

1 **Title: Not your private tête-à-tête: leveraging the power of**  
2 **higher-order networks to study animal communication**

3 *(Special issue: ‘The power of sound – unravelling how vocal communication shapes*  
4 *group dynamics’)*

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28 **Abstract**

29 Animal communication is frequently studied with conventional network representations  
30 that link pairs of individuals who interact, for example, through vocalisation. However,  
31 acoustic signals often have multiple simultaneous receivers, or receivers integrate  
32 information from multiple signallers, meaning these interactions are not dyadic.  
33 Additionally, non-dyadic social structures often shape an individual's behavioural  
34 response to vocal communication. Recently, major advances have been made in the  
35 study of these non-dyadic, higher-order networks (e.g., hypergraphs and simplicial  
36 complexes). Here, we show how these approaches can provide new insights into vocal  
37 communication through three case studies that illustrate how higher-order network  
38 models can: a) alter predictions made about the outcome of vocally-coordinated group  
39 departures; b) generate different patterns of song synchronisation than models that only  
40 include dyadic interactions; and c) inform models of cultural evolution of vocal  
41 communication. Together, our examples highlight the potential power of higher-order  
42 networks to study animal vocal communication. We then build on our case studies to  
43 identify key challenges in applying higher-order network approaches in this context and  
44 outline important research questions these techniques could help answer.

45

46 **Keywords:** *hypergraph, simplicial complex; synchronisation; quorum decision-making;*  
47 *chorus; social networks*

48

49

## 50 **1. Introduction**

51 Quantifying the role of communication in the social coordination of animals has  
52 long been a topic of considerable interest in ecology and evolution (1,2). Network  
53 analysis is a useful tool to study patterns of communication within animal groups (3,4)  
54 and populations (5). For example, vocal communication may be used to maintain close  
55 social bonds (3) or play a key role in wider group coordination by enabling individuals to  
56 maintain weak social connections without interacting closely (4). However, while it is  
57 widely acknowledged that vocal communication frequently involves more than two  
58 individuals within each “interaction” (2), most existing analyses have only used dyadic  
59 representations of these communication networks.

60 Dyadic representations can capture valuable aspects of animal communication  
61 network structure (1,2). However, there are often social mechanisms acting on  
62 interactions of three or more individuals at a time. Eavesdropping (6–8) and audience  
63 effects (9,10) both represent examples of when non-dyadic animal communication  
64 shapes ecological and evolutionary outcomes. Accounting for the multibody nature of  
65 such interactions prevents losing relevant information. Powerful new higher-order  
66 network approaches (11–14) encode these non-pairwise interactions between agents,  
67 helping us quantify the importance of multibody interactions in driving group dynamics  
68 and wider social coordination. By explicitly representing multibody interactions, higher-  
69 order approaches capture the rich set of dynamics introduced by including the non-  
70 dyadic components of communication networks.

71 Vocal communication involves the transmission of information encoded in sound  
72 from one (or more) signallers to one or more receivers (1,15). Individuals integrate  
73 information received to inform their social decision-making (e.g. (16–18)).  
74 Consequently, tools to understand social transmission from network science can help  
75 understand the outcomes of vocal communication. Typically, social transmission occurs  
76 as a *complex contagion* (19), in which the probability of an individual changing state (i.e.  
77 altering its behaviour in the light of the information it receives) is not an additive function  
78 of the state of its neighbours (i.e., each interaction with a signaller is associated with an  
79 independent probability of behaviour change). These social effects on behaviour spread  
80 are not limited to humans. For example, non-human animals can change their state

81 when most of their social connections behave in a particular way (conformity; (19)). For  
82 instance, complex contagion models best reproduce the outcome of behavioural  
83 transmission experiments in fish schools (20). While it is possible to model the  
84 dynamics of these complex contagions across dyadic networks, many forms of  
85 behavioural spread are inherently mediated by multibody interactions, naturally calling  
86 for higher-order network approaches (21).

87 Here we introduce higher-order network approaches such as hypergraphs,  
88 simplicial sets, and simplicial complexes (12,13). We illustrate how they can be applied  
89 to study animal communication using a series of toy models based on real-world case  
90 studies across a range of temporal scales. We then provide an overview of the tools  
91 available to empiricists keen to explore the higher-order structure of their data. Finally,  
92 we summarise potential future directions for research in this area, highlighting possible  
93 synergies between research advances for both the animal behaviour and network  
94 science communities.

95

## 96 **2. Structure of higher-order communication networks**

97 Higher-order network approaches make it possible to represent multibody  
98 interactions that involve two or more individuals at a time (Fig. 1). There are three  
99 common higher-order network representations applicable to vocal communication  
100 networks: hypergraphs (Fig. 1a), simplicial sets, and simplicial complexes (Fig. 1b) with  
101 overviews of these approaches provided elsewhere (12,13,22,23).

102 Hypergraphs extend dyadic networks to enable edges (termed hyperedges)  
103 among any number of nodes (Fig. 1a, Fig. 1c). Hypergraphs can still represent dyadic  
104 interactions between pairs of individuals but also capture situations in which  
105 communication occurs among any number of individuals as one hyperedge, rather than  
106 multiple dyadic edges (Fig. 1c). This is important as vocal communication dynamics  
107 may differ between situations with multiple signallers and/or receivers (whether intended  
108 or not) and those in which communication is only dyadic (5,8–10,24). The connectivity  
109 of a hypergraph can be encoded as an incidence matrix; an explicitly higher-order  
110 representation (Fig. 1e) that link individuals (nodes) to specific group interactions  
111 (hyperedges), akin to a group-by-individual matrix in animal social behaviour research

