

1 **Title Page**

2

3 **Network analysis reveals underlying syntactic features in a vocally learnt mammalian**
4 **display, humpback whale song**

5 Jenny A. Allen^{1,2}, Ellen C. Garland³, Rebecca A. Dunlop¹, and Michael J. Noad¹

6

7 ¹ The University of Queensland, Cetacean Ecology and Acoustics Laboratory, School of
8 Veterinary Science, Gatton, QLD 4343, Australia

9

10 ² Griffith University, School of Environment and Science, Gold Coast, QLD 4222, Australia

11

12 ³ University of St Andrews, Centre for Social Learning and Cognitive Evolution, and Sea
13 Mammal Research Unit, School of Biology, St Andrews, Fife, KY16 9TH, UK

14

15 Lead contact: Jenny A. Allen

16 Correspondence: j.allen3@uq.edu.au, jenny.allen@griffith.edu.au

17

18 Key words: syntax, vocal learning, song, humpback whale, network modelling

19 **Abstract**

20 Vocal communication systems have a set of rules that govern the arrangement of
21 acoustic signals, broadly defined as ‘syntax’. However, there is a limited understanding of
22 potentially shared or analogous rules across vocal displays in different taxa. Recent work on
23 songbirds has investigated syntax using network-based modelling. This technique quantifies
24 features such as connectivity (adjacent signals in a sequence) and recurring patterns. Here, we
25 apply network-based modelling to the complex, hierarchically structured songs of humpback
26 whales (*Megaptera novaeangliae*) from east Australia. Given the song’s annual evolving
27 pattern and the cultural conformity of males within a population, network modelling captured
28 the patterns of multiple song types over 13 consecutive years. Song arrangements in each
29 year displayed clear “small-world” network structure, characterised by clusters of highly
30 connected sounds. Transitions between these connected sounds further suggested a
31 combination of both structural stability and variability. Small-world network structure within
32 humpback songs may facilitate the characteristic and persistent vocal learning observed.
33 Similar small-world structures and transition patterns are found in several birdsong displays,
34 indicating common syntactic patterns among vocal learning in multiple taxa. Understanding
35 the syntactic rules governing vocal displays in multiple, independently evolving lineages may
36 indicate what rules or structural features are important to the evolution of complex
37 communication, including human language.

38

39 **Background**

40 While syntax in birdsong has been extensively studied, comparatively little is known
41 about the rules governing non-human mammalian vocalizations which likely share a closer
42 evolutionary lineage to our own (1). Humpback whale (*Megaptera novaeangliae*) song
43 provides a model to understand the evolution of complex vocal communication in mammals.
44 Their song repertoire is large and versatile, analogous to particularly complicated birdsong
45 displays. However, unlike birds, humpback whales produce songs in a stereotyped, nested
46 multi-level hierarchy (2, 3). Individual sounds or ‘units’ are arranged in a stereotyped pattern
47 called a ‘phrase’. Phrases then repeat multiple times to form a ‘theme’. A complete sequence
48 of four to seven themes sung in a particular order comprises a ‘song cycle’, which are
49 typically between seven and 30 minutes long (3). All male humpback whales in a population
50 usually conform to one song pattern at any given time, though there are often within-year
51 variants of that pattern. However, songs undergo incremental, progressive ‘evolutionary’
52 changes to their pattern each year, which singers adopt through social learning (4, 5). Songs
53 in the South Pacific populations additionally undergo periodic cultural ‘revolutions’ in which
54 the entire song pattern is replaced within a single breeding season (5, 6). Better understanding
55 of the structure of humpback whale song and learning mechanisms involved may provide
56 insight into how complex grammars and vocal learning evolved in a mammalian species (1,
57 7).

