# Reinforcement Learning Enables Resource-Partitioning in Foraging Bats

Aya Goldshtein, Michal Handel, Ofri Eitan, Afrine Bonstein, Talia Shaler, Simon Collet, Stefan Greif, Rodrigo Medellín, Yuval Emek, Amos Korman, et al.

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16

17 **Summary**

18 Every evening, from late spring to mid-summer, tens of thousands of hungry lactating female

19 Lesser long-nosed bats (*Leptonycteris yerbabuenae*) emerge from their roost and navigate

20 over the Sonoran Desert seeking for nectar and pollen [1,2]. The bats roost in a huge maternal

21 colony which is far from the foraging grounds, but allows their pups to thermoregulate [3]

22 while the mothers are foraging. Thus, the mothers have to fly tens of kilometers to the

23 foraging sites - fields with thousands of Saguaro cacti [4,5]. Once at the field, they must

24 compete with many other bats over the same flowering cacti. Several solutions have been

25    suggested for this classical foraging task of exploiting a resource composed of many

26    renewable food-sources whose locations are fixed. Some animals randomly visit the food

27    sources [6], some actively defend a restricted foraging territory [7–11], or use simple forms

28    of learning such as 'win-stay lose-switch' strategy [12]. Many species have been suggested to

29    follow a trapline, that is, to re-visit the food sources in a repeating ordered manner [13–22].

30    We thus hypothesized that lesser long-nosed bats would visit cacti in a sequenced manner.

31    Using miniature GPS devices, aerial imaging and video recordings, we tracked the full

32    movement of the bats and *all* of their visits to their natural food-sources. Based on real data

33    and evolutionary simulations, we argue that the bats use a reinforcement learning strategy,

34    that requires minimal memory, to create small non-overlapping cacti-cores and exploit nectar

35    efficiently, without social communication.

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40    **Results and Discussion**

41    The foraging task of the Lesser long-nosed bat is particularly complex. Saguaro fields

42    (*Carnegiea gigantea*) in the northern Sonora contain many hundreds of cacti per square

43    kilometer [23]. The cactus flowers open in the evening and start producing nectar ca.1.5

44    hours after sunset at a constant rate of $0.1\pm0.004$ ml/h per flower (Figure S1A, STAR

45    Methods). The quality of a specific cactus can vary dramatically according to the number of

46    flowers it opens on a given night, which translates linearly to its total rate of nectar

47    production (flowers produce nectar at similar rates and sugar concentration is similar, see

48    STAR Methods). Moreover, there is little correlation between the quality of neighboring cacti

49    (Figure 1A).

50     Energetic estimates (see STAR Methods) suggest that a lactating female needs to drink 14.1-

51     18.9 ml of nectar per night. Because a single cactus provides no more than 0.65 ml during the

52     hours that a bat spends in the field, a bat must visit many cacti. As high-quality cacti are rare

53     and most cacti have 0-1 open flowers (Figure 1A and Figure S1B), it is worthwhile for a bat

54     to invest time in exploring the field. Moreover, bats have to re-map the field every night.

55     Although we found a significant correlation between the number of flowers on a cactus on

56     consecutive nights, there was much inter-night variability (Spearman correlation test: r=0.6,

57     P<0.001, Figure S1C-D). Importantly, even if the exploration is effective, the corresponding

58     exploitation might not be trivial. In theory, a bat could memorize when it last visited a

59     profitable cactus [24] and plan to revisit it after some time interval, but it cannot be certain it

60     will find the expected nectar, since a conspecific might deplete it in the meanwhile (the bats'

61     behavior suggests that they do not know if a flower was recently visited, Figure S1E-F). We

62     thus set out to examine how bats make foraging decisions under such uncertainty.

63     We used miniature GPS devices to track bats' movement. We employed drone and aerial

64     imaging (of ~3600 cacti) to identify all resources available to the bats, that is, the positions of

65     the cacti that they visited and the estimated distribution of flowers. To complete our

66     understanding at the population level, we video-monitored tens of cacti over full nights,

67     recording all bat (and other pollinator) activity. Finally, all of these data were used to develop

68     a mathematical model that aims to explain the bats' foraging strategy.

69     In total, we GPS tracked 17 lesser long-nosed females. We then used aerial imaging to

70     reconstruct the location of all cacti at the foraging sites of eight bats (STAR Methods).

71     Henceforward, unless stated otherwise, all foraging analyses were conducted for these n=8

72     bats, with a mean of 2.9±2.1 nights per bat. Tracking revealed extreme commutes of tens of

73     kilometers, from the colony to the cacti fields (the average one-way commute was 55.4±17.2

74     km, Mean±SD, n=17 bats, with a record-holding bat that flew ~104 km to reach the field,

75    Figure 1A). On consecutive nights, bats typically returned to the same field (in 25 out of the

76    28 consecutive nights that we monitored for 8 bats, Figure 1B).
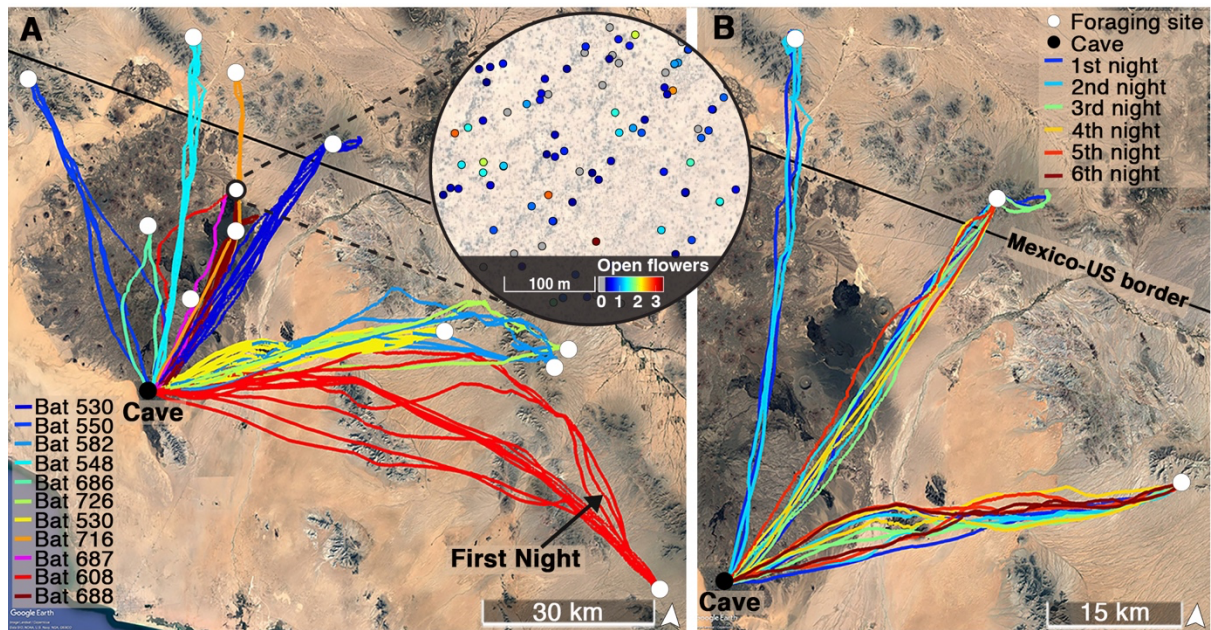


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78    Commuting to the foraging fields took 1.6±0.8 hours, in which bats flew at a mean ground

79    speed of 8.7±0.8 m/s, mean air speed of 9.1±0.9 m/s, and a mean altitude of 126±75 m above

80    ground (Mean±SD, n=17 bats, maximum ground speed was 18.3 m/s and maximum altitude

81    was ~1045 m). These long commute flights account for an average of ~46% of the total time

82    a bat spends out-doors, implying that the bats should use the remaining time for exploiting

83    the field efficiently.