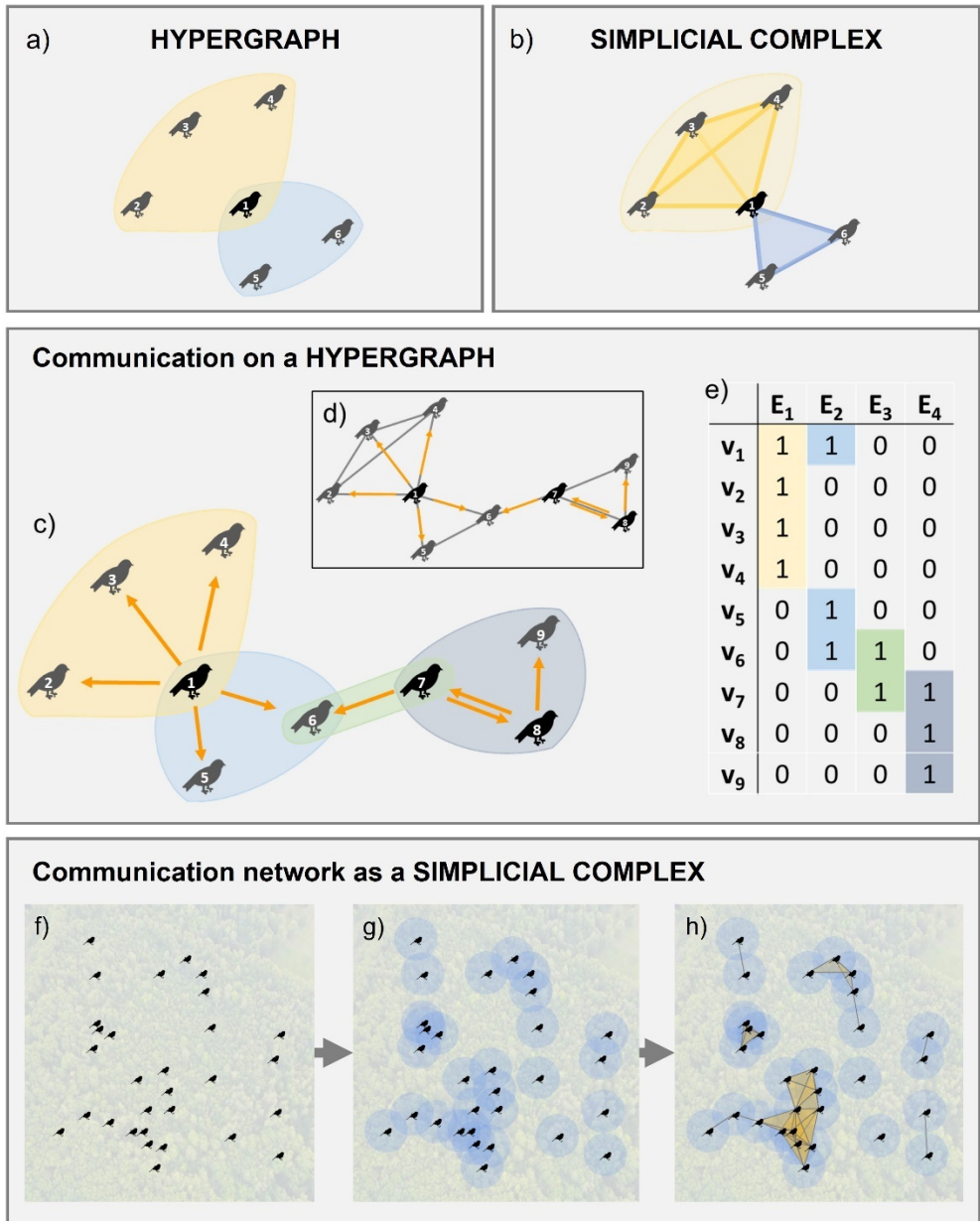
112 (25). Extensions to hypergraph approaches allows hyperedges to be directed —  
113 potentially weighted— hyperarcs (26), which may be useful to study some  
114 communication networks.

115         Simplicial sets (not illustrated) are broadly equivalent to hyperedges and  
116 represent an alternative mathematical framework to represent higher-order interactions  
117 (27). For example, a 0-simplex is the same as a node in a network, a 1-simplex the  
118 same as an edge, a 2-simplex an interaction involving three individuals, and so on.  
119 Unlike hypergraphs, one can represent the influence of interactions without the  
120 presence of the constituent individuals in a simplicial set representation (24,28).  
121 However, this extension will only occasionally be useful in studying communication  
122 networks, so we do not focus on it here.

123         We describe simplicial sets to introduce simplicial complexes (Fig. 1f-h). A  
124 simplicial complex is a specific type of simplicial set, which must contain all nested  
125 lower-order simplices, i.e., requires downward closure. For example, a simplicial  
126 complex that contains the simplex  $(i, j, k)$  must also contain the simplices  $(i, j)$ ,  $(i, k)$ ,  
127  $(j, k)$ ,  $(i)$ ,  $(j)$  and  $(k)$ . This extra requirement makes simplicial complexes somewhat  
128 limited in their ability to faithfully represent complex systems, as at times the inclusion of  
129 all the possible sub-interactions would result in a tight constraint. Nevertheless, working  
130 with simplicial complexes brings a lot of mathematical advantages, as it allows for the  
131 use of tools from *topological data analysis* (TDA). Readers interested in exploiting the  
132 recent advances in TDA to study higher-order communication landscapes can read  
133 (29).

134         One directly applicable approach for communication networks is to construct a  
135 simplicial complex of a random geometric hypergraph (30) based on individual locations  
136 and their audible radii. Constructing this representation is the same approach as (5) but,  
137 instead of constructing a dyadic network, builds a simplicial complex representing the  
138 potential for higher-order interactions. Similar higher-order structures that could be used  
139 are the Vietoris-Rips (Fig. 1h) and Čech complexes (31). The Vietoris-Rips complex  
140 adds higher-order simplices to cliques in a dyadic network, i.e. if the 1-simplices  $(i, j)$ ,  
141  $(i, k)$  and  $(j, k)$  all exist then the 2-simplex  $(i, j, k)$  will be added. The Čech complex  
142 corresponds to the distribution of 0-simplices in space, defining an interaction radius

143 and adding simplices corresponding to the intersection of the circles defined by each  
 144 radius. This could be used to construct the information landscape for receivers  
 145 navigating through a signalling collective, such as females listening to a chorus of  
 146 simultaneously vocalising males (e.g., (32)).  
 147



148  
 149 *Figure 1. An introduction to higher-order networks for animal communication based on*  
 150 *a) hypergraphs (network edges can connect any number of individuals) and b) simplicial*

151 *complexes (all nested lower-order interactions must be included in the network object).*  
152 *We then show examples of higher-order networks applied to animal communication. c)*  
153 *Communication as a dynamical process on a series of higher-order social interactions*  
154 *(indicated by the coloured hyperedges). Exploiting higher-order interactions in this way*  
155 *explicitly quantifies biological phenomena such as audience effects and eavesdropping*  
156 *effects that cannot be fully captured using d) the dyadic network representation of the*  
157 *same system. e) Hypergraphs are easily represented as incidence matrices that link*  
158 *individuals to social groupings or events (equivalent to group-by-individual matrices) or*  
159 *can be stored as lists of the events. Communication networks can often be well*  
160 *represented using simplicial complexes, such as that produced in the process illustrated*  
161 *by f-h): f) A researcher locates the position of all individuals within a population; g) using*  
162 *data on the audible radius of different individuals (here assuming no individual variation*  
163 *for illustrative purposes) they can then calculate different types of simplicial complexes*  
164 *to represent the higher-order communication network; h) we illustrate the first-order*  
165 *(grey lines) and second-order simplices (semi-transparent yellow polygons) of the*  
166 *Vietoris-Rips complex for this example.*

167

### 168 **3. Applications of higher-order communication networks**

169 An important consideration when applying these approaches is whether the higher-  
170 order structure is a) an aspect of the social structure over which communication occurs  
171 (Fig. 1a), or b) an integral part of the communication process itself (Fig. 1f). An example  
172 of the former case would be how individuals produce and respond to contact calls. In  
173 this case the contact call is a directed signal on a higher-order social network. The  
174 underlying social structure might influence whether the signaller produces a contact call  
175 or the response of receivers to the signal. For instance, a receiver may respond  
176 differently when in a dyad with the signaller versus when part of a larger group.  
177 Consequently, incorporating higher-order social structure can alter predictions about  
178 how vocal communication spreads information through a group. An example of the latter  
179 case would be a chorus. The vocal communication itself can be encoded into a higher-  
180 order network, as the information available is altered by whether a receiver can hear  
181 one, two, or more signallers. Our first case study is an example of modelling vocal

182 communication as a directed signal on a higher-order social structure. We then provide  
183 two examples that treat the structure of the communication network itself as higher-  
184 order; the first incorporates higher-order structure to vocal communication networks to  
185 model signal synchronisation, and the second explores how higher-order structure can  
186 shape long-term patterns of group coordination and culture.

