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1 Communal and efficient movement routines can develop
2 spontaneously through public information use

3
4 *Abbreviated title:* The emergence of shared movement routines

5 *Authors:* Louise Riotte-Lambert and Jason Matthiopoulos

6 *Affiliation:* Institute of Biodiversity, Animal Health and Comparative Medicine,

7 Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK

8 *Corresponding author:* Louise Riotte-Lambert, Institute of Biodiversity, Animal Health

9 and Comparative Medicine, Graham Kerr Building, University of Glasgow, Glasgow

10 G12 8QQ, UK, +44793-389-7590, louise.riotte.lambert@gmail.com

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17 Data accessibility statement

18 The Julia codes supporting this article are freely available on Figshare (Riotte-Lambert

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23 Abstract

24 Animal aggregations occur in almost all taxa and can be strongly influential for consumer-
25 resource dynamics and population health. Their adaptive value and underlying
26 mechanisms are thus fundamental questions. Many animals use information about
27 resource locations inadvertently broadcasted by other individuals through visual,
28 acoustic, or olfactory cues. Such simple, involuntary information transfer is commonly
29 employed in groups of social animals. However, it remains unknown whether public
30 information use could have been the initial cause of social aggregations. Here, using
31 agent-based modelling, in the absence of inclusive fitness benefits or direct conspecific
32 attraction, we show that the use of ephemeral public information about resource locations
33 can cause memory-based foragers to spontaneously and permanently aggregate into
34 communal home ranges that take the form of movement circuits (also called traplines)
35 along which individuals travel asynchronously. Even though experienced individuals
36 only rely on their personal memory to inform their movement decisions, we find that the
37 use of public information during the learning phase is very beneficial in the long term
38 because the communal circuits are more efficient than those established by non-publicly-
39 informed individuals. Our results reveal how simple, inadvertent information transfer
40 between naïve, selfish foragers can cause the emergence of long-term aggregations,
41 which are a prerequisite for the evolution of more complex social behaviours. They also
42 suggest that individuals may not necessarily need to witness the entire sequences of
43 actions performed by others to converge to the same behavioural routines.

44

45 Keywords

46 Behavioural stereotypy; collective space use; group living; movement routine; self-
47 organization; traplining

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51 Introduction

52 Animal aggregations can yield some of the most striking spatial patterns in nature. They
53 are observed in almost all taxa (Ims 1988; Sumpter 2006; Bruce and Bradford 2015;
54 Venkataraman et al. 2017), and may comprise several species (Heymann and Buchanan-
55 Smith 2000; Goodale et al. 2010). In some cases, they result directly from the existence
56 of large-scale resource heterogeneity, but in others, animals aggregate more than what
57 would be expected on the basis of resource distribution alone (Brown and Orians 1970;
58 Jeanson et al. 2005). This observation has stimulated several hypotheses on the
59 advantages of aggregations for individual animals, postulating improvements in as wide
60 a range of processes as foraging efficiency through the use of social information (Safi and
61 Kerth 2007; Evans et al. 2016), anti-predation protection (Jeanson et al. 2005), and
62 thermoregulation (Kerth and Reckardt 2003).

63 Despite recent theoretical and empirical investigations of the advantages of animal
64 aggregation, there is still no clear consensus about the circumstances and processes
65 leading to group living, both proximately and ultimately (reviewed, in the case of
66 coloniality, by Evans et al. 2016). Proximately, conspecific attraction (or taxis) inevitably
67 leads to the aggregation of individuals, and as a result, a large number of studies have
68 focused on the patterns that emerge from it, and on the circumstances in which it is
69 advantageous (Fletcher 2006; Sumpter 2006; Wood and Ackland 2007; Tania et al. 2012;
70 Shaw and Couzin 2013). Conspecific attraction is commonly defined and modelled as the
71 constant, context-independent tendency of individuals to move towards the conspecifics
72 that are within an attraction range (see for example Couzin et al. 2005). In the special case
73 of the settlement stage of dispersal, conspecific attraction can also be defined as the

74 tendency of dispersers to settle in areas of high population density (Fletcher 2006).
75 Conspecific attraction is often considered a necessary mechanism underlying the
76 emergence of aggregations when there are no large-scale resource heterogeneities
77 (Jeanson et al. 2005). But can aggregations emerge as a by-product of other types of
78 behaviours, i.e. through passive coordination of individuals? This question is of
79 fundamental evolutionary interest because conspecific attraction may not have been a
80 necessary part of the evolutionary origin of aggregations if they could have proximately
81 emerged from other processes. This question has important implications for our
82 understanding of the evolution of social behaviour, because the long-term aggregation of
83 individuals is a prerequisite for the emergence and development of cooperation
84 (Deneubourg et al. 2002; Lion and van Baalen 2008). It is also of practical importance,
85 because the empirical interpretation of aggregations in homogeneous environments as the
86 unequivocal sign of conspecific attraction (Brown and Orians 1970) may, in some cases,
87 be incorrect.