84    **Foraging dynamics throughout the night**

85    Once in the field, bats spent 2.2±0.7 hours foraging (n=11, Mean±SD). Even though a single

86    Saguaro field in this region can spread over a few square kilometers, each bat concentrated its

87    foraging on a relatively small area ($0.14±0.09$ km$^2$, the convex hull of all locations defined as

88    foraging, STAR Methods). Moreover, even within this restricted site, the bat did not visit all

89    cacti uniformly, but clearly preferred some cacti over others (Figure 2A). We defined a cactus

90    that was visited by a specific bat at least five times throughout the night as belonging to this

bat's *core cacti* (see STAR Methods and Figure S1G-H for the reasoning behind this definition).
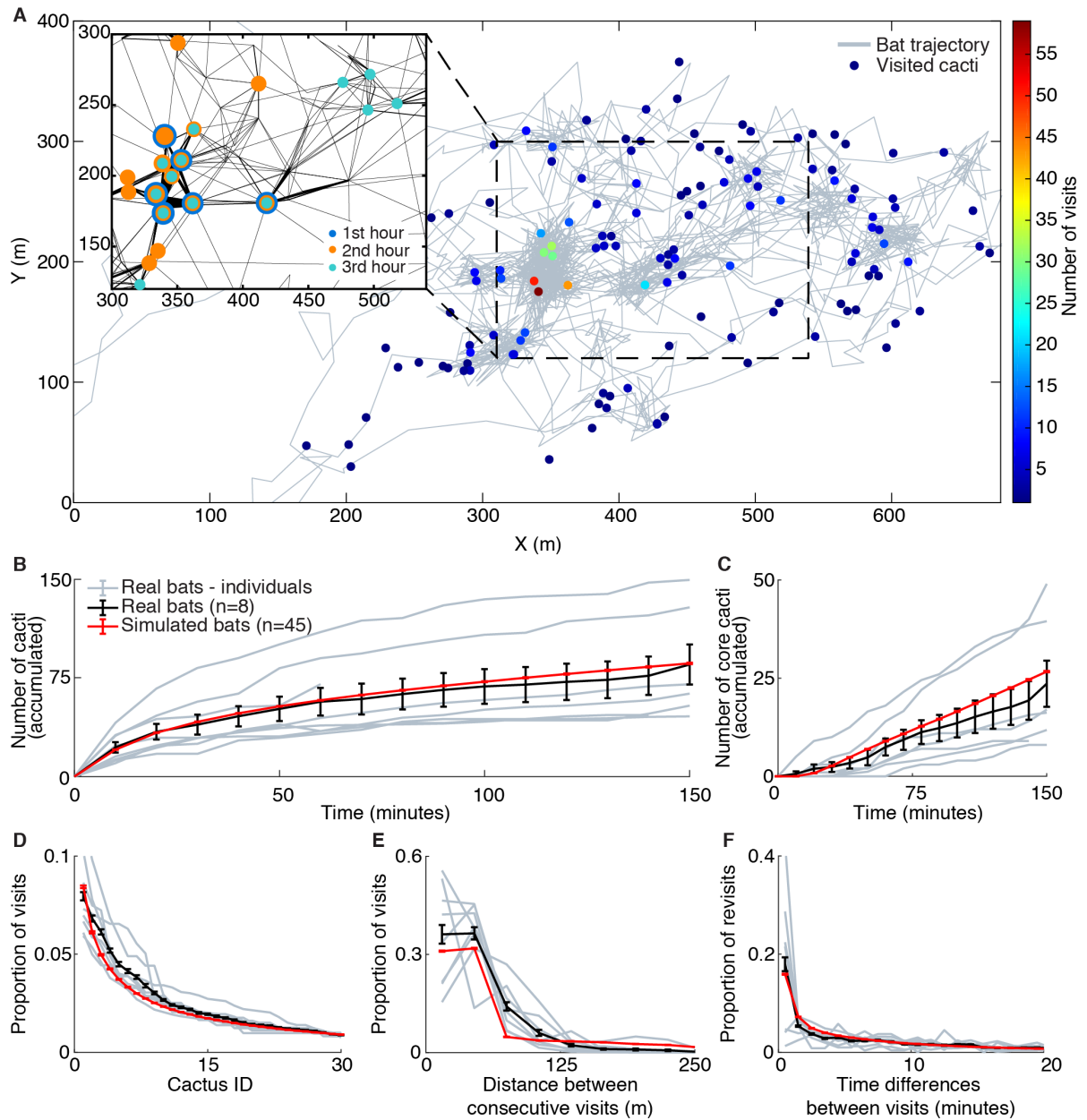


The bats combined exploitation of their core cacti with exploration of new unvisited cacti (Figure 2B-C and insert in Figure 2A), and they gradually increased the exploitation to exploration ratio at a steady rate throughout the night (Figure S1I). By the end of the night, a bat visited an average of 86±48 cacti, out of which, 28±26 (~33%) cacti were part of its core

99  cacti (Mean±SD, Figure 2B-C, Figure S1J). This accounts for drinking ~18 ml of nectar per

100  night, approximately the amount required by a lactating female (see STAR Methods).

101

102  **Information-based foraging**

103  Bats clearly did not visit cacti in the field in a deterministic ordered sequence, as a trapline

104  strategy would suggest (see Figure S1K-L for more details). However, the bats also did not

105  visit the cacti at random. Indeed, video analysis revealed that cacti with more flowers were

106  visited significantly more often (Spearman correlation test, r=0.40, P=0.02, n=33 cacti,

107  Figure S1M), suggesting that some kind of a reinforcement mechanism underlies the bats'

108  behavior.

109  In order to unravel the bats' visitation strategy, we developed a mathematical model that

110  simulates a single night of foraging under competition in a space with multiple replenishing

111  food-sources, using a rule inspired by reinforcement learning [25]. In the simulations, bats

112  start without prior knowledge on cacti quality, and remember the value ('nectar-weight') and

113  positions of the ten best cacti they experienced (see Figure S1J). At each visit, the bat updates

114  the nectar-weight of the cactus depending on the cactus' nectar yield as experienced by the

115  bat in previous visits and according to a learning rate $\alpha$. Then the bat samples its next visit

116  from the set of cacti that includes the ten remembered best cacti and the other cacti around it

117  (STAR Methods). The probability to pick a cactus in this set is proportional to its nectar-

118  weight, i.e., to the amount of nectar it provides, and inverse-proportional to its distance from

119  the current location of the bat.