58

59 Recent studies on syntax have begun to examine structural components such as
60 connectivity (i.e., which sounds appear adjacent in a sequence) or transitions between
61 connected sounds (8-13). For example, if the sequence “AB” occurs frequently, then A and B
62 are highly connected and A transitions to B. For a longer sequence example “ABCDEF”, A
63 and C are better connected than A and F because there is a short distance between A and C

64 (one step), but a larger distance between A and F (4 steps). Network modelling has emerged
65 as a tool for investigating these structural components. ‘Small-world’ networks have certain
66 elements which are more connected than others and any two elements can be linked within a
67 few steps (14). These small-world networks are common in some complex birdsong
68 repertoires (8-13). Additional common features are transition ‘motifs’ and unit usage.
69 Transition motifs describe the frequency with which certain element arrangements (e.g.,
70 reoccurring patterns) occur (15) and can be either ‘deterministic’ or ‘non-deterministic’ (8).
71 Deterministic motifs occur when a particular sound type is only followed by a few specific
72 other sound types, while sound types in non-deterministic arrangements may be followed by
73 a wide variety of other sound types (8, 12). Unit usage quantifies the frequency with which
74 each element occurs within the display. Zipf’s law stipulates that word usage in human
75 language has an inverse linear relationship with the rank of each word’s use, meaning there
76 are a few common words while most words are relatively rare (16, 17). Animal repertoires
77 often have a convex departure from this linearity (11, 18-20), known as a Zipf-Mandelbrot
78 curve. The greater the departure, the more redundancy within a repertoire and less potential
79 information is implied (21). Unit usage therefore provides a baseline metric for estimating a
80 system’s potential capacity for complex communication (21, 22).

81

82 Repertoire complexity (i.e. size and variety of sounds) has been quantified in
83 humpback whale song (23) but quantitative studies are limited for structural complexity and
84 syntactic rules (23-26). In the current study, recordings of the east Australian humpback
85 whale song were assessed over 13 consecutive years. We used directed network modelling,
86 which considers unit order, to measure three specific structural features of songs: 1) the
87 overall network structure, 2) the distribution of unit usage, and 3) transition patterns. It was
88 hypothesized that, given the structure of humpback whale song and its similarities to complex

89 birdsong, it will contain both small-world network structure and a Zipf-Mandelbrot
90 distribution as these features are common among similar complex and learned vocal displays.
91 Each of the three structural features was first assessed separately per year. Then each feature
92 was assessed across all years combined to quantify consistent patterns irrespective of song
93 arrangement (8). Identifying shared syntactic rules in animal vocal learning displays will help
94 determine common vocal learning strategies or evolutionary pathways across multiple taxa
95 (27, 28).

96

97 **Methods**

98 **Data collection**

99 Recordings were made from 2002 to 2014 at Peregian Beach (26°30' S, 153°05' E)
100 and at Point Lookout on North Stradbroke Island (27°43' S, 153°53' E), both on the coast of
101 southeast Queensland, Australia. Recordings were made using a variety of methods over this
102 time in including moored hydrophone arrays, boat-based recordings, and passive acoustic
103 monitoring. Methods and sample sizes are summarized in Table S1.

104

105 **Song transcriptions and theme classifications**

106 Spectrograms were generated using Raven Pro 1.6 so that recordings could be
107 inspected visually and aurally for quality. Songs of sufficiently high quality (at least 10dB
108 above background noise with no other overlapping singers) were transcribed at the unit level
109 into numerical sequences using an acoustic dictionary of 149 distinct units classified using a
110 self-organizing map in MATLAB (see Allen *et al.* (29) for method details). Thirty-six
111 complete song cycles from a minimum of six different singers were selected randomly from
112 the available high-quality recordings and transcribed from each year from 2002 to 2014. The
113 exceptions were 2006 (n=12 song cycles from 2 singers) and 2007 (n=4 song cycles from 1
114 singer) due to insufficient high-quality recordings. As recordings were made along the

115 migratory pathway, songs recorded on separate days were assumed to be from different
116 individuals. In total, 412 song cycles were transcribed from 95 singers. Song cycles had an
117 average length of 172 total units (range 101-228) and an average duration of 7.2 minutes
118 (range 4.3-11.1).