88 Several authors have proposed that aggregations could emerge from the use of public
89 information about the location of resources (reviewed in Evans et al. (2016), and, in the
90 case of multispecies aggregations, in Goodale et al. 2010). Inadvertent broadcasting of
91 resource location by a foraging individual, and the use of this information by other
92 individuals, is commonly observed in a broad range of taxa, particularly across
93 vertebrates (Pöysä 1992, reviewed in Galef and Giraldeau 2001, Danchin et al. 2004), and
94 can implicate conspecifics as well as heterospecifics (Seppänen et al. 2007). It can occur
95 through visual (e.g. in seabirds: Machovsky-Capuska et al. 2014, in vultures: Cortés-
96 Avizanda et al. 2014, in pigs: Nicol and Pope 1994, in crabs: Laidre 2010), acoustic (e.g.
97 in bats: Safi and Kerth 2007), or olfactory cues (e.g. in bees: Nieh et al. 2004), and also

98 through modifications of the environment (e.g. by trampling, rats: Calhoun 1962, in forest
99 elephants: Blake and Inkamba-Nkulu 2004). Despite the appeal of this hypothesis, no
100 study has yet investigated if the use of public information about resource location could
101 cause the aggregation of selfish foragers in the first place, what form these aggregations
102 would take, and what short- and long-term advantages it might confer (Evans et al. 2016).

103 Here, we investigate if such a simple mechanism of public information transfer can
104 spontaneously lead to the aggregation of individuals without the constraining assumptions
105 of central-place foraging, conspecific attraction, inclusive fitness benefits, or large-scale
106 resource heterogeneities, and what form these aggregations take. We developed a
107 parsimonious individual-based model in which foragers rely on perception and memory
108 to travel between resource patches. We mimicked information broadcasting by assuming
109 that the area over which a patch is detectable increases when it is visited by an individual,
110 and that this increase in detectability takes time to decay. Here, we consider inadvertent
111 broadcast of information, but our formulation could also apply to voluntary information
112 transfer. It can equally represent intra- or inter-specific information transfer and is also
113 flexible enough to be relevant to a wide range of mechanisms. If the broadcast area and
114 information decay rate are large, our model mimics processes such as visual transmission
115 of information, typical of some bird species (Machovsky-Capuska et al. 2014), or acoustic
116 transmission, typical of some bat species (Safi and Kerth 2007). However, if the
117 information decay rate is small relative to the broadcast area, public information is
118 persistent, emulating processes such as olfactory transmission of information, typical of
119 arthropods (Nieh et al. 2004), or a transmission of information mediated through a
120 physical modification of the environment, e.g. through trampling (Galef and Giraldeau
121 2001). Overall, the model we developed is fundamentally different from a conspecific

122 attraction (or taxis) model as defined above because (i) individuals are attracted to
123 patches, not to other individuals, which means that they do not move as a group as would
124 automatically occur with an attraction model, and (ii) an advertised patch will only attract
125 uninformed individuals, because those that already know the patch will base their
126 decision to revisit it or not upon their memory, not their perception (*Material and*
127 *Methods*).

128 Material and Methods

129 *Model Description*

130 We consider a 100×100 u (arbitrary length unit) continuous-space square arena with
131 reflective boundaries, containing 400 identical resource patches uniformly randomly
132 distributed in space. The environment is thus heterogeneous at a small spatial scale, but
133 homogeneous at a large spatial scale. Patches are modeled as dimensionless points in
134 space because we focus on behavioral decisions associated with inter-patch movements.
135 When a patch i is visited by an individual at time t , its circular detection area A_i is
136 instantaneously increased by an area B , which we will call the broadcast area, so that
137 $A_{i,t} = A_{i,t-1} + B$. As $r_{i,t} \propto \sqrt{A_{i,t}}$, the radius of the detection area of a patch $r_{i,t}$ is a
138 deceleratingly increasing function of the number of broadcast events (i.e. patch visits).
139 Such a relationship has been theoretically and empirically shown in the special case of
140 visual local enhancement in seabirds (Haney et al. 1992), and as a consequence it has
141 been used in other theoretical models of public information use (Buckley 1997). If the
142 patch i is not visited at time t , its detection area decreases linearly with time down to the
143 baseline detection area A_0 with an information decay rate d , such as: $A_{i,t} =$

144 $\max(A_0, A_{i,t-1} - d)$, where $A_0 = \pi r_0^2$ and r_0 is the minimum distance at which a patch
145 is perceived by a naïve passing animal.