120  Importantly, we did not fit the data in order to find the learning-rate $\alpha$. We ran evolutionary

121  simulations, in which multiple bats with different individual learning-rates competed with

122  each other. Bats that accumulated more nectar had higher chances to reproduce; and the

123  learning-rates in each generation were slightly mutated. After many generations, the

124     simulated bats converged to a learning-rate of 4.6, see STAR Methods. The simulated bats

125     with this $\alpha$ behaved very similarly to the real bats (compare the red and black lines in Figure

126     2B-F).

127     Similar to the real bats, the simulated bats showed a strong preference for specific core cacti,

128     but they also continued exploring other cacti (Figure 2B-C). The simulated bats increased the

129     exploitation to exploration ratio in a similar rate as the real bats and they showed a similar

130     preference for cacti with more flowers (Figures S1I and S1M, respectively). The simulated

131     bats hopped between cacti with a similar distance distribution as the real bats (Figure 2E),

132     and they revisited cacti after similar time-intervals (Figure 2F). Our model was also able to

133     predict the nectar consumption per visit of the actual bats, as we observed in the video

134     (Figure S1N). All the above suggests that our simple model, which assumes little memory

135     and a single free parameter can well-approximate the bats' behavior.

136     We also compared our model to two other models. The first, had no learning and bats visited

137     the cacti uniformly at random. The second model, a version of a trapline-model, is similar to

138     our model, except that cacti at the core are visited in an ordered manner that minimizes the

139     distance to the next cactus (Figure 3A-E, and STAR Methods). Both of these alternative

140     models performed worse in terms of their fit to the actual data (Figure 3F), and were also

141     significantly less efficient in terms of nectar consumption (One-way ANOVA: $F_{(2)}=28.5$,

142     $P<0.001$, Figure 3G).

143     We conclude that learning is a key feature of the bats' behavior. Because bats rarely

144     encounter conspecifics at the cacti (see below), the main way in which a bat experiences

145     competition is through depletion of cacti. We thus hypothesized that learning is particularly

146     useful in the face of competition. To examine this, we ran another simulation comparing the

147     model, in which cacti are visited uniformly at random in each step, to our reinforcement

148     algorithm strategy, under two circumstances: (1) when the forager is alone in the field and (2)

when it forages with conspecifics - unlike the simulations above, here we tested a situation

150 where half of the bats use the first strategy (i.e., random) and the other half use the second

151 strategy (i.e., learning). In the case of a sole forager, a purely random model was as good as

152 the learning model (Permutation-based t-test: P=0.3, n=10,000 simulations). This

153 phenomenon was reversed in the case of many competing bats, where the simulated bats that

154 used reinforcement learning consumed 43% more nectar than the randomly-visiting bats

155 (17.2 ml vs 11.9 ml in the learning and random models respectively, Permutation-based t-

156 test: P<0.0001, n=10,000).



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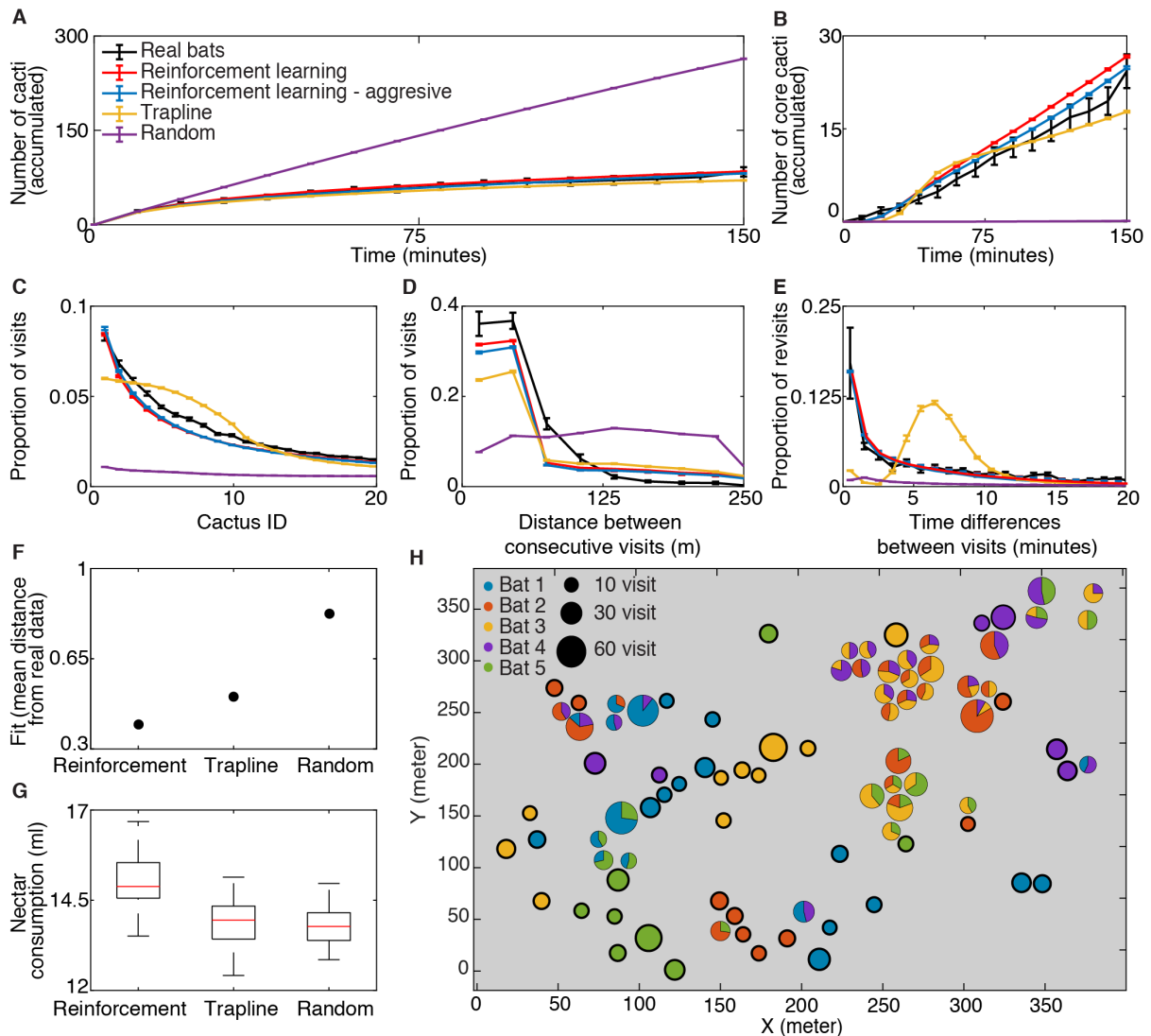
**Individual foraging cores with little overlap emerge from reinforcement learning**

160 A prominent feature of our model is the formation of foraging cores with little overlap

161 A prominent feature of our model is the formation of foraging cores with little overlap

162 between individuals (Figure 3H, we prefer the term "core" to "home range" [26] because

163 their important feature is the set of cacti they are composed of and not their area). The

164 sharing of core cacti by multiple bats in our simulations was significantly lower than

165 expected if the bats randomly visited the cacti (see STAR Methods, Permutation-based t-test:

166 P=0.0001, n=10,000 simulations). Data suggests that in reality bats also form disjoint cores

167 with little overlap - video analysis revealed an estimated overlap of 1.3 bats per cactus, while

168 in the simulations it was 1.5 bats per cactus, (Figure S2A-B).