119

120 Qualitatively assigned themes were verified quantitatively using a weighted
121 Levenshtein similarity index (LSI) (24, 30), with weightings ($\beta=1$) based on acoustic
122 similarity of units (29, 31). Hierarchical cluster analysis then grouped identified themes onto
123 major dendrogram branches based on the similarity of their unit sequence patterns,
124 confirming that theme assignments were robust. All dendrograms had a cophenetic
125 correlation coefficient (CCC) greater than 0.8, indicating a good representation of the data
126 (32).

127

128 **Small-world network analysis**

129 One network model for each year was generated based on the 36 song cycles from
130 that year (n=12 in 2006, n=4 in 2007), accounting for the consistent population-wide
131 conformity to one general song pattern in each separate year (3, 5). A separate model was
132 generated based on all years combined (n=412 for 2002-2014). Network analysis was
133 performed using the *PajaroLoco* software package (33) in Mathematica version 10.4. Models
134 were directed networks to account for sequential unit order. Each network model quantified
135 connectivity among units (i.e., units which were adjacent in a sequence) in the respective
136 dataset and compared it to a random Erdős-Renyi network which permuted the same number
137 of units and connections as the observed data (14, 35). This measure, termed the small-world
138 coefficient (S), is calculated following Humphries and Gurney (35) as:

139

$$S = \left(\frac{C}{C_{\text{rand}}} \right) / \left(\frac{L}{L_{\text{rand}}} \right)$$

140 where C is the clustering coefficient for the study dataset, L is the characteristic path length
141 for the study dataset, and C_{rand} and L_{rand} are values for C and L calculated for the randomly
142 permuted Erdős-Renyi network. ‘Small-world’ networks are characterised by 1) a small-
143 world coefficient (S) greater than 1 (35) and 2) clusters of units above a certain degree of
144 modularity, referred to here as ‘network communities’ and defined by having a higher
145 number of connections amongst each other than with units outside of the cluster (11, 14, 33,
146 35).

147

148 **Transition motifs**

149 Transition patterns or ‘motifs’ were based on the sequential arrangements of units. For
150 each year’s dataset, the number of different unit types that immediately preceded another unit
151 were counted (P_i) and averaged across all unit types ($\bar{P} = (\sum P_i)/N$). The number of different
152 unit types that immediately followed another unit were also counted (F_i) and averaged across
153 all unit types (Mean $\bar{F} = (\sum F_i)/N$) (8, 12). These averages were used to calculate transition
154 patterns, representing the frequency with which those patterns occurred across all song
155 variants in a given year. For example, if one male sung “AB” and another sung “BC”, the
156 motif calculations would reflect how often A immediately preceded B and how often C
157 immediately followed B across the dataset. Motifs fell into four categories as defined by
158 Sasahara *et al.* (8) (see Fig. 1):

- 159 1. Bottleneck – for a given unit type (X), a greater than average number of unit types
160 precedes and a less than average number of unit types follows ($P_x > \bar{P}$ and $F_x < \bar{F}$)
- 161 2. Hourglass – for a given unit type (X), a greater than average number of unit types
162 both precede and follow ($P_x > \bar{P}$ and $F_x > \bar{F}$)
- 163 3. Branch – for a given unit type (X), a less than average number of unit types precedes
164 and a greater than average number of unit types follows ($P_x < \bar{P}$ and $F_x > \bar{F}$)

165 4. One-way – for a given unit type (X), a less than average number of unit types both
166 precedes and follows ($P_x < \bar{P}$ and $F_x < \bar{F}$)

167

168 ‘Deterministic’ motifs (bottleneck and one-way) have fewer than average units

169 following any particular unit type ($F_x < \bar{F}$). ‘Non-deterministic’ motifs (hourglass and

170 branching) , have greater than average units following any particular unit type ($P_x < \bar{P}$) (8).