146 The memory and movement processes presented here derive from a memory-based
147 movement model that leads to the emergence of individual home ranges (Riotte-Lambert
148 et al. 2015). Individuals move with a constant speed of $1 u$ per time step. At the beginning
149 of the simulation, they are introduced into the environment at random locations, are naive,
150 and move following a correlated random walk characterized by a zero-centred wrapped
151 normal distribution of turns. If an unknown patch is perceived, the individual moves
152 towards it in a straight line and remains in it for one time step. Individuals rely on a long-
153 term, reference memory of duration T_R to remember the locations of the patches they
154 previously visited, and a shorter-term, working memory of duration T_W to avoid patches
155 they have recently visited.

156 Aggregation can only be advantageous when resources can be shared between
157 conspecifics. As the primary motivation of our study is the effect of public information
158 use on space use patterns, we first considered a simple, baseline model where resources
159 are unaffected by individuals' visits, and where individuals are encouraged to keep on
160 moving by their working memory durations. Individuals can have several reasons to move
161 away from a food patch before full depletion. For example, many animals need several
162 types of resources that are available in different places (Raubenheimer et al. 2009).
163 Moreover, animals may also move from place to place to maintain an up-to-date cognitive
164 map of their home range (Powell and Mitchell 2012). Individuals may maintain a familiar
165 area larger than what is usually required to meet their needs, so as to ensure food intake
166 sufficiency in the face of environmental stochasticity (Sutherland and Moss 1985). Here,
167 we encoded the tendency of individuals to be continuously on the move by using the

168 generic concept of the working memory. The working memory duration can act both as
169 a propensity to diversify food sources (it is then pre-adapted to the time needed for an
170 individual to visit a sufficiently large number of different patches to reach its minimal
171 nutritional diversity requirements), and/or as a propensity to maintain an accurate
172 knowledge of several food patches, as a risk-alleviating strategy. In the “nutritional
173 diversification” scenario, this formulation is parsimonious because it will be functional
174 even if individuals cannot directly distinguish between different food types.

175 Although the assumptions of no-depletion and of a substantial working memory
176 duration are of course not valid for all real systems, they are nonetheless relevant for
177 many of them, as discussed in the *Discussion* section. In *Supplementary Information 1*,
178 we explored a wide range of working memory durations, including a very short duration,
179 such that individuals can revisit patches quickly without getting permanently trapped into
180 a single patch. In *Supplementary Information 2*, we relaxed the assumption of no
181 depletion.

182 Every time an individual finishes exploiting a patch, it chooses the closest known
183 patch that has been visited more than T_w time steps ago and travels to it along a straight
184 line. The distance separating the individual from a known patch acts as a proxy for the
185 inverse of the expected rate of intake when the individual decides to revisit the patch
186 (Boyer et al. 2006; Van Moorter et al. 2009; Riotte-Lambert et al. 2015; Janson 2016;
187 Merkle et al. 2017), because the time required to reach a patch is proportional to its
188 remoteness, and all patches have equal profitability (see in *Supplementary Information 2*
189 how we adapted these conditions when there is resource depletion). If no known patch
190 has been visited more than T_w time steps ago, the individual will rely on random search
191 until for such time as a previously visited patch becomes attractive again (i.e. time since

192 it was visited exceeds T_w) or an unknown patch is encountered. If while the individual is
193 on its way to a known patch, it detects an unknown patch that is closer, it changes focus
194 and walks directly towards it.

195 All simulations were performed using the Julia programming language v. 0.5.1 (Bezanson
196 et al. 2012) and were run for 50,000 time steps. The Julia code supporting this article has
197 been uploaded on Figshare and will be made freely available upon publication. We
198 investigated the effect of food depletion, population size, information transfer parameters,
199 and memory parameters, on emerging space use patterns and the foraging efficiency of
200 individuals (see Table 1 for default parameter values and their variation range). All
201 analyses were performed using R v.3.3.3 (R Core Team 2017).

202

203 *Overlap Computation*

204 We computed the overlap between every pair of foragers as the ratio, over the last 5,000
205 simulation time steps of the simulation, of the number of patches used by both individuals
206 divided by the total number used by either of them (i.e. the intersection over the union of
207 the sets of used patches). We defined groups of highly-overlapping individuals by
208 hierarchical cluster analysis within R (R Core Team 2017). We used complete clustering
209 so that a group is formed when all overlaps between pairs of individuals in the group are
210 higher than a threshold level. We fixed the cut-off level to 0.9 to highlight groups of
211 almost-perfectly overlapping individuals and because this degree of pairwise overlap
212 rarely happens (<0.1 % of cases) when individuals do not use public information.