169 Importantly, foraging cores are unlikely to be a result of territorial behavior: bats' core cacti

170 spread over 0.04 km$^2$, an area far too large for a bat to defend - flying from one side to the

171 other would require ~40 seconds while a visit of a conspecific to one of the bat's cacti

172 requires less than a second (Video S1). Moreover, the range from which a bat could detect a

173 conspecific based on its echolocation is limited [27], and visual detection range is even more

174 limited, reaching only ~50 m [27,28].

175 To further understand the potential impact of interference competition, we added to the

176 simulation a component of aggressive defense where a bat deters conspecifics it encounters at

177 its core cacti (Figure 3A-E, blue lines, see STAR Methods). Consistent with our hypothesis

178 that core formation is not a result of territorial defense, this aggressive model did not differ

179 from the previous non-aggressive model.

180 Moreover, the formation of foraging cores was also not a result of the limited memory of the

181 simulated bats (10 remembered cacti). We ran the model with unlimited memory where the

182 bats remember the positions and weights of all cacti in the field, and the same type of core

183 cacti evolved (Figure S2C-F). In fact, what appears to determine the size of a foraging core is

184 the learning rate α, where a larger α generates smaller cores (Figure S2G-J). This is intuitive

185    as a larger α drives more exploitation of previous profitable cacti at the expense of exploring

186    new cacti.

187    The little overlap between neighboring cores in the simulation appears to result from a

188    combination of two factors. First, bats initially visit cacti randomly, and then a positive

189    feedback effect enhances the profitable initial discoveries through reinforcement learning.

190    Second, the nectar-weights of profitable cacti are reinforced accumulatively, increasing their

191    weight in the eyes of the owner bat and, at the same time, decreasing their nectar-weights in

192    the eyes of occasional visitors that are likely to find the cacti empty. When this reinforcement

193    learning strategy is employed in parallel by many bats, it enables the partitioning of the

194    resources in the field without active communication and reduces the number of conflicts.

195    Indeed, very few social agonistics interactions were observed - only in 5% of the 1123 visits

196    documented on video.

197    **<u>The efficiency of core formation</u>**

198    Despite its simplicity, the proposed reinforcement learning strategy results in highly efficient

199    foraging: as a group, the simulated bats consumed 91% of the total amount of nectar that was

200    accumulated in the field during the night (14.9±0.8 ml per bat). This means, in particular, that

201    *any* other foraging algorithm could not improve nectar consumption by more than 10% on

202    average.

203    In principle, one might expect that a more sophisticated (non-realistic) algorithm, that, e.g.,

204    maintains a complete memory of the qualities of all cacti and visits them accordingly, would

205    perform significantly better than one that only selects a small subset of core-cacti. However,

206    an analytic analysis of a simplified model suggests that this intuition is wrong (see [29]). We

207    mathematically analyzed a simplified setting in which a (single) bat aims to exploit a set of n

208    cacti with different refill rates ($r_i$ is the rate of the i'th cactus). Competition is modeled as

209    uncertainty, i.e., a cactus i is emptied at each round with some "depleting probability" $0 < s_i$

210   <1. Furthermore, distances between cacti are neglected, and in each round a new cactus can

211   be visited. We restrict attention to purely-stochastic strategies that are characterized by a

212   probability vector p = ($p_1$, ..., $p_n$), determining the probability $p_i$ that the bat visits cactus i in

213   each round. We prove analytically that when cacti are visited often by other bats (modeled by

214   higher depleting probabilities) a purely-stochastic strategy based on exploiting a relatively

215   small core will be almost as good as the best strategy. In our simulations, smaller cores can

216   be achieved by increasing α. Indeed, the reinforcement learning literature shows that α can be

217   tuned by an animal, based on the environment [30].

218   Another interesting result of our analytical analysis (mentioned above) is that the cacti bats

219   should choose for the core are those that have higher refill rates $r_i$ relative to low depletion

220   probabilities $s_i$. In the analytical model, those cacti with higher $r_i/s_i$ ratios are expected to

221   accumulate larger amounts of nectar. This nicely corresponds to the reinforcement learning

222   algorithm in our simulations, that assigns a large weight to a cactus that contains much nectar

223   upon our bat's visit.

### **Conclusions**

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225   Foraging is a fundamental task which entails many decisions. In this study, we used

226   comprehensive continuous tracking of lesser long-nosed bats in parallel to estimating their

227   available resource to study their foraging decisions as they explore and exploit food resources

228   in their natural environment. Interestingly, a single parameter model based on reinforcement

229   learning was able to closely reproduce the bats' behavior.

230   This model has three main characteristics: 1. The emergence of individuals foraging cores

231   through reinforcement learning and competition. 2. Exploitation of the cores through

232   stochastic sampling that is dependent on the cacti quality and distances. 3. Exploration of the

233   field in search of new profitable cacti and update of the core accordingly, in parallel to

234   exploitation.

235 Another foraging strategy that is adopted by many species including insects and birds is

236 trapline [31]. In our system, however, we do not see evidence for trapline. In principle, the

237 bats could have used a reinforcement-learning component to identify a core with high quality

238 cacti and then exploit the core using a trapline. However, as we show, it turns out that this

239 combined strategy is inferior to the reinforcement-learning strategy (Figure 3G). Perhaps the

240 reason for this, is that distances between cacti in a core are small and their qualities still vary.

241 Hence, a strategy that specializes in minimizing traversal lengths such as trapline would be

242 less effective than the reinforcement-learning strategy that effectively incorporates both

243 qualities and distances despite being memoryless.

244 Due to the simplicity and effectiveness of the reinforcement-based strategy, we hypothesize

245 that other species facing similar foraging tasks also adopt a similar strategy. A key

246 characteristic of which would be dividing the resources between individuals without direct

247 communication and without a need for aggressive territoriality.

248

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262  **Author Contributions**

263  A.G., Y.Y. and R.A.M., designed the experiments; A.G., M.H., O.E., A.B., T.S., S.C., S.G.

264  and Y.Y. conducted the experiment; A.G. conducted the analysis, carried out drone imaging

265  and analysis. A.K., S.C., Y.Y. and A.G. designed the model and A.G. implemented the

266  model. A.K and Y.E conducted the analytic analysis of the simplified model. A.G, Y.Y. and

267  A.K. wrote the manuscript.

268  **Declaration of Interests**

269  The authors declare no competing interests.

270  **Figure Legends**

271  **Figure 1. Typical movement of lactating nectar-feeding bats.** (**A**) Bats fly tens of

272  kilometers from the cave to their foraging site (colors represent different individuals, n=11

273  bats for which we had at least one full night). The bat that flew farthest (red) flew a one-way

274  distance of ~104 km on her first night (depicted by a black arrow) to her foraging site (white

275  circle). The zoomed in circle panel shows how the cacti quality - the number of open flowers

276  - differ greatly within one of the Saguaro fields, with 0-4 open flowers on an average night (0

277  flowers are presented as grey circles and 1-4 flowers are presented as blue to red circles). See

278  also Figure S1. (**B**) Bats typically visited the same Saguaro field on consecutive nights

279  (colors from blue to red depict different nights for each bat, three bats with a mean of 4.3±2.0

280  nights per bat are shown). When returning to the same site, the bats visited ~75% of the cacti

281  that they visited on the previous night (n=8 bats, see also STAR Methods and Table S1).