187

### 188 **3.1 Case Study 1: Group coordination and consensus decision-making**

189 In many species that rest or feed in groups, group departures are coordinated using  
190 vocal communication (33,34). Frequently, quorum decision-making allows group  
191 departures to be fully or partially coordinated (33,35). For example, in western jackdaws  
192 *Corvus monedula* call intensity increases immediately prior to a group departure and  
193 experimental playback leads to earlier departures from communal roosts (33). Similarly,  
194 red-fronted lemurs *Eulemur rufifrons* also increase call frequency prior to collective  
195 departures enabling group coordination (34).

196 We can model these behavioural states as contagions on social networks to  
197 quantify transitions from individuals a) not calling to calling and b) being present in the  
198 group to departed. Because social contagions are often best considered complex  
199 contagions and animal groups frequently contain higher-order social structures such as  
200 subgroups (11) or family units (36), these systems are suited to modelling as a directed,  
201 dyadic signal (vocal communication) across a higher-order network structure.  
202 Incorporating this higher-order social structure could make meaningful differences to the  
203 predictions made about group coordination, helping to elucidate how partial- and full-  
204 consensus decisions are reached.

205 Here we provide an example of vocally-coordinated departures from a group  
206 containing higher-order social structure. Our example is inspired by foraging and  
207 roosting flocks of light-bellied brent geese *Branta bernicla hrota*. In the non-breeding  
208 season, this species feeds and roosts in fission-fusion social groups (Fig. 2a). Groups  
209 contain multiple family units as juveniles accompany adult individuals for their first  
210 winter. As in other goose species, group departures are typically preceded by increased  
211 vocalisation (37).



212 We define a group that contains a pre-specified number of family units ( $n=20$ ),  
213 reproductive pairs ( $n=10$ ), and unpaired individuals ( $n=2$ ). We stochastically determine  
214 family unit size to be between 3 and 8 individuals (38). We distribute family units (here  
215 including reproductive pairs within our definition) uniformly at random across 2D space,  
216 with the spatial location of individuals drawn from a normal distribution centred on the  
217 family centroid. As a simplifying assumption we assume individuals remain static—  
218 equivalent to a resting group or a foraging group over a short timescale.

219 We then define subgroup membership by constructing a social proximity network  
220 defining proximity as two individuals within a threshold distance. Each connected  
221 component in the proximity network represents a subgroup hyperedge. A second set of  
222 hyperedges connects individuals within the same family unit (including reproductive  
223 pairs). We can alternatively represent these family and subgroup networks as dyadic  
224 networks in which pairs of individuals are connected by edges if they are both in the  
225 same sub-group or family unit.

226 We then simulate the transmission of calling behaviour across the group. First,  
227 we define a threshold audible radius over which individuals can hear each other and  
228 use this to generate a network to indicate who can hear whom. We then select two  
229 individuals at random to be initial callers. We model the uptake of calling behaviour as  
230 the function of a dose-response curve, in which the “dose” is modified by the social  
231 relationship between two individuals. We assume the probability of an individual  
232 transitioning from a non-calling to a calling state is a function of the dose. In our network  
233 model, we calculate the probability of transition independently for each dyadic  
234 connection and take a corresponding draw from a Bernoulli distribution. We consider an  
235 individual to have started calling whenever at least one possible transmission event  
236 occurs. In our hypergraph model, we calculate the total “dose” an individual receives  
237 based on its hyperedge membership. We use this total dose to calculate the transition  
238 probability of an individual from non-calling to calling. The transmission model is  
239 equivalent to that described in (27). We model the behavioural contagion for 1000  
240 timesteps (timesteps are arbitrary).

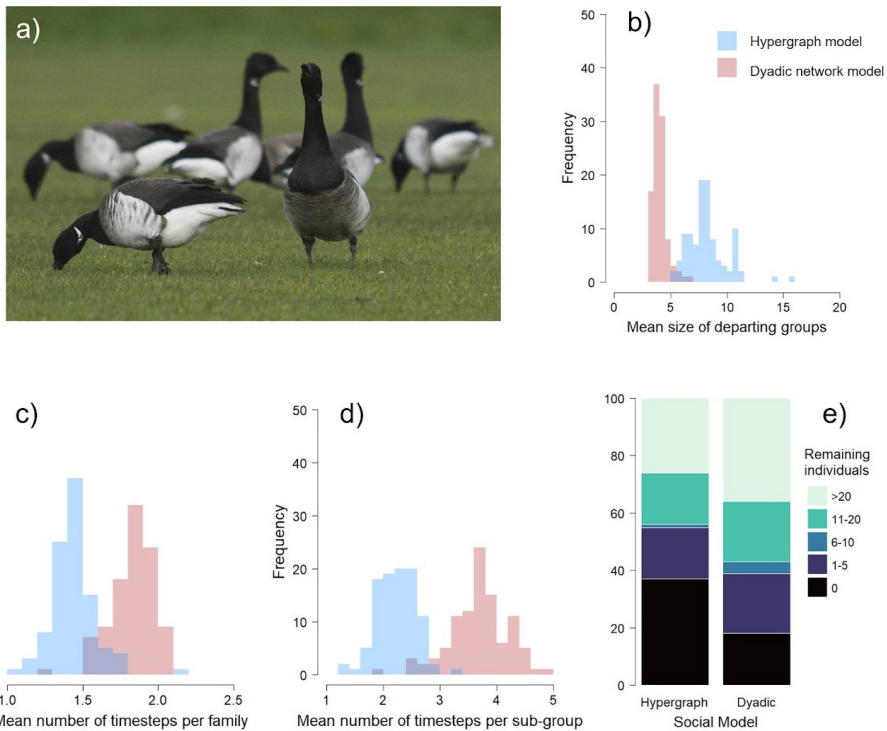
241 We then simulate departure decisions of individuals (i.e., transition from a  
242 present to a departed state) based only on the proportion of calling individuals within the

243 audible radius. For these simulations, we set this threshold such that individuals only  
244 depart when 90% of others within this radius are calling. We record when each  
245 individual departs and whom it departs with.

246 Comparing the outcomes of our network and hypergraph models demonstrates  
247 that including a complex behavioural contagion specified on the hypergraph depiction of  
248 the social network leads to improved coordination in the departure of family units and  
249 sub-groups. When transmission depends on the higher-order social structure of the  
250 group then: a) the mean size of departing groups is larger (Fig. 2b); b) the departures of  
251 both family units (Fig. 2c) and sub-groups (Fig. 2d) are more coordinated; and c) fewer  
252 individuals are likely to remain (undeparted) at the end of the simulation (Fig. 2e) as  
253 compared to when transmission depends on dyadic interactions.

254 Our example highlights how incorporating higher-order social structure can help  
255 construct effective models of complex behavioural contagions within groups based on  
256 vocal communication. While you could model these same complex contagions using  
257 dyadic networks, it is more straightforward when conceptualised as a higher-order  
258 network. The results demonstrate that incorporating the higher-order structure found  
259 within groups can substantially alter the predictions made when quantifying the outcome  
260 of information transmission through groups using vocal communication. Given our  
261 hypergraph model predicts improved coordination in departure, especially among  
262 individuals that share higher-order social connections, it seems likely these types of  
263 social structures will be important in explaining partial- and full-consensus decisions  
264 during collective departures (as well as for other collective action problems). More  
265 generally, comparing the predicted outcomes of higher-order and dyadic network  
266 models with empirical data can be used to infer the best performing model and  
267 ultimately estimate the importance of higher-order social structures across different  
268 species. This can reveal how vocal communication contributes to complex behavioural  
269 contagions within groups.

