cases until the juvenile arrives at the target roost represents anecdotal evidence
411 that at least in some cases deliberate, evolved signals rather than inadvertent social cues are
412 used. The existence of evolved signals and the strong bias towards information transfer
413 among mother-pup pairs suggests that the observed behaviour is best explained by kin
414 selection. Some studies have reported on the use of social information in bats for finding
415 suitable roosts, however, studies are scarce and the mechanisms are in parts poorly
416 understood, in particular when it comes to naïve juveniles. Studies on a range of
417 vespertilionid species including the focus species *N. noctula* have shown that conspecific calls
418 enhance roost finding efficiency in captive experiments as well as in the wild (Ruczyński,
419 Kalko & Siemers 2009; Schöner, Schöner & Kerth 2010; Furmankiewicz *et al.* 2011). These
420 studies demonstrate that bats may eavesdrop on vocalizations to localize an occupied roost
421 once within hearing distance. Since playbacks from varying contexts have been used we
422 conclude that the studied bats relied on inadvertently broadcasted public information. On the
423 contrary, Spix's disk winged bats deliberately produce signals to facilitate group cohesion, by
424 a remarkable call-and-response system among flying bats in search of a roost and bats
425 occupying a roost (Chaverri, Gillam & Vonhof 2010; Chaverri, Gillam & Kunz 2012). A
426 common theme of all abovementioned studies is that the mechanism of recruitment of
427 conspecifics is best explained by local enhancement, i.e. the social information is acquired at
428 the new roost, when searching bats are in hearing distance. Kerth and Reckardt (2003) were
429 first to present experimental evidence for information transfer about roosts in bats. The
430 authors presumed that naïve Bechstein's bats are recruited to a novel roost already at the
431 dayroost by experienced conspecifics, however, they could not unequivocally exclude local
432 enhancement at the target roost. Our study finally demonstrates that this inferred mechanism
433 does exist in roost-switching bats.

434 We classify the advertent information transfer from mothers to their young as a form of
435 maternal care which has to the best of our knowledge not been observed in free-ranging bats,

436 so far. Mammalian offspring is usually strongly dependent on maternal care for food,
437 protection and warmth (Balshine 2012) and maternal investment in young is also wide-spread
438 in bats (Smith, Lacey & Hayes 2017). Besides weaning maternal care has been demonstrated
439 in form of post-weaning food provisioning (Wilkinson 1990; Geipel *et al.* 2013), grooming
440 (Kleiman 1969; Wilkinson 1986; Kozhurina 1993) or pup guarding (Bohn, Moss &
441 Wilkinson 2009). Carrying young in flight is also commonly observed and Jones (2000)
442 summarizes some reports where young are possibly carried to temporary roosts or feeding
443 grounds. However, this is the first study to document maternal guidance to roosts, which has
444 been hypothesized as a plausible explanation for young to reach swarming and hibernation
445 sites, but could not be confirmed, possibly due to the lack of appropriate tracking technology
446 (Sachteleben 1991; Burns & Broders 2015; Stumpf *et al.* 2017).

447 Previous work on bats indicated that roosts may act as information centres where bats may
448 obtain information on food by inadvertent cues (Ratcliffe & ter Hofstede 2005; O'Mara,
449 Dechmann & Page 2014). A considerable part of the diet of Greater noctule bats consists of
450 insects, which fly in swarms and often over water (Gloor, Stutz & Ziswiler 1995). Such rich
451 and patchy, but ephemeral foraging sites are required for the establishment of information
452 centres (Ward & Zahavi 1973) and juveniles in particular might benefit from rich food
453 patches when collecting experience on where and how to forage. However, we did not
454 observe recruitment at the roost to feeding grounds in young noctules, which complies with
455 most foregoing studies that showed that 'ICH' operates in colonial roosts, but is rarely
456 demonstrated in breeding colonies (summarized by Evans, Votier and Dall (2016)). Our
457 observation that juveniles start foraging bouts considerably later than their mothers suggests
458 that juvenile noctules conduct opportunistic, explorative foraging flights. Rare and short
459 contacts to tagged colony members other than the mother during foraging bouts suggest that
460 local enhancement by eavesdropping on conspecifics while hunting may play a role as it has
461 been shown for several insectivorous bat species (Gillam 2007; Dechmann *et al.* 2009; Cvikel

462 *et al.* 2015). However, our data cannot unequivocally prove this theory since the exact context
463 of the meetings remains unknown.