282  **Figure 2. Nectar-feeding bats foraging dynamics.** (**A**) Flight trajectory of one bat is shown

283  (grey line) and the cacti it visited are colored according to the number of visits (unvisited

284   cacti are not presented). Top left insert shows hops between cacti, where the width of the

285   black lines represents the number of hops between cacti and colored circles represent only the

286   core cacti that were visited more than 5 times at different hours throghout the night. In all

287   panels B-F colors are as follows: grey - real bats data; black - Mean±SE of 8 real bats; red -

288   Mean±SE of 45 simulated bats (30 simulations). (**B**) The accumulated number of visited cacti

289   and (**C**) core cacti throughout the night (see also Figure S1J). (**D**) The proportion of visits per

290   cactus are sorted according to cactus ID, i.e., cactus 1 is the cactus that received most visits.

291   (**E**) The distribution of distances between consecutive visited cacti. (**F**) The distribution of

292   time lags between revisits to the same cactus. Core cacti were close to each other (25.1±13.6

293   m apart) and bats revisited them very often (consecutive visits to core cacti were on average

294   8.9±3.5 minutes apart, Figure 2E-F).

295   **Figure 3. Comparison of different models.** (**A-E**) Foraging behavior of real bats (black),

296   and simulated bats using different foraging models: reinforcement learning (red),

297   reinforcement learning with aggression (blue), trapline (yellow) and random (purple).  (**A**)

298   Accumulated number of visited cacti and (**B**) core cacti (first 2.5 hours). (**C**) Sorted

299   proportion of visits per cactus (in the 20 most visited cacti). (**D**) The distribution of distances

300   between consecutive visited cacti (30 meters bins). (**E**) The distribution of time lags between

301   revisits to the same cactus (first 20 minutes). (**F**) The fit of different foraging models

302   (normalized mean distance from real data, data was normalized to a max of 1 before fitting).

303   (**G**) Bats' nectar consumption in different foraging models. (**H**) Core cacti of five simulated

304   bats in the reinforcement learning model. Cacti of different individuals are depicted by

305   different colors and circle size represents the number of visits (accumulated over a full night).

306   Cacti that were in the core of more than one bat appear in multiple colors according to the

307   relative number of visits of each bat; and cacti that were in the core of a single bat are circled

308   by a black line. See also Figure S2.

309

**STAR Methods**

**Lead Contact**

Further information and requests for resources should be directed to and will be fulfilled by

the Lead Contact, Yossi Yovel (yossiyovel@gmail.com).

**Materials Availability**

This study did not generate new unique reagents.

**Data and Code Availability**

The datasets and code generated during this study are available at Mendeley, doi:

10.17632/jxghjjsttw.1

**EXPERIMENTAL MODEL AND SUBJECT DETAILS**

All experiments were conducted under permit number 443 # 04019/15, 03946/15 14509/16

from the Dirección General de Vida Silvestre (=Wildlife Service). All experiments on *L.*

*yerbabuenae* and *C. gigantea* has been conducted in El Pinacate Biosphere Reserve and in

the surrounding Saguaro fields (in the Sonoran Desert in northwest Mexico).

**METHOD DETAILS**

**Tracking bats' movement**

During May-June 2015-2017, we successfully monitored the movement of a total of 17

lactating female lesser long-nosed bats (*Leptonycteris yerbabuenae)*. We used miniature GPS

data-loggers (Lucid Ltd., Israel) combined with a synchronized ultrasonic microphone (FG-

23329, Knowles) [27] to tag bats roosting in a maternity colony with more than 50,000

lactating bats in El Pinacate Mexico [32]. A telemetry unit (either LB-2X 0.3 g, Holohil

Systems Ltd. Carp, Ontario, Canada or Pico pip Ag379 0.37 g, Biotrack Ltd, Dorset, UK)

was attached to the GPS, to enable its recovery after falling off the bat. Tracking bats'

333     movement for up to eight days in a row revealed fundamental aspects of their foraging

334     strategy.

335     The device's total weight was 4.1±0.1g (mean±SD), which accounted for less than 14% of

336     the average body mass of the bats (the average mass of the bats was: 30.0±2.7g, n=17). We

337     have already mounted these tags on similar sized bats (e.g., *Rhinopoma microphyllum,*

338     *Myotis vivesi* and *Myotis myotis*) for which we performed several control experiments to test

339     the effect of the extra loading on their well-being and behavior (see detailed information in

340     Cvikel et al. [27] and Egert-Berg et al. [33]). Here too, we made sure that this additional

341     weight did not affect foraging: all tagged bats left the cave and flew to remote foraging sites,

342     sometimes as far as ~100 km from their roost where they exhibited vast foraging. We also

343     conducted several control experiments ensuring that flight and foraging abilities of the bats

344     were maintained. To test bats' ability to forage, we captured three non-lactating females,

345     mounted the same GPS tags on their backs, and recorded their behavior while feeding on

346     flowers on a cut Saguaro branch placed inside a flight tent. All bats were able to approach the

347     flowers, hover in front of them and drink (See Video S2). Bats were allowed to feed *ad-lib*

348     and were released in good condition at the cave at the end of the experiment. To test the

349     effect of the additional weight on the overall flight duration, we tagged 10 bats with

350     lightweight (1g) telemetry unit (without GPS). The bats that were tagged with heavier GPS

351     devices spent a similar amount of time outside the cave (6.3±1.4 hours, n=9) as the bats that

352     were tagged with light tags (5.9±1.3 hours, n=10, Wilcoxon rank sum test, P=0.84).

353     Additionally, one bat that we tagged and was caught a week later (at the same time of the

354     night), was found in a very good condition and gained 1.3g during this period when it carried

355     the extra tag-weight.

356     **Movement analysis**

357    GPS positions were sampled every 2, 5, 15 or 30 seconds for different bats (Table S1

358    summarizes which bats were used in which of the analyses). GPS positioning standard

359    deviation was estimated to be 8 m in the horizontal plane and 11 m in height [27]. Bats'

360    ground speed was estimated as the derivative of distance over time between GPS points that

361    were 15s apart, and outliers with ground speed above 30 m/s were removed. Bats' airspeed

362    was calculated by subtracting the estimated wind speed in the direction of the flight from the

363    bat's ground speed. Wind data was collected from a weather station located between the cave

364    and the foraging sites (31.679985, -113.304831). The bats' height above the surface was

365    estimated by subtracting the geoid and the elevation above the surface from the altitude

366    above the ellipsoid (provided by the GPS). The geoid height was estimated to an accuracy of

367    0.001 m using the EGM2008 Geopotential Model and surface elevation was extracted using

368    Google Maps Elevation API. The height over-time was smoothed using the 'LOESS' local

369    regression smoothing filter [34]. Bats' movement was divided to commute and foraging using

370    the straightness index that measures the ratio between the actual path length and the direct

371    distance between two points [35]. The straightness index was calculated for segments of five

372    minutes and revealed a bimodal distribution with a trough at 0.4 separating the two modes.