270



271  
 272 *Figure 2. An illustration of hypergraph and dyadic network models of the vocal*  
 273 *coordination of collective departure. a) Light-bellied brent geese form fission-fusion*  
 274 *social groups during non-breeding periods with foraging or roosting groups sub-*  
 275 *structured by space and family ties. Hypergraph models of vocally-coordinated group*  
 276 *departures inspired by this species predict b) larger departing sub-groups; c) greater*  
 277 *coordination among family units in departure timing; d) greater coordination among*  
 278 *spatially-defined units in departure time; and e) a greater frequency of all individuals*  
 279 *being involved in partial consensus departure decisions than dyadic models.*

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### 287 **3.2 Case Study 2: Synchronisation in vocal signalling**

288 Animal choruses are widespread (found in insects, anurans, fish, birds, and mammals)  
289 and impressive vocal displays characterised by high rates of signalling by many  
290 individuals. By their very nature, as opposed to duets, they are thus best described in  
291 terms of higher-order interactions because multiple signallers simultaneously advertise  
292 and could interact vocally with one or multiple nearby individuals. Additionally, choruses  
293 are dynamic, and individuals may be involved in multiple simplices at different points in  
294 time. Rich information is available to receivers from both individual and interactive  
295 communication displays. We illustrate how the dawn choruses of territory-holding  
296 songbirds may be explained by modelling their higher-order interactions using simplicial  
297 complexes; we showcase how many-body interactions could give rise to self-organised  
298 coordination within choruses.

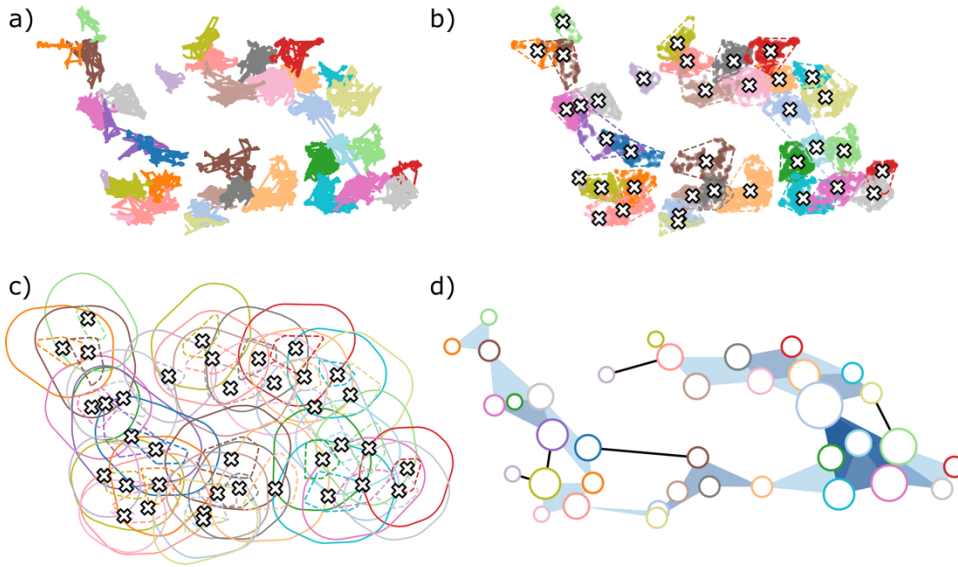
299 Black-capped chickadee dawn vocal communication networks provide a good  
300 example to illustrate the types of higher-order interactions that may exist in territorial  
301 systems. Chickadees have a relatively unique social system among songbirds. In  
302 winter, several pairs and unpaired individuals form winter flocks with linear dominance  
303 hierarchies where males are dominant to females and older individuals dominate  
304 juveniles (39,40). In spring, pairs defend breeding territories within their winter flock  
305 home range (39). Female black-capped chickadees prefer higher-ranking males as both  
306 within and extra-pair mates (41–43). As such, information about social familiarity (flock  
307 membership) and social rank has been linked to vocal behaviour and fitness (44).  
308 Chickadees sing a pronounced dawn chorus in which all territorial males sing and  
309 choruses honestly signal both age and winter dominance rank (45,46).

310 Multi-microphone array recordings revealed that dawn chorus interactions are  
311 influenced by both winter dominance rank and flock membership, and that higher-order  
312 processes are features of these networks (47,48). Black-capped chickadees sing a  
313 simple two-note song ‘fee-bee’ that they can shift up and down a continuous frequency  
314 range (49). During vocal interactions or in response to song playback, males change  
315 their song frequency relative to their opponent (50), with frequency matching perceived  
316 as more aggressive than singing at a different frequency (51). Frequency matching  
317 occurs in dyads at dawn but can also include three or even four individuals (48).

318 Frequency matching patterns matched predictions based on social relationships, with  
319 more matching between males from different flocks or of similar dominance rank (47).  
320 Matching interactions extended from dyadic to triadic in a predictable way, beginning  
321 more often with two males from different flocks joined by a flockmate of one of them  
322 (48). In black-capped chickadees and other vocal territorial species, whether the  
323 synchrony in timing of the chorus or in timing of signals within the chorus is influenced  
324 by higher-order processes could be studied using the methods we outline here.

325         As an example, we consider the configuration of territories from a population of  
326 another songbird species — ovenbirds *Seiurus aurocapilla* — for which we had GPS  
327 tracks of singing males used to map territories throughout the 2022 breeding season  
328 (Figure 3). We looked at the overlaps of buffered territory boundaries (Figure 3c) to  
329 construct an empirical higher-order structure that could exist in a vocal network of  
330 territorial ovenbirds. We used a 25m buffer beyond the territory boundary, in which we  
331 estimated most songs would be within the comfortable communication or recognition  
332 distances of neighbours as estimated previously for other songbird species (52) and as  
333 the likely area in which we would expect most higher-order interactions to occur. The  
334 higher-order structure (Figure 3d) suggests that simplices are likely features of territorial  
335 vocal communication networks and that some ovenbirds are involved in larger or more  
336 simplices than others. The simplices identified by the model match behavioural  
337 observations of multi-way vocal interactions documented during breeding activity  
338 surveys (J Foote *pers obs*).