213 To investigate the spacing patterns of individuals within populations, we looked at
214 (i) the median pairwise overlap between individuals, which provides a measure of the
215 overall aggregation of individuals within the population, and (ii) the number of groups of

216 highly-overlapping individuals in the populations divided by the total number of
217 individuals, which provides a more spatially-explicit measure of aggregation. We looked
218 at the number of groups in the population divided by the population size to account for
219 the fact that a population of 10 individuals clustered in 3 groups is less aggregated than a
220 population of 30 individuals clustered in the same number of groups.

221

222 Results

223 *Emerging space use patterns*

224 A home range is the stable area to which an animal restricts its movement (Börger et al.
225 2008). Here, home range behavior is characterized by the stabilization of the set of
226 patches an individual regularly uses (see Riotte-Lambert et al. (2015) for the stability
227 criterion). Our simulation duration was sufficient for stable home ranges to emerge (with
228 the parameter default values, for any population size, by the end of the simulation more
229 than 99% of individuals had stable home ranges). We found that use of public information
230 leads to the permanent aggregation of their home ranges (example spatial pattern in Fig.
231 1b). The average routine movement index of individuals, as defined in Riotte-Lambert et
232 al. (2017), is extremely close to 1 (mean \pm SD: 0.9997 ± 0.0016 , calculated over 100
233 simulations per population size) and equal to 1 for more than 92% of individuals. This
234 shows that the communal home ranges take the form of circuits of patches (also called
235 traplines: Thomson et al. 1997) along which the individuals of the group indefinitely
236 travel mostly asynchronously (Fig. S1). Individuals remember patches between two entire
237 circuit rotations, because the time it takes for them to circle their entire home range (for
238 default parameters, mean \pm SD: 267.4 ± 64.0 time steps; maximum observed: 991.4) is

239 smaller than the reference memory duration ($T_R = 1,000$ time steps). Therefore,
240 irrespectively of an individual's ability to use public information, when it has established
241 a circuit, it makes every movement decision exclusively by using its personal memory,
242 and thus independently of others' behaviour. Individuals that can use public information
243 therefore only use this ability while they are still naïve and exploring the environment.
244 The use of public information during individuals' learning phase leads to the convergence
245 of their routine circuits, but, once established, these circuits are entirely maintained by
246 individual memory processes.

247 We found that within populations with public information, the distribution of pairwise
248 overlap is bimodal (Fig. 2a), indicating a tendency for a randomly selected pair of
249 individuals to either use the same set of patches, or share no patches at all. As the
250 population size increases, more and more pairs of individuals overlap. The median
251 overlap increases until reaching 69% (Fig. 2a) and the number of groups divided by the
252 total number of individuals decreases, down to a mean number of 4.8 ± 1.8 groups for 30
253 individuals (Fig. 2b). This indicates that when the population size increases, fewer unique
254 groups are being formed, and additional individuals simply join one of the existing
255 groups. The increase in the degree of aggregation with population size cannot be simply
256 attributed to a crowding effect, because, in populations without public information, the
257 aggregation measures are not impacted by population size (Fig. 2).

258 The median overlap increases with the broadcast area and the information persistence
259 time (defined as the time it takes for the detection area to go down to its baseline after a
260 single broadcast event, Fig. 3a), while the number of groups decreases rapidly with the
261 broadcast area and is comparatively little affected by the information persistence time
262 (Fig. 3b). In the case of visual and acoustic cues, where public information does not

263 persist in the environment, aggregation will thus emerge only if the visual or acoustic cue
264 can be perceived over sufficiently large distances. Inadvertent broadcast of information
265 through visual cues is thus expected to lead to aggregation only in open habitats, which
266 is consistent with the current theory and empirical knowledge of visual local enhancement
267 (Pöysä 1992; Buckley 1997). In the case of olfactory cues and physical modifications of
268 the environment, which persist for some time in the environment, the cue does not need
269 to be perceived from very far to lead to aggregation.