373    hence, GPS positions with a straightness index lower than 0.4 were considered as foraging

374    and GPS positions with straightness index greater than 0.4 were considered as commute

375    (Figure S2K-L). Short flights inside the foraging sites were considered as foraging even if

376    their straightness index was higher than the threshold (0.4).

377    **Foraging behavior analysis**

378    Some of the bats briefly visited secondary foraging sites on the way to the main one

379    (spending no more than 10 minutes in these sites). We restrict our analyses to foraging in the

380    main site.

381     ***A visit.*** A visit to a cactus was defined as flying at a distance of less than 15 meters from a

382     cactus, in an altitude of less than 20 meters. The video analysis revealed that bats typically

383     lingered in the area of a cactus for a few seconds before visiting it which made GPS-based

384     visit recognition easier. We also validated our visit detection method using the video

385     recordings (See Video S1 and Figure S2M). Notably, all of our analyses are based on the

386     proportions of visits and not the absolute number of visits, so even if our method for

387     detecting visits under- or over-estimated their number, this should not have affected our

388     results.

389     Consecutive visits to the same cactus less than 60 seconds apart were considered as one visit

390     since the video recordings (below) showed that bats tend to fly around the cacti and approach

391     it repeatedly during a visit. In cases where a bat visited a patch with several cacti less than 15

392     m apart, one of the cacti in the patch was chosen randomly and considered as the visited

393     cactus. For every visited cactus, number of visits, visits duration, distance and time past

394     between consecutive visits were calculated.

395     We examined the influence of the lower GPS sampling rates on the results, by reducing the

396     sample rate of bats that were sampled every two seconds to five, 15 and 30 seconds. We

397     found no difference between the bats' behavior using sample rates of every two and five

398     seconds, and corrected the results for only three bats that were sampled at a lower rate (one

399     bat that was sampled every 30 seconds and two bats that were sampled every 15 seconds).

400     ***The definition of core cacti.*** Cacti that were visited more than five times during the night by

401     a specific bat were defined as the bat's core cacti. We used a criterion of five revisits to the

402     same cactus because the distribution of revisits drops rapidly above five visits (Figure S1G-

403     H).

404     **<u>Cacti locations and number of open flowers</u>**

405 Several approaches were used to assess cactus and flower distribution: (1) cacti locations in

406 specific areas where the tagged bats foraged were identified using (a) drone-imaging (using a

407 DJI Phantom 3 advanced drone with its built-in camera 12.4M pixel, DJI Science and

408 Technology Co. Ltd., Guangdong, China); (b) Google Earth satellite and aerial images (in

409 cases where flying a drone in the area was prohibited). In total, we managed to map the cacti

410 in the foraging sites of eight bats. (2) The flowering of 414 cacti from three cacti fields

411 around El Pinacate biosphere reserve were characterized: 327 cacti (121 flowering cacti) in

412 an area of ~84 $m^2$ were monitored over 8.3±2.8 days per cactus (22/5/2016-7/6/2016) by

413 remote-imaging using the same drone and camera as above. The drone was flown above the

414 field early in the morning when the flowers are still open. A 3D model of the field was

415 created using Pix4Dmapper Pro version 2.2.25 allowing to count the number of open flowers.

416 Additional cacti were monitored every morning in a manual census during 10.7±3.4 days per

417 cactus (26/5/2015-11/6/2015 n=48 cacti, 6/5/2016-28/5/2016 n=23 cacti, 25/4/2017-2/5/2017

418 n=6 cacti, 13/5/2017-27/5/2017 n=10 cacti).

419 **<u>Video observations</u>**

420 33 saguaro cacti were videoed for an average of 1.8±1.2 nights (n=62 nights in total) during

421 the flowering season (11/5-1/6/2016, 12/5-18/6/2017) using IR video cameras (Full Spectrum

422 POV Cam, GhostStop, Florida, USA or Panasonic Action Cam HX-A1, H.264 1920x1080,

423 30fps). Each camera was placed on a two m pole at a distance of two m from the cactus for a

424 period of nine hours (starting at sunset). Bats' echolocation and social calls were recorded in

425 45% of these observations using Ultrasonic recorders (Song meters SM4BAT, Wildlife

426 Acoustics Inc., Massachusetts, USA) that were placed <50 cm below the flowers. In cases

427 where the cactus had more than one branch with flowers, we used a separate camera for each

428 branch, so that all approaching bats to all of the cactus flowers could be observed. The videos

429 were fully analyzed and all visits of all pollinators (bats, moths and birds) were denoted.

430     Social interactions between conspecifics were also noted (based on the video or based on the

431     detection of social calls in the audio recordings).

432     **<u>Nectar refill rate and nectar consumption</u>**

433     To estimate the nectar refilling rate throughout the night, the upper part of eight cacti were

434     covered with mesh (20D nylon tulle) to prevent access to their flowers. During two

435     consecutive nights (20-21/5/2017), nectar was extracted from the flowers every 90 minutes

436     (from 21:00 at least until 03:00, during the bats' presence in the field) using a 1 ml syringe,

437     and the amount of nectar was measured (n=17 flowers, 1.4+0.8 flowers per cactus per night).

438     Sugar concentration was measured using Bellingham-Stanleylow-volume Eclipse

439     refractometers (0–50 Brix). We found little variation in sugar concentration (24.5±2.7%), in

440     nectar rate and in the accumulative nectar quantity (0.73±0.13 ml) at the end of the night, and

441     no correlation between the accumulative nectar quantity at the end of the night and the

442     number of open flowers (Pearson correlation test: r=0.1, P=0.6). The amount of nectar in a

443     flower (ml) can thus be predicted according to the time passed since 21:00 (~1.5 hours post-

444     sunset) using a linear equation: $0.13 + 0.102 \times$ time (hours), $R^2$=0.89, P<0.001, n=40 flowers

445     (Figure S1A). To assure that repeated nectar depletion does not affect nectar secretion, we

446     conducted another experiment where we measured the nectar quantity throughout the night in

447     different flowers (each flower was depleted and measured only once). When comparing the

448     two experiments, with and without repeated depletion, we found that nectar secretion rate

449     throughout the night is not affected by repeated nectar depletion (Generalized linear mixed-

450     effects model: P=0.381, n=202 flowers that were measured once, 20 flowers that were

451     repeatedly depleted throughout the night, and depletion status as fixed effect).

452     To examine how much nectar a bat drinks in a visit, five bats were released in a flight tent for

453     four nights (21:00-03:00), and video-recorded while feeding ad libitum on 25% sugar water

454     from 1-ml tubes which were placed inside 10 Saguaro flowers that were mounted on the top

455    of two 20 liter water bottles (mimicking the cylinder structure of a Saguaro cactus). After

456    every feeding event, the amount of nectar was measured, and the tube was refilled. Drinking

457    duration of each drinking event was measured from the tube. We found that drinking amount

458    per feeding event could be predicted by the feeding duration, according to a linear equation:

459    nectar feeding amount (ml)=0.052 + 0.44 × feeding duration (s) $R^2$=0.36, P<0.001, n=187,

460    Figure S2N-O). Based on this equation, we concluded that a bat in the field drinks 0.04±0.04

461    ml (mean±SD, n=2492 observations) in an average visit.