171 Each of the four transition motifs were counted per song cycle (including all phrase

172 repetitions of all themes) and averaged for each year’s dataset separately. All years were then

173 combined and similarly analysed as a single data set. The proportions of deterministic and

174 non-deterministic transitions were compared to one another within each year and among all

175 years to determine whether their relative proportions were consistent across years.

176

177 **Unit usage**

178 Units were ranked based on how frequently they occurred in each year’s dataset.

179 Rankings and frequency of occurrence were plotted logarithmically, generating a distribution

180 of unit usage for each year (18-20, 36, 37) to determine the “openness” of the repertoire. A

181 repertoire with a slope of -1 (a ‘Zipf Curve’) indicates that a small number of sounds are used

182 frequently and many sounds are used infrequently (10, 16, 20, 37). A ‘closed’ system has a

183 slope of less than -1 indicating that a few specific units dominate use whereas an ‘open’

184 system has a slope between 0 and -1, indicating that many units are used with similar

185 frequency. The same calculation was repeated using all years combined based on the 412

186 song cycles. Unit usage parameters were calculated using the *PajaroLoco* software package

187 (33) in Mathematica version 10.4.

188

189 **Results**

190 **Small-world networks**

191 Directed network models for each year's song had clear small-world network
192 structure (i.e. small-world coefficient ($S > 1$), with an average S value of 3.0 (range: 1.2 to 5.1
193 per year) (Fig. 2 & 3, Table 1). Therefore, unit types within song sequences clustered into
194 highly connected groups with short distances between unit types. Song arrangements for each
195 year contained an average of 4.7 (range: 3-7, Table 1) network communities (i.e., clusters of
196 adjacent unit types) and a short average path length (mean=2.1, range: 1.8-2.4, Table 1),
197 meaning that any pair of unit types only needed a few steps to connect them. A directed
198 network model for all years combined had a small-world coefficient of 2.6, average path
199 length of 1.9, and 12 network communities (Table 1). Network communities for each year
200 contained an average of 10 unit types (range: 1-38). However, song themes contained an
201 average of 3 unit types (range: 1-10), suggesting that network communities did not
202 correspond with song themes (stereotyped patterns of units within a song type). Additionally,
203 there was no difference between small-world coefficients and whether songs changed by
204 evolution or revolution (heteroscedastic t-test, $p=0.28$).

205

206 **Transition motifs**

207 Deterministic motifs (i.e., few unit types following any particular unit) were more
208 common than non-deterministic motifs (i.e., many unit types following any particular unit) in
209 every year (average of deterministic motifs=59%, range 50-71%), except for 2006 which had
210 equal proportions of transitions. When all years were combined into a single analysis, the
211 percentages of deterministic and non-deterministic motifs were 56% and 44%, respectively.
212 Therefore, songs have more motifs which indicate stability than motifs indicating variability.

213

214 One-way motifs (where few unit types precede and follow a unit) were the most
215 common in each year (range: 43-63%, Table S2). Hourglass motifs, which have many units
216 both preceding and following a unit, were the second most common motif (range: 20-41%).
217 Branch motifs (few units precede a unit, but many units follow) and bottleneck motifs (many
218 units precede a unit, but only a few units follow) were far less common in each year (branch
219 range: 6-20%, bottleneck range: 4-19%). These trends suggest that song sequences primarily
220 contain sequences with either restricted, stable patterns (one-way motifs), or variable patterns
221 (hourglass motifs). This is reinforced by how rarely transitions occurred between stable and
222 variable patterns (bottleneck and branch motifs).