270 The median pairwise overlap slightly increases when the duration of the reference
271 memory is halved, but the number of groups is unaffected by changes in this parameter
272 (Fig. S2a and c, *Supplementary Information 1*). The median pairwise overlap increases
273 with the duration of the working memory, but the number of groups of individuals sharing
274 at least 90% of their patches is comparatively little affected (Fig. S3a and c). For a very
275 short memory duration, the number of tightly-aggregated groups divided by the number
276 of individuals is equal to 0.69 ± 0.13 (mean \pm SD), thus showing that aggregation occurs
277 even in this case. Aggregation measures are little affected by food depletion as long as
278 the proportion of food collected by individuals during a patch visit is smaller than 50%
279 (Fig S5 in *Supplementary Information 2*). When individuals collect more than 50% of
280 available food during a patch visit, the number of groups relative to the population size
281 increases but the median pairwise overlap is comparatively unaffected (Fig S5 in
282 *Supplementary Information 2*).

283

284 *Short- and long-term foraging efficiencies*

285 We assumed that individuals incur constant metabolic costs, because they always move
286 at the same speed. In the baseline scenario where no depletion occurred, we measured the

287 short- and long-term foraging efficiencies of individuals as the number of patches visited
288 during the first and last 5,000 time steps respectively, because all patches were of equal
289 value. Long-term foraging efficiency is of high importance to an individual's fitness
290 because it determines the amount of energy it will be able to allocate to reproduction.
291 Short-term foraging efficiency is of high selective importance if individuals are at risk of
292 dying from low intake levels during their learning phase (cf. the high juvenile mortality
293 in many species: Daunt et al. 2007).

294 We found that the use of public information benefits all individuals both in the
295 short term, i.e. during the learning phase when they are naïve about the environment (Fig.
296 4a), and in the long term, i.e. when they have established a movement circuit (Fig. 4b),
297 even if individuals only use public information when they are naïve (see *Emerging Space*
298 *Use Patterns*). Both short- and long-term foraging efficiencies of public information users
299 increase with the number of individuals in the environment (Fig. 4). The long-term
300 foraging efficiency of public information users reaches levels 29% greater than those of
301 non-public information users (Fig. 4b). The short-term foraging efficiency of public
302 information users increases with the broadcast area and the information persistence time
303 (Fig. 5a). The long-term foraging efficiency roughly plateaus for a broadcast area of 200,
304 although it slightly tends to decrease when both the broadcast area and the information
305 persistence time are very big (Fig. 5b).

306 Both short- and long-term foraging efficiencies are unaffected by changes in the
307 reference memory duration (Fig. S2b and d). The short-term foraging efficiency decreases
308 for both types of populations when the duration of the working memory increases (Fig.
309 S3b), whereas the long-term foraging efficiency of public information users increases
310 when the working memory lengthens and tends to decrease for non-public information

311 users (Fig. S3d). For a short working memory duration ($T_W = 15$), there is a high
312 variability in the efficiency of the movement circuits that are established, because
313 individuals do not explore much before settling into a home range and initial conditions
314 have thus a high relative importance. Foraging efficiencies of public information users
315 are on average larger than that of non-public information users, but the standard deviation
316 ranges overlap. Overall, the use of public information tends to lead to better foraging
317 efficiency irrespectively of any memory parameter (Figs S2b,d and S3b,d).

318 When relaxing the assumption of no depletion, we measured the short- and long-
319 term foraging efficiencies of individuals as the amount of food consumed during the first
320 and last 5,000 time steps respectively. A clear prediction of the depletion model is that
321 the relative efficacy of public information use will be smaller than one when both the
322 population size and the proportion of food collected by individuals during a patch visit
323 (k_{Eat}) are large. However, our analyses show that public information use is advantageous
324 both in the short and long terms up to substantial thresholds of population size and k_{Eat} .
325 Public information use is advantageous up to $k_{Eat} = 80\%$ for small population sizes (i.e.
326 with fewer than 10 individuals), and up to $k_{Eat} = 40\%$ for big population sizes (i.e. with
327 approx. 30 individuals; Fig. S4 in *Supplementary Information 2*). Below this threshold,
328 the energetic intake of public information users relative to non-public information users
329 increases with population size, whereas it decreases with population size above this
330 threshold (Fig. S4).

331

332 Discussion

333 Here we have shown that beneficial, large-scale and permanent group-living can emerge
334 from the use of inadvertently broadcast information, in the absence of large-scale resource
335 heterogeneities, inclusive fitness benefits, conspecific attraction, or any constraint on
336 individual movement. Individuals spontaneously develop communal movement routines.
337 These resemble patterns observed in nature where several individuals (or groups of
338 individuals, and not always of the same species) share common movement routines (Di
339 Fiore and Suarez 2007). The use of public information increases both the short- and long-
340 term foraging efficiencies of individuals. In the short term, individuals are still learning
341 about their environment, and public information enables them to discover resource
342 patches more quickly. Even if individuals only use memory to inform their movement
343 decisions when they have established a home range, the use of public information during
344 the learning phase has a long-term effect because it enables the establishment of more
345 efficient movement habits, by decreasing the distance travelled between the patches that
346 are routinely and successively visited. As the information transfer process considered here
347 can equally represent intra- or inter-specific information transfer (reviewed in Seppänen
348 et al. 2007), our results apply to both single- and multi-species group living.