462    **Estimating the bats' energy consumption**

463    In order to examine whether the nectar consumed by our bats is enough to cover their

464    energetic demands, we used literature estimates of their energetics. According to Horner et al.

465    [36], a 23g non-reproductive lesser long-nosed bat spends 1.05, 0.97, 0.32 Watts during

466    commute, foraging and day roosting, respectively. Converting these values to kJ according to

467    the average duration our bats spent in each activity (commuting for 3.1±1.2 hours, foraging

468    for 2.2±1.0 hours and day roosting for 18.7±1.5 hours, n=11) results in a mean energy

469    demand of 40.9 kJ per day. Kunz & Nagy [37] estimated the energy consumption of lactating

470    bats as 50-100% higher than non-reproductive individuals, hence we estimate the energy

471    consumption of a lactating lesser long-nosed bats as 61.4-81.8 kJ. Since 0.1 ml of Saguaro

472    nectar provides 0.43 kJ [36], lactating bats need to drink between ~14-19 ml of nectar and

473    non-reproductive bats need to drink ~9.5 ml of nectar per night.

474    Based on our GPS monitoring and video analysis, the lactating bats conducted ~450 feeding

475    visits on average throughout the night, drinking 0.04 ml on an average visit (according to our

476    video observation and nectar model, Figure S1N). That accumulates to drinking 18 ml of

477    nectar during a full night, nicely corresponding to the calculation above.

478

479    **The foraging model**

480    In order to unravel the bats' visitation strategy, we developed a mathematical model that

481    simulates a single night of foraging under competition in a space with multiple replenishing

482    food-sources. At each step, each agent (bat) in our model decides which cactus to visit next

483    based on its previous experience and current location. To capture the fact that bats visited

484    profitable cacti more often (Figure S1M), we modeled this decision process using a rule

485    inspired by reinforcement learning [25], in which the agent learns to prefer rewarded stimuli.

486    In the simulation, each bat associates each cactus with two parameters: a 'nectar-weight' and

487    a 'score'. The nectar-weight of a cactus depends on the cactus' nectar yield as experienced by

488    the bat in previous visits, and the score of a cactus depends on both the nectar-weight and the

489    distance of the cactus from the current location of the bat. After every visit to a cactus, the bat

490    updates its nectar-weight (see below) and it then visits the next cactus with probability that is

491    proportional to its score. If higher nectar is found in a cactus, it will have more nectar-weight

492    and hence a higher score, which means that the probability of returning to it can only

493    increase.

494    In the simulations, the bats start without prior knowledge on cacti quality. At any point in

495    time, bats remember the nectar-weights and positions of only 10 cacti (we chose this number

496    because this is the number of cacti we observed in the core in time slots of 30 minutes (see

497    Figure S1J). Moreover, nectar feeding bats have been shown to have an immense spatial

498    working memory [24]). "In the eyes" of a bat, the nectar-weights of all other cacti are set to

499    1. Cacti scores are proportional to their nectar-weights and inversely proportional to their

500    distance, that is, the score $S_b(c,t)$ that a bat '$b$' associates with cactus 'c' at time 't' is:

501    Eq 1. $S_b(c, t) = \frac{W_b(c,t)}{T_b(c,t) + \tau}$,

502    where $W_b(c,t)$ is the nectar-weight that bat '$b$' gives to cactus 'c' at time 't' (see below),

503    $T_b(c,t)$ is the duration of flight to cactus 'c' from the current location of bat '$b$' (which is

504    proportional to the corresponding distance) and $\tau$ is the time duration of a visit.

505    Similarly to the reinforcement learning framework [25], bats update nectar-weights at each

506    visit based on how much nectar they drank (relative to an average expectation). At time 't',

507    the nectar-weight of the last visited cactus 'c' is updated:

508    Eq 2. $W_b(c,t) = W_b(c,t-1) + [N - Avg] \times \alpha$ ,

509    where $W_b$(c,t) is the nectar-weight of cactus 'c' at time 't' in the eyes of bat 'b', N is the

510    volume of nectar consumed during the visit, Avg is the average consumed volume (set to

511    0.04ml based on field observations) and $\alpha$ is a scaling parameter equivalent to the learning

512    rate in reinforcement learning.

513    The list of remembered cacti is updated as follows: if the nectar-weight of a visited cactus

514    exceeds the nectar-weight of at least one of the 10 remembered cacti, it will replace the

515    remembered cactus with the lowest score. In turn, the latter cactus will go out of the list and

516    its nectar-weight will be set to 1. In order to keep exploring, the bats can also visit

517    unremembered cacti (i.e., with nectar weights = 1) but since they do not remember the

518    location of these cacti, they will only visit unremembered cacti within their visual sensing

519    range [28,38].

520    The fixed parameters of the model, namely, the numbers of bats and cacti (45 bats with a

521    ratio of 1 bat per 12 flowering cacti), cacti locations, flower distribution and nectar filling

522    rate, were all set based on our field measurements (see below).

523    The model thus has one free parameter, $\alpha$ - the learning rate. We used an evolutionary

524    algorithm [39] in order to predict the value of $\alpha$ (an evolutionary algorithm searches for a

525    solution that is at equilibrium under the modeled conditions). The value of $\alpha$ in our

526    evolutionary simulations converged to an average of 4.6, with all individuals converging to a

527    range around it (4.6±4.8 Mean±SD). Importantly, although we did not fit the data to the

528    model ($\alpha$ was determined evolutionary) the simulated bats with this $\alpha$ behaved very similarly

529    to the real bats (compare the red and black lines in Figure 2B-F).

**The Fix factors of the model** A bat in our simulation arrives at a field with a fixed number of cacti that are distributed over a plane according to an actual field whose cacti-positions have been reconstructed. The simulated field has 1125 cacti and 45 bats. This agrees with our observed bats-cacti ratio estimations: ~200,000 bats are estimated to roost in the El Pinacate cave using annual bats counting and ~5,700,000 cacti were estimated to be in a radius of 100 km from the cave based on satellite imaging analysis, see sensitivity analysis for this parameter in Figure S3A-F). Each cactus has a certain number of open flowers that are sampled from a real distribution (Figure S1B) and it refills all of them in a constant rate according to our field measurements (Figure S1A).

**Initial nectar weight** Bats start at random positions in the field (real bats can fly from one side of the field to the other in ~40 seconds), without prior knowledge on cacti quality (all cacti receive initial equal nectar-weights = 1). We chose the value of 1, since if we choose any other positive constant instead of 1, say c, the system will behave the same by replacing alpha with c times alpha. Since we are aiming to evolve and learn alpha, we will get the same result, only named differently. At any point in time the bats remember the values (i.e., nectar-weights) and positions of only 10 cacti and can visit these remembered cacti and other cacti within their vision detection range. Because a bat always sees additional cacti in its range it will never hold in its memory a cactus with weight smaller than the default value (1), therefore we don't have to worry about negative weights.