464 Our observations raise the following question: Why is social information transfer among
465 mothers and their offspring context dependent? One possible explanation is that group
466 cohesion is crucial for energy-saving social warming and prolonged lactation periods in bats
467 require mothers to stay in contact with their young for 3 weeks to 2 months depending on the
468 species (reviewed by Kerth (2008)). Extended weaning, which was observed in captive
469 noctules for up to 2 months (Kleiman 1969), and the broad spectrum of insects they feed on
470 (Gloor, Stutz & Ziswiler 1995) may in turn enable juveniles to forage opportunistically and –
471 if available – make use of social information by local enhancement. In general, suitable roosts
472 of high quality may be harder to find opportunistically than insect prey and information on
473 roosts is likely to accumulate in adults, in particular in philopatric females. This should favour
474 information transfer on roosts since failing to relocate at an occupied roost might be more
475 costly than low foraging success, which might subsequently be balanced by extended
476 weaning. Adverse climatic conditions may have detrimental effects on single bats (Lindström
477 1999) and might therefore be a strong driver of the evolution of the observed guidance
478 behaviour, since local enhancement by vocalization at the roost (Furmankiewicz *et al.* 2011)
479 might not be functional for long-distance localization of roosting partners.

480

481 **Conclusions**

482 Bats are facing ideal prerequisites for social information transfer, since they are long-lived
483 and the vast majority of species is living in group. Regarding information use in offspring
484 Wilkinson and Boughman (1999) speculated already 20 years ago that young bats almost
485 certainly follow adults in situations other than foraging. However, this is also how long it took
486 to unequivocally track mother-pup pairs switching among roosting sites. Our study shows that

487 the current revolution in tracking technology provides powerful tools to investigate
488 behavioural ecology and sociobiology in free-ranging small bodied animals such as bats.

489

490 **Authors' contributions**

491 SR and FM conceived the ideas and designed the sampling scheme; MH, ND, AK, BC and
492 RK developed and tested all tracking equipment. SR, LG, FM and HW collected the data; SR
493 and LG analysed the data; SR and FM led the writing of the manuscript. All authors
494 contributed critically to the drafts and gave final approval for publication.

495

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500 113-G0008/16).

501

502 **Data accessibility**

503 Data will be deposited on GFBio and made available upon acceptance.

504

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- 659
- 660

661 **Supporting information**

662 The following Supporting Information is available for this article online.

663 Table S1: Results from allele frequency calculations with CERVUS v. 3.0 (Kalinovski et al.

664 2007).

665 **Tables**

666 Table 1: Summary of joint roost switching events of pups and associated partners. Switching
 667 durations were only determined when both roosts were known and equipped with base
 668 stations, while NA represents unmonitored sites or uncertain switching mode.

pupID	sex	partnerID	start time	end time	duration	Switching
		(mother)	[date-time]	[date-time]	[hh:mm:ss]	mode
9307	f	9338 (m)	2016-07-21 02:59:35	NA	NA	NA
9311	f	9330 (m)	2016-07-16 23:26:22	2016-07-17 01:15:06	01:48:44	3*
9311	f	9330 (m)	2016-07-20 03:18:35	2016-07-20 03:19:31	00:00:56	1
9318	f	9330 (m)	2016-07-16 23:26:33	2016-07-16 23:28:31	00:01:58	1*
9318	f	9330 (m)	2016-07-20 04:14:25	2016-07-20 04:14:54	00:00:29	3
9319	f	9327 (m)	2016-07-16 22:48:01	NA	NA	NA
9312	f	9334 (m)	2016-07-17 01:29:14	NA	NA	1
9323	m	9340 (m)	2016-07-16 23:58:13	2016-07-17 01:37:06	01:38:53	2
9323	m	9340 (m)	2016-07-19 02:05:26	NA	NA	1
9325	m	9336 (m)	2016-07-17 02:44:31	2016-07-17 03:55:19	01:10:48	2
9376	f	9383	2017-07-20 04:23:43	2017-07-20 04:23:49	00:00:06	1
9376	f	9383	2017-07-22 02:25:53	NA	NA	1
9370	f	9368 (m)	2017-07-20 04:35:41	NA	NA	1
9373	m	9412	2017-07-22 02:38:13	2017-07-22 02:38:39	00:00:26	1
9380	m	9413	2017-07-20 04:17:52	NA	NA	1
9391	f	9385 (m)	NA	2017-07-22 02:22:25	NA	1

669 Switching mode: 1 quick, direct switch among two roosts; 2 switch included a joint stopover
 670 at an unknown site indicated by stable meetings; 3 roost switch after commuting flights by
 671 mother; * see Fig. 3 for a schematic representation of these events

672

673 **Figures**

674

675 Figure 1: Unpackaged proximity sensor (a) and tagged adult Greater noctule bat (*Nyctalus*
676 *noctula*) ready for take-off (b).