223 **Unit usage**

224 The repertoire size for each year ranged from 21 to 73 (average=45) unit types per
225 year and a total of 142 unit types over the 13-year study period. Unit types were shared by an
226 average of 4 separate years (range: 1-11) and an average of 50% of unit types in a given year
227 were shared between at least two song themes (range: 29-73%). The Zipf-Mandelbrot curve
228 was present for each separate year, as well as for all years combined, with a plot of log rank
229 of usage vs. log frequency of occurrence displaying a clear convex departure from linearity
230 (Fig 4). All linear regressions had negative slopes with an average of -1.9 (range: -1.1 to -
231 2.2), indicating a more “closed” system in which song repertoires were composed of a few
232 (~10% of units) common units while most units were rarely used. There was no difference
233 between slopes of songs changing via evolutions vs revolutions (heteroscedastic t-test,
234 $p=0.51$). Commonly used units near the top of the curve were mainly hourglass units, while
235 most rarely used units near the bottom of the curve were one-way units (Fig 4).

236

237

238 **Discussion**

239 Humpback whale song contained several features indicating a degree of structural
240 complexity and syntax. All analysed song patterns (2002 to 2014) displayed a small-world
241 network structure. Small-world structure was also present when data were combined into one
242 network model. Changes to small-world structure were not driven by changes to song
243 arrangement since there were no significant structural differences between songs that
244 underwent evolutionary (incremental) versus revolutionary (rapid) changes. Therefore, while
245 song patterns changed to varying degrees each year (5), some degree of small-world structure
246 was always present. This suggests that small-world structure is a consistent feature of
247 general song structure and not of any one particular arrangement.

248

249 Unexpectedly, each year's network communities (clusters of highly connected units)
250 did not coincide with that year's identified song themes (the repeating and stereotyped
251 patterns of units). Instead, on average about half of all unit types in a given year occurred in
252 at least two song themes rather than each song theme containing a unique set of units.
253 Similarly, unit types occurred across multiple years, even in instances where song patterns
254 were unrelated due to a cultural revolution event. Thus, even unrelated song types did not
255 seem to have entirely unique repertoires. Potentially shared units between both song themes
256 and song types from different years could facilitate song learning because even when the
257 song arrangement is novel, some unit types may be familiar.

258

259 Unit type arrangement within the network structure showed that common song
260 features were versatile in some aspects, yet restricted in others. This dichotomy stemmed
261 from the prevalence of both one-way and hourglass motifs. One-way motifs indicate that
262 many unit types 'direct' song patterns toward a specific sequence, limiting variability. These

263 units were typically found on the network's periphery because they connected with few unit
264 types and are likely to only appear within a single year's song variants. Conversely, hourglass
265 motifs demonstrate the common use of some units as 'hubs' or points of high connection that
266 facilitate sequence variability (9). Their role as hubs placed hourglass units at the centre of
267 the network communities within broader song networks, as they occurred in multiple themes,
268 within-year song variants, or yearly song types. While repertoires contained more one-way
269 unit types, hourglass unit types occurred more frequently within song sequences themselves.
270 Therefore, hourglass units mostly comprise the top of the unit usage curve, while one-way
271 units tended to make up the lower portion of the curve (Fig. 4). Based on visual inspection of
272 the units classified, hourglass units were primarily low frequency (~300-500Hz), flat, tonal
273 calls such as "moans", "groans" or "cries", while one-way units covered the spectrum of
274 acoustic features. The dominant use of stable one-way and diverse hourglass transitions
275 reflects the combination of stereotypy and variability (8) which is observed in multiple levels
276 of humpback whale songs (3, 24). The presence of these patterns across song variants and
277 unrelated song types further suggests fixed roles in the song structure. The common use of
278 hourglass units may allow incorporation of novelty by individuals, while the range of one-
279 way units support stability in that year's general arrangement which all singers must conform
280 to.

281

282 Overall, song structure featured stability and stereotypy by having considerably more
283 deterministic motifs (e.g., one-way and bottleneck) than non-deterministic motifs (e.g.,
284 hourglass and branching). Deterministic motifs encourage stereotypy by limiting which units
285 follow them, thus restricting variation (8). Unit usage (overall and per year) always followed
286 a similar distribution to that of human languages (16). In other words, each song type
287 contained sequences with a few commonly used unit types while most units were rare.