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342 *Figure 3. Constructing a higher-order structure based on audibility range from empirical*  
 343 *data of bird positions. a) Individual trajectories from GPS tracks of singing and foraging*  
 344 *males where each colour represents the position in time of a different bird. b) The*  
 345 *centroid of each trajectory is computed (white cross) together with the associated*  
 346 *convex hull (dashed line) representing a proxy for the area covered by each bird. c)*  
 347 *Each area is expanded by adding a buffer distance of 25m, in which we estimate most*  
 348 *songs from within the territory would be recognized by neighbours representing the*  
 349 *approximated hearing range. d) Finally, a simplicial complex is constructed from the*  
 350 *many-body intersections within the buffered areas. The colour of the simplexes is*  
 351 *proportional to the order; the size of the nodes is proportional to the number of attached*  
 352 *simplices.*

353

354 We use the ovenbird position data (Fig. 3) as the backbone structure to run a  
 355 higher-order generalisation of the classic Kuramoto model (53) proposed by Adhikari et  
 356 al. 2023 (54). Coupled oscillators have been widely used to model emergent  
 357 synchronisation patterns in various networked populations (55). We consider a  
 358 hypergraph (Figure 4), where each bird is associated to a node and birds can interact  
 359 by means of pairwise or three-way interactions (higher order interactions are possible  
 360 but neglected for simplicity). Each node  $i$  is associated to a natural frequency  $\omega_i$   
 361 (randomly drawn from a normal distribution) and a state variable  $\theta_i \in [0, 2\pi[$  representing

362 the central “object” of the synchronisation dynamics, which could be, for example, the  
 363 signal content (e.g., song frequency or type) or song timing (e.g., overlapping or  
 364 alternating pattern of singing) to be matched upon an interaction. It is easier to think of  
 365 this state variable, called the *phase* of the oscillator, as an angle in the unit circle. With  
 366 this approach, we can easily quantify the degree of synchrony in our system by  
 367 measuring how much our oscillators rotate together around the circle. After embedding  
 368 the phases in the complex plane via the transformation  $z = e^{i\theta}$ , we can thus measure  
 369 the level of synchrony as the average vector of these complex numbers:

370

371 
$$z = \frac{1}{N} \sum_{i=1}^N e^{i\theta}$$

372

373 The magnitude  $r = |z|$  represents the Kuramoto order parameter, also called phase  
 374 coherence, that takes its maximum value  $r = 1$  for perfectly synchronised phases.  
 375 The equation of motions governing the dynamics of the  $N$  nodes are:

376

377 
$$d_t \theta_i = \omega_i + K_2 \sum_{j=1}^N a_{ij} \sin(\theta_j - \theta_i) + K_3 \sum_{k,j=1}^N b_{ijk} \sin(2\theta_k - \theta_j - \theta_i),$$

378

379 where the free parameters  $K_2$  (dyadic) and  $K_3$  (multi-body) are the coupling strengths  
 380 associated to the interactions at different orders. Positive coupling will induce synchrony  
 381 among the interacting individuals. In our case, these interactions are mediated by the 1-  
 382 and 2-simplices encoded into the respective adjacency tensors: A represents the  
 383 standard adjacency matrix — for 1-simplices —, with elements  $a_{ij} = 1$  if nodes  $i$  and  $j$   
 384 share a 1-simplex (otherwise  $a_{ij} = 0$ ). Similarly, the adjacency tensor B for 2-simplices  
 385 will have elements  $b_{ijk} = 1$  when nodes  $i, j$ , and  $k$  participate in the same 2-simplex.  
 386 We assume a simple sinusoidal function for the coupling, but the model naturally  
 387 extends to interaction functions of any form.

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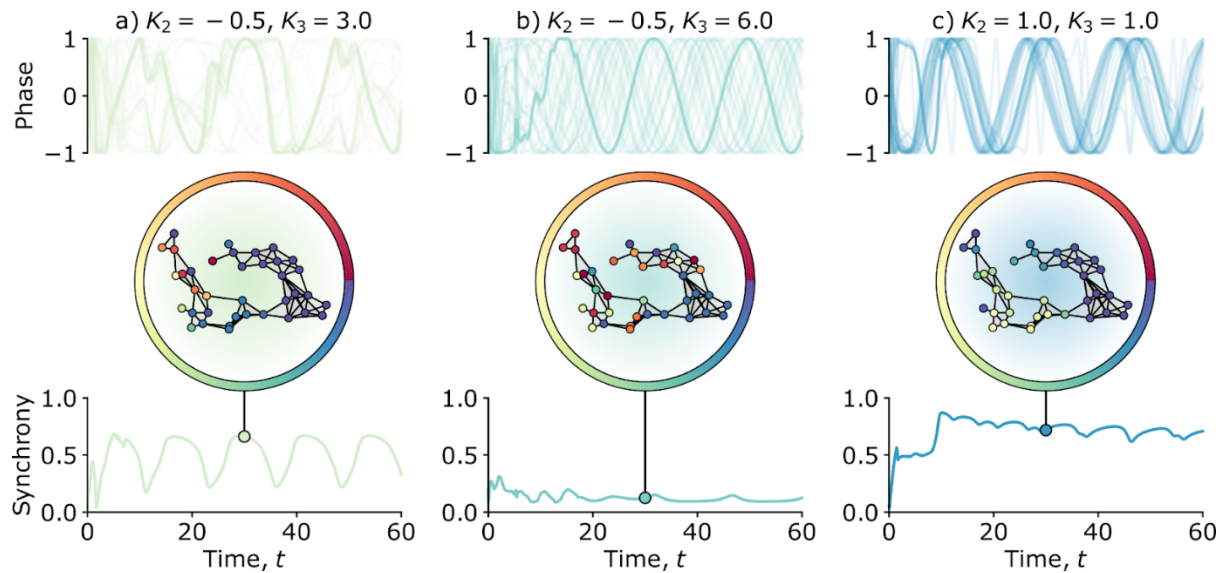
389 The model suggests that synchronisation can emerge in neighbourhoods with  
 390 higher-order interactions (Fig. 4). A periodic pattern of synchrony emerges (Fig. 4a)  
 under moderate positive three-body coupling and mild divergent coupling in dyads. This

391 pattern could emerge if chorusing individuals somewhat attend to their two closest  
392 neighbours simultaneously when singing but shift attention between neighbours over  
393 time as they move within their territory, leading to clusters of synchrony at different time  
394 points. If we increase the coupling strength of three-body interactions, the overall  
395 synchronisation of the whole chorus is reduced, and no local synchrony occurs (Fig.  
396 4b). Finally, for positive coupling strengths for both dyadic and three-body interactions,  
397 we get synchronisation in clusters (Fig. 4c). Local patterns emerge, where  
398 neighbourhoods display phase-locking behaviour. This pattern likely matches nicely  
399 what we see in black-capped chickadee dawn choruses where individuals synchronise  
400 song frequency with individual neighbours in turn and also with two neighbours  
401 simultaneously (48), indicating similar behaviours could occur in ovenbirds and other  
402 species.

403         While these approaches remain untested in songbird territorial networks,  
404 pairwise phase coherence associated to volume oscillations as a function of their spatial  
405 distances has been shown in cicadas (56), with spatial synchrony also found to be  
406 patchy in this example. Similarly, in field crickets *Gryllus campestris*, with increased  
407 number of singing rivals, males were more likely to sing leading to moderate singing  
408 overlap but singing was inhibited by close proximity (57). Models of synchronisation  
409 have also been applied to frog choruses (58). Additionally, there is scope for higher-  
410 order vocal communication networks influencing synchrony across a wider diversity of  
411 species. For example, indris (*Indri indri*) use long-range songs to communicate between  
412 territorial groups (pairs and their offspring), and encounters in peripheral areas are  
413 mediated mostly through long-range vocalizations (59) meaning synchrony involving  
414 multi-body interactions could emerge where peripheral edges of multiple territories  
415 overlap. Further technological advances (e.g. in underwater recording) could extend  
416 research to aquatic systems such as territorial chorusing fish, for example the territorial  
417 defense and mate attraction calls of damselfish produce territorial calls used in both  
418 mate attraction and territorial defense (60).