349 Intriguingly, the long-term foraging efficiency of individuals (i.e. once their home
350 ranges are established) roughly plateaus for a threshold broadcast area. This threshold
351 broadcast area (~200) is also associated with an abrupt change in aggregation patterns:
352 for smaller broadcast areas, the median pairwise overlap drops to 0 and the number of
353 groups abruptly increases (Fig. 3). Overall, this indicates that although the availability of
354 public information will always increase the foraging efficiency of naïve individuals, over
355 time, the emerging movement circuits will reach maximum efficiency and individuals
356 will aggregate into the same small number of groups. This is consistent with theoretical

357 expectations and empirical observations in ants where colonies under a critical size fail
358 to establish efficient pheromone trails (reviewed in Sumpter 2006). A broadcast area of
359 about 200μ corresponds approximately to a four-fold increase of the distance of
360 perception at the time of the information broadcast event. This is not unrealistically large
361 compared to what has been quantified in real systems. We can derive a factor of increase
362 of detection distance following public information use of about 9 for parti-coloured bats
363 (Safi and Kerth 2007), and of at least 13 for bottlenose dolphins (Janik 2000). Even if
364 reliable estimates of perceptual ranges are still lacking for many systems (Lima and
365 Zollner 1996), we can expect that the factor of social increase in detectability for foragers
366 relying on visual cues in open landscapes is large. This should be amplified when the
367 resources do not move, as moving objects (conspecifics) are easier to detect than non-
368 moving objects (Hirsch 1982). For example, Grünbaum and Veit (2003) set plausible
369 perceptual ranges for black-browed albatrosses that correspond to a minimal increase in
370 detectability between direct detection of a krill swarm and a flock of conspecifics of factor
371 5.

372 We observed a slight tendency for the long-term foraging efficiency to decrease
373 when both the information broadcast parameters are very big: for $B=1,000$ and $T=20$, the
374 long-term foraging efficiency of a population of 10 individuals was 5% smaller than the
375 maximum long-term foraging efficiency reached for a population of the same size (Fig.
376 5). This suggests that at a very high level of information broadcast, individuals are
377 exposed to too much social information to explore sufficiently and establish the best-
378 possible movement circuits.

379 It is commonly expected that aggregation, in the absence of any other advantage such
380 as thermoregulation or predation defense, should only be beneficial when resources can

381 be shared between conspecifics (Buckley 1997). Here, we first implemented this
382 condition in a baseline model by assuming that the depletion of resource patches is
383 negligible. Patches can represent any kind of fragmented resource. In the case of non-
384 food (i.e. non-depletable) resources, they can represent resting or refuge sites. For
385 example, baboons regularly alternate between sleeping sites (Hausfater and Meade 1982).
386 In the case of food patches, our assumption implies either that food is replenished very
387 quickly after depletion, or that the amount of food harvested by an individual during a
388 single visit is negligible compared to the total amount of food available in the patch.
389 Although the assumption of negligible consumption during a patch visit is of course not
390 valid for all systems, it is consistent with what has been observed in several real systems
391 (Illius, Andrew et al. 2002; Merkle et al. 2015). Illius, Andrew et al. (2002) have also
392 suggested that this could be much more widespread than commonly thought and
393 popularized by the Marginal Value Theorem. Note also that even under the Marginal
394 Value Theorem, individuals are generally expected to leave patches before their complete
395 depletion (Charnov 1976). When relaxing the assumption of no depletion, the precise
396 profitability of aggregations will be determined by the interplay of resource dynamics,
397 information broadcast, and memory processes. Quantifying fully these interactive effects
398 was outside the scope of the present article but should be the subject of future
399 investigations. Nevertheless, the large energetic advantage of public information we
400 found both in the short and long terms indicates that resource depletion should be quite
401 severe to render the use of public information deleterious. We confirmed this expectation
402 by showing that our results still apply for considerable ranges of depletion scenarios
403 (*Supplementary Information 2*).