288 However, all plots were convex rather than linear, displaying the ‘Zipf-Mandelbrot’ curve
289 that is often observed in animal communication (20, 22, 36). This indicates that each song’s
290 repertoire contained a high level of redundancy, likely due to its repetitive hierarchical
291 structure. This is consistent with the relatively low estimates of mean unit-level entropy (~1.0
292 bits) found in other studies across song sequences within both this population (23, 26) and
293 Hawaii (25), which indicates predictability in unit arrangements and further supports the
294 presence of stereotypy and redundancy within humpback song. Disproportionately high usage
295 of the few central hourglass units (e.g., “moans”, “groans”, or “barks”) encouraged small
296 variations within the stereotyped song sequences, while the remainder of the units were used
297 in these small variations. Although following Zipf’s law is not sufficient evidence of
298 language, it does illustrate that some animal vocal repertoires contain a surprising amount of
299 complexity in their organisation (21).

300

301 The same syntactic features we have identified in humpback whale song (e.g., small-
302 world structure, deterministic motifs, and redundant unit usage) also occur in the songs of
303 certain songbirds (8-13, 20). Small-world coefficient values in humpback whale songs are
304 comparable to those calculated for birdsongs ($S=1.69-4.70$ for seven species, summarized in
305 Table 2). Reflecting network structure, deterministic transition motifs also occurred in similar
306 proportions across these species. One-way transitions are the most commonly used motif,
307 followed by hourglass “hub” elements central to small-world structure (Table 2).

308 Additionally, the network communities identified here are equivalent to the ‘small-world
309 themes’ identified in some bird songs (11, 12). Such parallels indicate that the network
310 structures of these displays cluster their song elements (units in humpback whales, phrases in
311 birds) in similar ways and encourage stability in their song arrangements. Stability through

312 small-world structures may therefore be taxon-general based on their presence in the vocal
313 learning displays of multiple, taxonomically diverse species.

314

315 Small-world structure is also found in human language (22, 38), with a relatively
316 small number of key words used often as important syntactic components. Evidence suggests
317 that small-world structure results from the need for language to have ‘optimal navigation’, in
318 which word arrangement can express an intended message efficiently using the smallest
319 number of steps (39, 40). While humpback whale songs do not contain information in the
320 same way as human language, consistent small-world structure is likely to increase song
321 learning efficiency. This may explain how singers learn a song’s pattern so quickly, as well
322 as the song’s ability to spread through an entire population within a single year or across
323 large spatial scales as shown in the South Pacific (5).

324

325 The concept of song structure facilitating learning is reinforced by the common
326 presence of repeating patterns across song types, shown as loops within the networks (Fig. 2,
327 Fig. S2). Doublets, triplets, and alternating repetitions were common one-way transitions.
328 Longer bouts of multiple repetitions of the same unit type appeared to involve mainly short
329 duration, low frequency, broadband calls such as “grunts” or “croaks”. Several previous
330 studies have found repetitions to be common through fine-scale qualitative analyses (41-43).
331 Both Guinee and Payne (42), and Payne (43) characterised these repetitions as “rhyme-like”,
332 suggesting that they could be used as mnemonic devices to better remember song content.
333 The prevalence of repetitions quantified here supports this suggestion that repetitions may aid
334 in song learning by making songs easier to remember.

335

336 **Conclusion**

337 The current study quantified fine-scale structural complexity and syntactic patterns of
338 humpback whale song. Although similar network modelling has been applied to birdsong (8-
339 13), studies are lacking for mammalian songs or hierarchical displays. By filling these gaps
340 using humpback whale song, the vocally learned displays of multiple species can be
341 compared. Convergence of small-world structure occurs in complex birdsong arrangements
342 (13); its presence in humpback whale song indicates that this convergence occurs in complex
343 songs across multiple vocal learning species. While these vocal displays may serve different
344 functions within their respective species, they share a common need for individuals to learn
345 them efficiently. If small-world structure does facilitate learning, then it is likely to be an
346 important feature of vocally learned displays. The ability to learn syntactic rules for syllable
347 arrangement is a fundamental component of vocal learning and development in humans (44,
348 45), birds (46), and humpback whales (47). Studies that quantify syntactic rules across
349 distantly related species are therefore invaluable for understanding the origin and evolution of
350 vocal learning and language.