419  
420





421  
 422 *Figure 4. Examples of a synchronisation problem mediated by higher-order interactions.*  
 423 *Top panels report the temporal evolution of the phases associated to each node ( $\sin(\hat{i})$ )*  
 424 *), representing the song frequency. Bottom panels report the evolution of the*  
 425 *associated order parameter — a proxy for the degree of synchrony of the system. For a*  
 426 *visual aid, we also display the network together with the status of each oscillator at time*  
 427  *$t=30$  by means of different colours picked from a circular colormap: nodes with similar*  
 428 *colours will have similar phases. To illustrate the different behaviours that can be*  
 429 *obtained through higher-order approaches, we consider three different scenarios of*  
 430 *coupling strengths  $K_2$  and  $K_3$ , where negative values indicate divergence and positive*  
 431 *values convergence and the magnitude of coupling strength (e.g., how fast you try to*  
 432 *keep up with neighbours or not) is variable. The interplay between these coupling*  
 433 *parameters at different orders lead to different phenomena: a) a partially synchronised*  
 434 *system with periodic signs of synchrony within the most connected nodes; b) an almost*  
 435 *asynchronous system with no signs of coordination among the nodes; c) a system*  
 436 *where clusters of nodes are synchronised.*

437

438

### 439 **Case Study 3: Long-term patterns of group coordination and culture**

440 Vocal communication signals are socially learned in many species (61). Socially learned  
 441 signals often vary within and among social groups, through cultural fission and fusion  
 442 (62). For example, male humpback whales *Megaptera novaeangliae* within particular

443 populations in the Pacific Ocean conform to a particular song type, but due to  
444 aggregations of individuals from different populations at migratory stopovers, there is a  
445 striking pattern of directional cultural transmission on songs across the overall  
446 metapopulation (63,64). We can examine the fission-fusion dynamics of cultural groups  
447 using higher-order communication networks. Here, we focus on socially learned  
448 vocalizations—an important signal of cultural identity in many songbirds—to show how  
449 differences in who can hear whom will influence how different cultural groups form and  
450 are maintained.

451         White-crowned sparrows *Zonotrichia leucophrys* are a useful example to  
452 illustrate outcomes of higher-order interactions during the process of learning a social  
453 signal. Adult males typically produce one song type, and most males in an area share  
454 the same song type; a cultural group also known as a ‘dialect’. Males from different  
455 areas produce different dialects (65). Cultural groups are thus separated geographically  
456 but not defined by geographic barriers – males can move between dialects (66). Males  
457 can memorize multiple song types from multiple tutors when young, overproduce these  
458 song types, and then selectively drop those that do not match the song of interacting  
459 males (66). Despite this selection for conformity, individuals are recognizable from their  
460 songs (67). There is subspecific variation in this song learning process, though, and it is  
461 thought that this variation could, in part, explain differences in the degree of geographic  
462 structure of dialects between resident and migratory subspecies (68).

463         One potential route to cultural fission is through detectability in the soundscape –  
464 if individuals cannot hear each other, they cannot influence each other’s song.  
465 Decreasing coordination among individuals over spatial scales greater than an  
466 individual’s audible range therefore leads to the emergence of different songs as  
467 individuals spread out or the population expands into new areas: group fission.  
468 Conversely, if individuals sing dissimilar songs within each other’s audible range, they  
469 can learn from each other and songs can become more similar (within and across  
470 generations): group fusion.

471         As a potential explanatory model of these dynamics, we construct a higher-order  
472 network model in which interactions are determined by audible distance,  $A$ . In our  
473 model, individuals favour song variants within the boundaries of their cultural group

474 norms, while maintaining sufficient distinctiveness to be individually recognizable. From  
 475 just this simple scenario, we propose the following model:

476 Consider a population of individuals,  $x_j$ . We describe the geographic distance  
 477 between the position,  $x_j^p$ , of any two individuals to be  $GeoD(x_j, x_i) = GeoD(x_i, x_j) =$   
 478  $|x_j^p - x_i^p|$ . We describe their song,  $x_j^s$ , as a real valued number, such that we can define  
 479 the distance between the songs of two individuals to be  $SongD(x_j, x_i) = SongD(x_i, x_j) =$   
 480  $|x_j^s - x_i^s|$ . We then call  $\epsilon$  the range of distinctiveness, such that if  $SongD(x_i, x_j) \leq \epsilon$ , then  
 481 both individuals incur a fitness penalty due to lack of distinctiveness and therefore, if  
 482 capable, alter their song.

483 We define a simplex  $G_{x_j} = \{x_i \mid i \neq j, GeoD(x_j, x_i) < A\}$ . We then define  $Med(G_{x_j})$   
 484 as the median value of the song of all individuals within  $G_{x_j}$

485 We can then define how  $x_j^s$  changes over time by a two-step rule:

486 1) If there exists any  $x_i$  such that  $SongD(x_j, x_i) \leq \epsilon$  then  $\dot{x}_j^s = x_j^s \pm rj\epsilon$ , where  $r$  is a  
 487 random value drawn from the uniform interval  $[-R, R]$ . This moves the song away  
 488 from its current value by a small random distance, pulled from a distribution tied  
 489 to its ordinal position within the population. This decreases the likelihood that any  
 490 two individuals with songs within the range of distinctiveness will simultaneously  
 491 alter their songs to remain indistinct from each other after they both shift.

492 2)  $\dot{x}_j^s = \begin{cases} x_j^s + \frac{Med(G_{x_j}) - x_j^s}{f} & \text{if } Med(G_{x_j}) \geq x_j^s \\ x_j^s - \left(\frac{x_j^s - Med(G_{x_j})}{f}\right) & \text{if } Med(G_{x_j}) < x_j^s \end{cases}$  where  $f$  is an integer  $\geq 2$  to reflect

493 song flexibility over time. (nb. 1 indicates maximum flexibility, allowing individuals  
 494 to converge to their audible community's median song). This moves each  
 495 individual's song closer to the median within their audible range,  $A$ .

496

497 This model can either be interpreted to reflect an individual changing their own song  
 498 (66), or an individual's offspring inheriting parental territory and learning/defining their  
 499 own song (69).

500 We consider a discrete time simulation of this model under two scenarios. In the  
 501 first scenario, individuals do not move and the only differences will arise as an outcome