404 The working memory has substantial consequences for both the aggregation pattern
405 and the foraging efficiency, both on the short and long terms. Even with minimally short
406 working memory, aggregation occurs. However, the degree of aggregation increases with
407 the working memory, because increasing the working memory postpones the time when
408 individuals begin to use their memory to revisit known places and thus lengthens the
409 exploration time during which individuals can learn about their environment, including
410 by using public information. It thus leads individuals to encounter more public
411 information during their learning period, thus to aggregate and to establish more efficient
412 movement circuits in the long term. This, however, is done at the expense of the short-
413 term foraging efficiency because it forces them to explore for a longer time. This result
414 is the manifestation of an exploration vs exploitation tradeoff: as exploring is costly
415 because it takes time (Stephens 1987), but also exposes animals to mortality risks (Lima
416 and Dill 1990), there is a trade-off between the benefits of spending more time exploring
417 the environment, vs exploiting the places that are already known (Hills et al. 2014).

418 Our study advances the conceptual thinking about the definition of spatial
419 aggregation. As revealed by our analysis, the degree of aggregation of a population cannot
420 be measured by a single summary. The mean degree of overlap between pairs of
421 individuals is not very informative in our simulations, because the distribution of overlap
422 is strikingly bimodal in populations with public information use (Fig. 2). The median
423 overlap provides a measure of the overall aggregation of all individuals. The number of
424 groups of almost-perfectly overlapping individuals provides a more spatially-explicit
425 measure of aggregation (Coulson et al. 1997; Mayor and Schaefer 2005; Wronski and
426 Apio 2006). As revealed by our sensitivity analysis on the working memory, one can get
427 a low median overlap but the same number of groups (Fig. S3), because groups can

428 overlap with each other, thus increasing the median overlap. Thus, both measures of
429 aggregation give complementary insights on the aggregation pattern. In the existing
430 literature on animal aggregation, studies focusing on almost sessile organisms (reviewed
431 in Taylor 1961) or on tightly grouped individuals (Jeanson et al. 2005) are abundant
432 compared to studies focusing on aggregations of home ranges, i.e. when aggregation
433 occurs at the scale of the area routinely used by individuals but where individuals do not
434 necessarily move together (but see for example: Brown and Orians 1970, Ims 1988, Rood
435 1989, Gehrt and Fritzell 1998, Rémy et al. 2013). This might be because few
436 methodological attempts have been made to quantify aggregation at this scale (but see
437 Coulson et al. 1997, Wronski and Apio 2006, Rémy et al. 2013).

438 Public information use does not lead to group movement as would be observed
439 from a classic conspecific attraction movement model (see for example Shaw and Couzin
440 2013). We showed that public information use during foraging movement leads to the
441 aggregation of home ranges (not individuals directly) and thus to areas of higher density,
442 which can also emerge from conspecific attraction during dispersal settlement decisions
443 (Fletcher 2006). However, and intriguingly, here individuals did not only aggregate into
444 communal home ranges of any shape but converged to shared movement circuits
445 (traplines). To our knowledge, no conspecific attraction model has shown the emergence
446 of such a pattern. The observation of communal traplines could therefore be taken as the
447 sign of public information use in nature.

448 Our model is different from a traditional collective evaluation of the traveling
449 salesman problem, where individuals look for the shortest route connecting all patches
450 only once and return to the origin (Applegate et al. 2006), because there were many more
451 patches in the environment than needed for one circuit, and individuals were free-ranging

452 and not central-place foragers. Our results thus provide the demonstration of a new
453 powerful self-organization mechanism, which could have practical applications for
454 optimization algorithms (Bonabeau et al. 2000). The pattern-forming mechanism we
455 demonstrated could also have implications for our understanding of the formation of other
456 types of behavioural routines. The distance separating patches can be an abstraction for
457 the cost of transitioning between two behavioural actions of any kind. It is already known
458 that individual habits, or stereotyped behavioural sequences, can develop through
459 sensitivity to local costs (Desrochers et al. 2010). Our study thus expands this knowledge
460 by suggesting counterintuitively that individuals may not necessarily need to copy entire
461 behavioural sequences to converge to the same behavioural stereotypies and to
462 collectively improve them.

463 Many authors have proposed that enhanced rate of food discovery is one of the main
464 reasons for the evolution of colonial breeding (reviewed in Evans et al. 2016). However,
465 all previous modelling investigations of this hypothesis have assumed that a tendency
466 towards aggregation already exists, and did not focus on the mechanisms leading to its
467 emergence (Buckley 1997; Evans et al. 2016). Here, we showed that public information
468 use can lead to the emergence of colonial living. The substantial energetic benefit of
469 public information use indicates that it could be at the evolutionary origin of colonial
470 living, if its costs do not exceed this benefit. Public information use can incur competition
471 costs, increased parasite or predation exposure, a loss of opportunities because of time
472 limitation, imperfect information processing, and misinformation if public information is
473 of lower quality than personal information (Dall et al. 2005; Bonnie and Earley 2007).
474 Quantifying these costs is difficult because they do not all act on the same currency, but
475 future studies should strive to integrate them (Evans et al. 2016).