**Remembered cacti** The number 10 was chosen because on average, the bats visited 10 core cacti at every moment throughout the night. We divided the night into time period of 30 min and during this period real and simulated bats visited 9.6±0.5 (n=8) and 10.2±1.1 (n=45) core cacti, respectively. Figure S1J). We also show that there is no advantage in remember more than 10 cacti, since even bats that remembering all cacti in the field perform very similar to bats that remember only 10 cacti (Figure S2C-F).

555 ***Bats' detection range*** In the simulation, we assumed that the bats' detection range of a cactus

556 is 50 meters. There is very little behavioral data on bats' vision. In a previous study we found

557 that the night vision of *Rousettus aegyptiacus* is similar to humans' [38]. Lesser long-nosed

558 bats have smaller eyes (ca. 0.23 diameter of those of *Rousettus aegyptiacus)* and should thus

559 be less sensitive. To estimate their visual detection range of a cactus, we first estimated

560 humans' detection range and we used this as an over estimation for the bats' detection range.

561 Four humans (adjusted to scotopic vision) were able to detect cacti (n=10) from a distance of

562 $55\pm9$ m. To estimate this, we had them move towards a cactus from a distance of 100 m and

563 report when they first detected it. On the one hand, as explained above, the bats are less

564 sensitive, but on the other hand, their task should have been easier since they observe the

565 cacti from above (unlike the humans) and can search for white flowers. We thus estimated

566 the bats' detection range to be within a range of 30-70 m. To validate that our results are not

567 sensitive to an error of up to 40% in this parameter, we ran our model with cacti detection

568 range of 30, 50 and 70 meters (Figure S3G-J).

569 ***Maintaining core cacti on consecutive nights*** Notably, our model assumes that bats are

570 naïve at the beginning of the night, while in reality bats' foraging cores on consecutive nights

571 heavily overlap (on a certain night, bats visited ~97% of the core cacti that they visited on

572 previous nights, Figure S3K). This suggests that bats incorporate information gathered on

573 previous nights when forming their foraging core on a given night. Relying on information

574 over consecutive nights probably reduces the costs of finding and mapping the positions of

575 flowering cacti. We also observed that bats reused the same flying pathway between cacti on

576 consecutive nights (Figure S3L), a strategy which could ease navigation in the field. One of

577 the bats that we tracked switched the field it visited while we were tracking it, allowing us to

578 examine its movements in a new field over time. In contrast to all other bats we tracked, in its

579 first nights in the field, this bat spent more time scanning the field and less time foraging, in

580  comparison to the other bats. Over several consecutive nights, it gradually increased the

581  proportion of foraging (Figure S3M). In order to account for this knowledge, we allowed our

582  simulated bats to scan quickly for a short period at the beginning of the night. Thus, at the

583  beginning of the night, our simulated bats explored cacti with a detection range of 250 m.

584  This exploration phase lasts ~10 minutes, until each bat acquires 10 remembered cacti.

585  Despite the fact that we neglect this issue of information transfer across nights, our

586  approximated model well captures the general characteristics of bat foraging dynamics.

587  ***Learning rate ($\alpha$)*** We used an evolutionary algorithm (using Matlab's Global Optimization

588  Toolbox) in order to predict the value of $\alpha$. We ran 30 simulations with 100 generations each

589  and took the average $\alpha$. We used a population size of 45 bats, with initial values of $\alpha$ that are

590  randomly distributed between 0 and 100. At each generation, 20% of the bats best fitted $\alpha$

591  (i.e., bats) survived, out of the rest remaining 80%, 62% randomly survived and 18% were

592  crossed with mutation. The values of $\alpha$ always converged within 100 simulations. Nectar

593  consumption was used to estimate fitness.

594  ***Modeling aggressive response*** A similar model with an aggressive response (aggressive

595  model) provided us the ability to estimate whether social interactions play a role in shaping the

596  foraging behavior of the bats. In this model, simulated bats foraged in the same manner as in

597  the non-aggressive model, except for when two bats simultaneously chose the same cactus. In

598  this case the dominant bat (the bat that has a higher nectar-weight for this cactus) drank from

599  the cactus, and the subordinate bat drinks nothing and is moved near a random cactus 200-500

600  m from its current location mimicking the result of a territorial agonistic interaction.

601  ***Alternative models*** We compared the real bats' behavior to two additional models (random and

602  trapline) using the same fixed parameters as in the reinforcement learning model, except for

603  the following changes: In the random model $\alpha=0$, and thus the bats did not learn from previous

604  experience. In the trapline model, bats used reinforcement learning during ~10 minutes at the

605     beginning of each simulation to acquire the first 10 remembered cacti (with α=6.1 that was

606     found using a genetic algorithm). Once the remembered set was established, the simulated bats

607     exploited the core in an ordered manner – always flying to the next closest cactus (as in a

608     trapline). They still occasionally explored additional cacti (according to the same rules of the

609     original model). Finally, we also ran the exact same foraging model with a single bat (and 125

610     cacti) to compare the nectar consumption of a learning (α=4.6) and a random (α=0) simulated

611     bat.

612     ***Estimating the overlap of cores*** We used the results of 100 simulations to compute how

613     many bats shared each of the core cacti. For each simulation, we collected the core cacti of all

614     bats into one set S, and then randomly selected a core for each bat, while maintaining the

615     number of core cacti per bat the same as in the specific simulation. That is, if a bat had x cacti

616     in its core in the simulation, we now randomly select x cacti in S to be in its random core. We

617     used a permutation test to compare the overlap in a typical core cactus in these two situations.

618     **QUANTIFICATION AND STATISTICAL ANALYSIS**

619     All statistical analysis conducted using MATLAB R2018a unless stated otherwise.

620     Comparison between groups were conducted using two tailed tests, unless stated otherwise.

621     Non-parametric Wilcoxon rank sum tests were used to examine the influence of the GPS

622     weight on the time bats spent outside the cave because of the small sample size. One-Way

623     ANOVA was used to compare bats' nectar consumption in different foraging models and all

624     other comparisons between models were conducted using Permutation based t-test, to avoid

625     influencing the power of our analysis by changing the sample size (i.e., the number of

626     simulations). We used Linear regression to find the equation of nectar secretion throughout

627     the night and nectar feeding quantity according to feeding duration, and GLM test used to

628     estimate the influence of depletion status (as a fixed factor) on nectar secretion rate

629     throughout the night. Monte-Carlo test conducted using R 3.6.1, ade4 package.

630 **Supplemental videos legends**

631 **Video S1. Bats foraging behavior. Related to STAR Methods.** Bats typically lingered in the

632 area of a cactus for a few seconds: they fly near the cactus, approach it, approach a specific

633 flower and drink from it. Most foraging behavior is solitary, and social interactions are seldom.

634 **Video S2. GPS weight control. Related to STAR Methods.** Bats successfully maneuver and

635 feed on Saguaro's flowers in a flight tent – a comparison of feeding behavior of a bat with and

636 without GPS device attached to its back. Related to Tracking bats' movement in STAR

637 Methods.

638

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