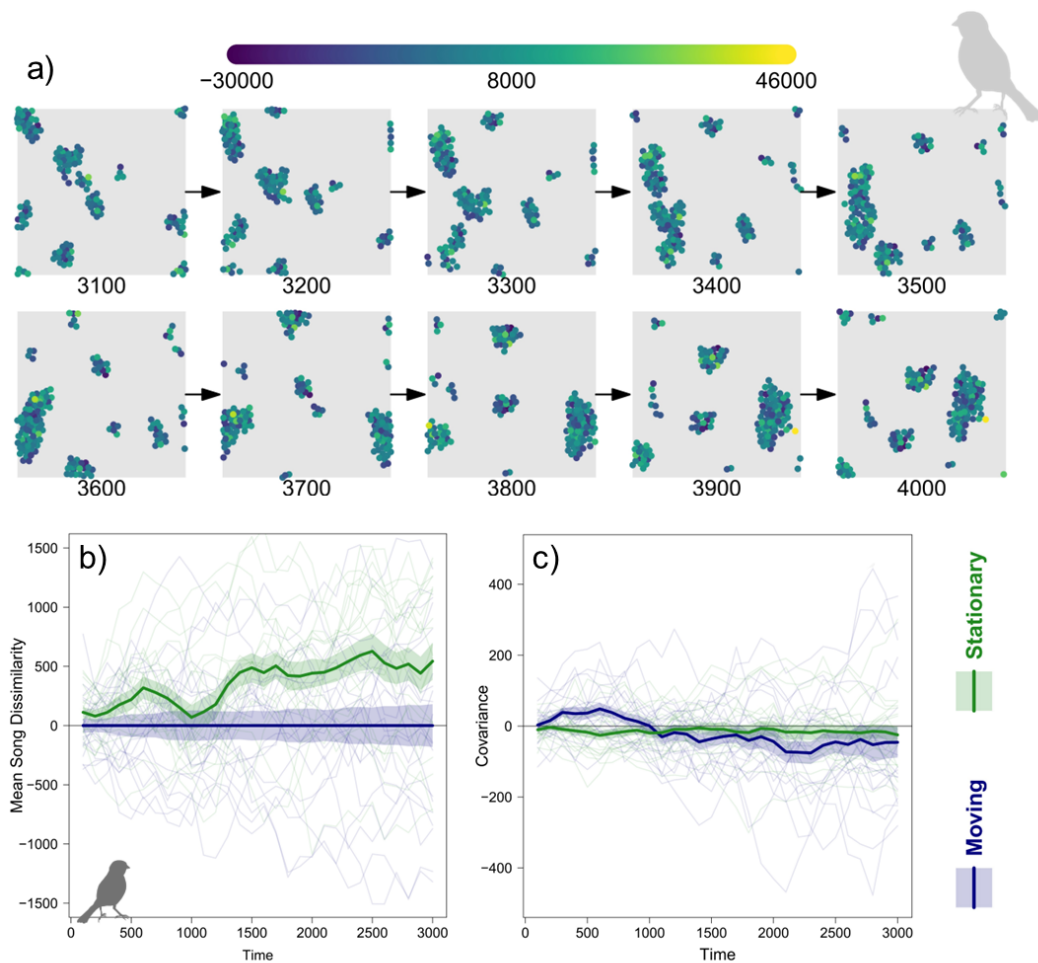
502 of changes in song, as influenced by others in a static set of simplices. In the second  
503 scenario, individuals move according to a standard flocking behaviour model (70). The  
504 simplices therefore change over time depending on movement-altered geographic  
505 distance altering who can hear whom, but otherwise independent of song.

506 From this simple model, we contrast the impact of static versus dynamic  
507 simplicial structures on population-wide emergent patterns in song (Fig 5). Individuals  
508 within the static spatial structure have more dissimilar songs (Fig 5b), consistent with  
509 the lack of interaction fostering divergence among subgroups akin to more geographic  
510 structure of dialects in resident white-crowned sparrow subspecies as compared to  
511 more migratory ones. However, a more nuanced story is revealed by examining the  
512 covariance between geographic and song distance over time in the two scenarios.  
513 While highly variant across scenarios, there are indications that geographically closer  
514 individuals have more dissimilar songs on average in the stationary scenario, while in  
515 the dynamic scenario, the mean scenario is for geographically close individuals to  
516 initially converge in song distance before then diverging to a more strongly negative  
517 correlation (Fig. 5c). Such a prediction has not been considered nor tested in this long-  
518 studied model species. This finding would be consistent with the initial formation of  
519 smaller groups with their own cultural identity and converging songs, but then fission-  
520 fusion dynamics in song-independent flocking behaviour causing these small cultural  
521 groups to encounter each other, intermix and form new small groups with different sets  
522 of individuals more rapidly than the convergence in song allows.

523 Our higher-order network model helps us characterise features that would be  
524 opaque in a dyadic framework. For example, one native output is a prediction of fission-  
525 fusion dynamics over time and space. An easily measurable feature of the emergent  
526 dynamics is the overlap in subsimplices shared by groups, i.e., “sub-simplicial density”.  
527 Greater numbers of shared subsimplices would suggest maintenance or emergence  
528 (i.e., fusion) of a single cultural group, whereas regions of sparse sub-simplicial density  
529 between two clusters of greater density would suggest fission. In this way, we can  
530 predict the emergence or loss of cultural groups from a landscape. This model is easily  
531 extendable to other songbirds which vary in their song learning process along multiple  
532 dimensions (71). For instance, we could also predict the song-trajectory of individuals

533 from open ended learners over their lifespans, depending on their geographic location  
 534 and the influence of audible cultural groups. The group’s cultural norms themselves will  
 535 shift over time as individuals change their songs and move into and out of audible  
 536 range. Extending this model to bias flocking behaviour towards similar song could then  
 537 yield complex bidirectional feedback between song type and movement, generating  
 538 valuable predictions about the relationships between culture formation and movement  
 539 ecology.

540



541

542 *Figure 5. An example of our Case Study 3 model in action. a) An illustration of a single*  
 543 *model run of the “moving” condition in which individuals follow basic rules of collective*  
 544 *action. Points are coloured according to their song values. Only the final part of the*  
 545 *simulation is illustrated but the full simulation can be watched in the Supplementary*  
 546 *Video. b) An illustration of how song dissimilarity increases faster for the “stationary”*

547 *than the “moving” condition for the selected parameter set. All values are scaled to the*  
548 *mean of the “moving” condition for illustrative purposes. c) An illustration of how the*  
549 *covariance between song dissimilarity and distance between individuals changes over*  
550 *time under the “moving” and “stationary” conditions. For panels b) and c) Time is the*  
551 *time since individual song values were free to change (i.e., from time step 1000). The*  
552 *thick lines show the mean song dissimilarity over time for 20 simulations runs and the*  
553 *shaded area the standard errors around the mean. Semi-transparent lines illustrate the*  
554 *mean song dissimilarity in each simulation run. Parameters used for these simulations*  
555 *were  $R = 5$ ,  $A = 100$ ,  $f = 500$  and  $\varepsilon = 50$ .*

556

557

#### 558 **4. Toolkit for higher-order networks**

559 Accessible software tools are not as well developed for higher-order network  
560 approaches as they are for dyadic networks, although this is changing rapidly. There  
561 are recent broad overviews of higher-order methods (12,13) and Silk et al. (27) provide  
562 an overview of the main tools available to ecologists, so here we focus on the most  
563 relevant tools available. The XGI *Python* library (72) provides a comprehensive toolkit  
564 for working with higher-order networks. It includes tools for calculating descriptive  
565 measures, some basic generative models, and visualisation tools alongside flexible core  
566 data structures for handling, converting, filtering, and storing hypergraphs and simplicial  
567 complexes. Alternatives in Python also include HypergraphX (73), while scikit-TDA  
568 represents a more general collection of libraries for Topological Data Analysis (74). In  
569 *R*, the *tdaverse* (<https://github.com/tdaverse/tdaverse>) provides tools for working with  
570 simplicial complexes, including plotting of Vietoris-Rips and Čech complexes while the  
571 packages *HyperG* (75) and *rhype* (76) provide various algorithms for descriptive  
572 measures, basic generative models and plotting. Basic tools for working with  
573 hypergraphs and simplicial complexes are also available in *Julia* (e.g.  
574 *SimpleHypergraphs.jl*: (77); *Simplicial.jl*: <https://github.com/nebneuron/Simplicial.jl>).