476 Generally, spatial clustering of individuals is thought to be a prerequisite to the
477 evolutionary emergence of cooperation (Buckley 1997, Deneubourg et al. 2002, reviewed
478 in Lion and van Baalen 2008). This has been repeatedly shown theoretically in the case
479 where conspecifics are attracted to each other (Joshi et al. 2017), and in the case where
480 low dispersal rates or small mobility lead to passive spatial self-structuring of populations
481 (Lion and van Baalen 2008). Dispersal behaviour is a specific movement phase that
482 connects populations within a metapopulation (Palmer et al. 2014), and therefore acts on
483 a longer temporal scale (metapopulation dynamics) and a larger spatial scale (between
484 populations) than foraging movement, on which we have focused here. We have thus
485 provided here the first minimally realistic set of movement assumptions that could hint at
486 the evolutionary origins of cooperation for mobile species, which does not necessitate the
487 preliminary evolution of conspecific attraction, and which can operate at the within-
488 population level.

489

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651

652 **Table 1**

653 Parameter names, definitions, default values and range

Parameter name	Interpretation	Default value	Variation range
n	Number of individuals	10	2 - 30
B	Information broadcast area	500	50 - 1,000
T or $d = T/B$	Information persistence time or Information decay rate	10 or 50	2 - 20 or $B/20 - B/2$
T_R	Reference memory duration	1,000	500 - 2,000
T_W	Working memory duration	200	100 - 400
k_{Eat}	Proportion of food eaten by an individual during a patch visit	0	0 - 1

654

655

656 **Figure legends**

657 **Figure 1:** Movement of 10 individuals during the last 5,000 time steps of two example

658 simulations, without (a) or with (b) public information. Each individual's trajectory is

659 represented with a different colour and different line widths to ease visualisation.

660 Individuals have established stable traplines and routinely cover their entire personal

661 circuit several times during the time window (movement speed is $1 u$ per time step and

662 each patch visit lasts for one time step). In the population with public information, 9

663 individuals out of 10 have aggregated and use the same movement circuit, their movement

664 tracks are thus superimposed. Note that the movement of aggregated individuals is not

665 synchronous along the circuit (see Fig. S1). Black points represent resource patches.

666 Parameters were set to: $A_0 = \pi * 2^2$, $T_W = 200$, $T_R = 1,000$, $B = 500$, $d = 50$.

667 **Figure 2:** Aggregation metrics depending on the population size. (a) Distribution of the

668 degree of overlap per couple, depending on the number of individuals in populations of

669 public information users. The plain line represents the median pairwise overlap. The
670 triangles represent the median pairwise overlap in populations without public
671 information. The widths of the distribution plots in the horizontal direction represent the
672 relative frequency of a particular pairwise overlap value for a particular population size.
673 (b) Mean \pm SD number of groups of individuals divided by the number of individuals
674 within the population. Circles and triangles: populations of individuals using public
675 information or not, respectively. 1,000 simulations per population size. Parameters were
676 set to: $A_0 = \pi * 2^2$, $T_W = 200$, $T_R = 1,000$, $B = 500$, $d = 50$.

677 **Figure 3:** Aggregation metrics depending on the information broadcast parameters. (a)
678 Median pairwise overlap and (b) mean number of groups per population. 10 individuals
679 in each population. 100 simulations per parameter condition. Other parameters were set
680 to: $A_0 = \pi * 2^2$, $T_W = 200$, $T_R = 1,000$.

681 **Figure 4:** Mean \pm SD intake of individuals using public information (circles) or not
682 (triangles), during the first (a) and the last (b) 5,000 time-step-windows of the simulation,
683 depending on the population size. The variation shown is the standard deviation of the
684 mean intake between simulations. 1,000 simulations per population size. Parameters were
685 set to: $A_0 = \pi * 2^2$, $T_W = 200$, $T_R = 1,000$, $B = 500$, $d = 50$.

686 **Figure 5:** Mean intake of public information users during the first (a) and the last (b)
687 5,000 time-steps of 10 simulated individuals divided by the mean intake of individuals
688 that do not use public information, depending on the broadcast area and the information
689 persistence time. 100 simulations per parameter condition. Other parameters were set to:
690 $A_0 = \pi * 2^2$, $T_W = 200$, $T_R = 1,000$.