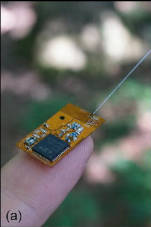
677

678 Figure 2: Visual representation of foraging bouts and roost switches based on presence signals
679 at bat boxes (base stations) and meeting data. (a) A foraging bout is characterized by an
680 interrupt of the presence signals of an individual bat which are received by a base station at a
681 specific roost. Usually, variation of the received signal strength indicator (RSSI) increases
682 when a bat is leaving a roost compared to when it is roosting (notice the pronounced spike
683 upon departure and return). (b) A roost switch among two monitored sites is displayed. The
684 presence signals interrupt at base station two while the strong variation in RSSI indicates that
685 the bat is flying. Presence signals are then received by base station 1. (c) A roost switch
686 occurs among an unmonitored to a monitored site. Roosting at the unmonitored site is
687 indicated by long-lasting stable meetings among three bat individuals. Meetings interrupt
688 when a bat individual leaves the unmonitored site followed by signal beacons being received
689 by the base station at the monitored site.

690

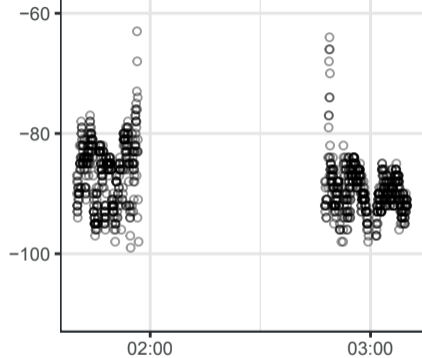
691 Figure 3: Schematic representation of a mother and its twins switching roosts: repeated
692 commutes indicate intentional behaviour of the mother. (a) A mother and its twins jointly
693 leave roost 1 and the mother successfully transfers to roost 2 with pup 1. The meeting to pup 2
694 aborts and pup 2 is flying back to roost 1. (b) Pup 2 moves solitarily from roost 1 to an
695 unknown location where it is joined by its mother after a few minutes. Both fly in company
696 towards roost 2, but pup 2 flies back to roost 1 while a meeting starts among the mother and
697 pup 1 at roost 2. (c) The mother joins pup 2 in an unknown location and they jointly switch to
698 roost 1. They jointly leave roost 1, but only the mother arrives at roost 2 starting a meeting

699 with pup 1, while the pup 2 flies back to roost 1. (d) The mother joins pup 2 in an unknown
700 location, around 00:50 am the meeting is interrupted for several minutes (possibly because at
701 least one individual left), before the mother commutes twice between its two pups. Finally,
702 around 01:15 am the mother successfully switches with pup 2 to roost 2 while a meeting is
703 ongoing. The triad stays at roost 2 until shortly before 2 am.
704

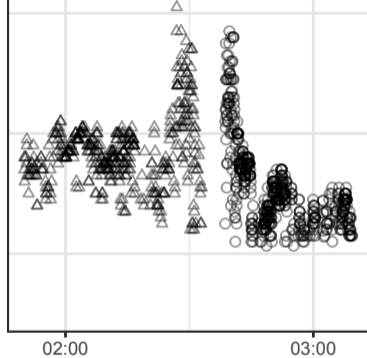


RSSI at base station

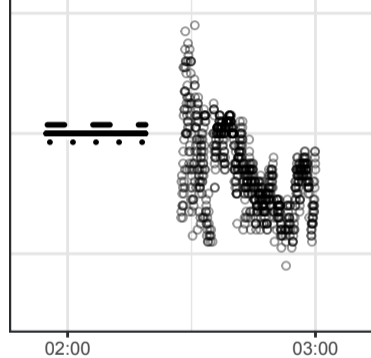
(a) foraging bout



(b) roost switch among monitored sites



(c) roost switch from an unmonitored to a monitored site



Local time Berlin

Legend: ○ Presence signal at base station 1
△ Presence signal at base station 2
— Presence at unknown roost indicated by stable meetings among three individuals