575

#### 576 **5. Key considerations and challenges**

577 It is important to discuss the general applicability of the proposed framework. An  
578 important caveat is that higher-order network approaches only benefit cases to which  
579 the theory applies well; just because something can be described as a hypergraph or  
580 simplicial complex, does not mean that it is always convenient to adopt such  
581 representation, nor that the higher-order dynamics are ecologically or evolutionarily  
582 meaningful. Some theoretical constructs may not be of practical use in real-world  
583 systems if assumptions central to the model are not realistically satisfied by any real-  
584 world scenario. There will also be cases where, even if the observed system naturally  
585 fits within the domain of many-body interactions, pairwise approaches already provide  
586 enough complexity to correctly capture the essential underlying mechanisms. For  
587 example, recent results have shown that dynamical systems defined on hypergraphs (at  
588 the node level) can be effectively reduced to dynamics on dyadic networks if the many-  
589 body interactions enter exclusively through linear functions of the states of the nodes  
590 (78). Other recent advances have also shown that, in some cases, it is possible to  
591 “lower” the order of some hyperedges without affecting the dynamical outcome —  
592 reducing the overall complexity of the model (79). In general, Occam’s razor remains a  
593 core principle: if a pairwise model is sufficient to explain the observed dynamics, there is  
594 no need to go higher with the order of the interactions. Higher-order models could  
595 indeed present further computational challenges that one might want to avoid if not  
596 strictly necessary. Consequently, methods that could provide meaningful insight, and  
597 satisfy the assumptions that make their interpretation valid, are limited by tractability.  
598 This can be particularly common as the size of simplices or hyperedges increases. In  
599 these cases, the application of higher-order network methods is ill advised unless  
600 limiting them to hyperedges or simplices of a particular size (or smaller) can be justified.  
601 As with all research, these limitations do not represent firm endpoints, but opportunities  
602 for cutting edge methodological research to extend the boundaries of capability.

603

## 604 **5.1 Data requirements**

605 A key challenge to applying higher-order network approaches to study animal vocal  
606 communication will be collecting appropriate data, something that is only recently  
607 possible with the advancement of acoustic and biologging technology. We envision an

608 ideal data collection protocol to gather simultaneously both movement and vocalization  
609 data of tracked individuals, for example, using acoustic location systems (80) or animal-  
610 borne microphones (81) or accelerometers (82). In general, it will be important to obtain  
611 longitudinal data, akin to recent efforts in human social networks (83), whose spatial  
612 and temporal extent goes beyond more traditional data collection procedures.

613         Quantifying the distance of communication in territorial networks will also be  
614 important to effectively model higher-order communication networks. We need to  
615 quantify not only how many individuals a receiver can hear, but also the distance at  
616 which information can be extracted (84). These distances can vary among species and  
617 with background noise levels (85). A further challenge is that for species with a single  
618 vocalisation type that is relatively invariable, it can be difficult to discern several  
619 independent signalers from dyadic or higher-order interactions. However, advances in  
620 autonomous acoustic location systems (86) could record networks of territory holders  
621 where position information can alleviate these issues.

622

## 623 **5.2 Model fitting versus prediction**

624 Following the discussion above, a key challenge in applying higher-order network  
625 models to communication networks will be in finding effective ways to: a) parameterise  
626 them to fit empirical datasets; and b) make suitably cautious predictions about how the  
627 system might respond to demographic or environmental change. For the former,  
628 choosing the correct outcome measures to compare between the empirical data and  
629 model predictions will be important. A second important point is that just because a  
630 higher-order model makes predictions that fit an empirical dataset does not necessarily  
631 mean we have identified the correct underlying mechanism. In fact, in absence of a  
632 ground truth — that is how nature operates — model selection becomes particularly  
633 crucial, especially against models that only incorporate dyadic network structures, to  
634 mitigate the risk of overfitting (the same argument also applies when adding in individual  
635 heterogeneity, temporal dynamics, etc.). For the latter, a potential strength of using  
636 these approaches is to forecast either ecological or evolutionary responses to scenarios  
637 such as reduced population density, habitat fragmentation or anthropogenic noise.  
638 However, these predictions must be made carefully as it is challenging to accurately



639 parameterise how individual behaviour may change in response to these factors, and  
640 this would alter the higher-order network structure. For example, if individuals respond  
641 to anthropogenic noise by moving more around their territory or targeting vocal  
642 communication at specific individuals, then predictions that did not incorporate these  
643 changes would likely be incorrect. Consequently, we advocate that when making  
644 predictions related to higher-order communication networks, researchers are very clear  
645 about their assumptions and any caveats to interpretation.

646

## 647 **6. Concluding remarks and future directions**

648 As demonstrated by our case studies, higher-order networks allow us to address  
649 questions that earlier models could not easily interrogate on behavioural, ecological,  
650 and even evolutionary scales. This means that not only already-posed questions can be  
651 revisited and addressed anew, but also future studies may benefit by framing  
652 hypotheses and gathering empirical data to anticipate the parameterization and/or  
653 validation of higher-order models.

654

### 655 **6.1 The value of interdisciplinarity**

656 Animal vocal communication network research offers an exciting opportunity to shape  
657 the direction of theoretical and methodological advancements in network science across  
658 boundaries of traditional research disciplines. Current advances in higher-order network  
659 modelling have been predominantly shaped by applications to sociological and  
660 engineering questions, and the intrinsic intuition of network scientists and complexity  
661 theorists. It is tantalising to imagine what new capabilities can be developed once  
662 interdisciplinary teams work together to envision their role in biological discovery.  
663 Through these collaborations “if only this concrete next concept were measurable,  
664 quantifiable, or computationally tractable to analyse” becomes a call to action, shaping  
665 basic methodological research. This is an opportunity for true bi-directional synthesis  
666 among biologists and network scientists that can extend the scope of both disciplines  
667 and answer questions together that would otherwise have been out of reach.

668 Two key examples of where animal vocal communication networks can inspire  
669 the development of new theoretical models are in the incorporation of individual

670 heterogeneity and the development of new models for the temporal dynamics of higher-  
671 order networks (87). Individuals may vary in how they receive and respond to signals,  
672 as well as their loudness of vocal communication. Developing approaches to  
673 incorporate this heterogeneity into theoretical models of higher-order social and  
674 communication networks could have important implications for general understanding of  
675 their dynamics. Similarly, developing computationally-tractable methods to deal with  
676 new model challenges brought by temporally-dynamic higher-order networks is a key  
677 area of methodological development that could be influenced by empirical challenges in  
678 animal communication. For example, a truly temporally explicit extension of Case Study  
679 2 that accounts for the movements of each individual would: a) require highly  
680 sophisticated data collection that tracked the location of every vocalisation of each  
681 individual (e.g. a time-synchronised recorder array; (88)); b) increase the complexity of  
682 the analysis pipeline to correctly identify the type or frequency of song while accounting  
683 for changes in background noise; c) induce further computational challenges to identify  
684 the correct temporal scales for modelling the dynamical process.

685

## 686 **6.2 Conclusion**

687 Researchers studying animal vocal communication have long recognised that these  
688 interactions are not dyadic, and their non-dyadic nature has important ecological and  
689 evolutionary consequences. We highlight how developments in modelling higher-order  
690 networks provide tools to explicitly account for these non-dyadic interactions. Our case  
691 studies demonstrate how higher order approaches can transform our understanding  
692 across diverse social contexts and help tackle new research questions. We also show  
693 the potential for animal communication networks to inspire and test new theoretical  
694 models in network science. Overall, we hope this article provides the motivation and  
695 tools to develop and test new models of higher-order communication networks in the  
696 wild.

697

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701

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710

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