351

352 **Acknowledgements**

353 We thank the staff and volunteers of the Cetacean Ecology and Acoustics Laboratory
354 for data collection, maintenance and storage over the course of the study. Data were collected
355 during the HARC project (2002–2004 and 2008–2009) and the BRAHSS project (2010–2012
356 and 2014). HARC was funded by the US Office of Naval Research, the Australian Defence
357 Science and Technology Organisation, and the Australian Marine Mammal Centre. BRAHSS
358 was funded by the E&P Sound and Marine Life Joint Industry Programme and the US Bureau
359 of Ocean Energy Management. Thanks to Douglas Cato for his significant role in instigating
360 and participating in all these field programmes. J.A.A. was funded by an Australian

361 Government Research Training Program Scholarship and the Australian American
362 Association University of Queensland Fellowship. E.C.G. was funded by a Royal Society
363 Newton International Fellowship and a Royal Society University Research Fellowship.
364 Particular thanks to Héctor Castellanos for his advice regarding the use of PajaroLoco
365 software and the application of network analyses within this study. We thank Adam Pack and
366 Christopher Templeton for providing comments on a previous version of the manuscript, as
367 well as the editor and two anonymous reviewers for their comments to greatly improve the
368 clarity of the manuscript.

369

370 **Data accessibility statement**

371 Data for this manuscript will be available on Dryad

372 **References**

- 373 1. Kershenbaum A, Ilany A, Blaustein L, Geffen E. Syntactic structure and geographical
374 dialects in the songs of male rock hyraxes. *Proceedings of the Royal Society of London B:*
375 *Biological Sciences*. 2012;279(1740):2974-81.
- 376 2. Catchpole CK, Slater PJ. *Bird song: biological themes and variations*. 2nd ed.
377 Cambridge, UK: Cambridge University Press; 2008. 1-348 p.
- 378 3. Payne RS, McVay S. Songs of humpback whales. *Science*. 1971;173(3997):585-97.
- 379 4. Payne K, Tyack P, Payne R. Progressive changes in the songs of humpback whales
380 (*Megaptera novaeangliae*): a detailed analysis of two seasons in Hawaii. *Communication and*
381 *behavior of whales*. 1983:9-57.
- 382 5. Garland EC, Goldizen AW, Rekdahl ML, Constantine R, Garrigue C, Hauser ND, et
383 al. Dynamic horizontal cultural transmission of humpback whale song at the ocean basin
384 scale. *Current Biology*. 2011;21(8):687-91.
- 385 6. Noad MJ, Cato DH, Bryden MM, Jenner MN, Jenner KC. Cultural revolution in
386 whale songs. *Nature*. 2000;408(6812):537.
- 387 7. Janik VM, Slater PJ. The different roles of social learning in vocal communication.
388 *Animal Behaviour*. 2000;60(1):1-11.
- 389 8. Sasahara K, Cody ML, Cohen D, Taylor CE. Structural design principles of complex
390 bird songs: a network-based approach. *PLoS One*. 2012;7(9):e44436.
- 391 9. Weiss M, Hultsch H, Adam I, Scharff C, Kipper S. The use of network analysis to
392 study complex animal communication systems: a study on nightingale song. *Proceedings of*
393 *the Royal Society of London B: Biological Sciences*. 2014;281(1785):20140460.
- 394 10. Deslandes V, Faria LR, Borges ME, Pie MR. The structure of an avian syllable syntax
395 network. *Behavioural processes*. 2014;106:53-9.

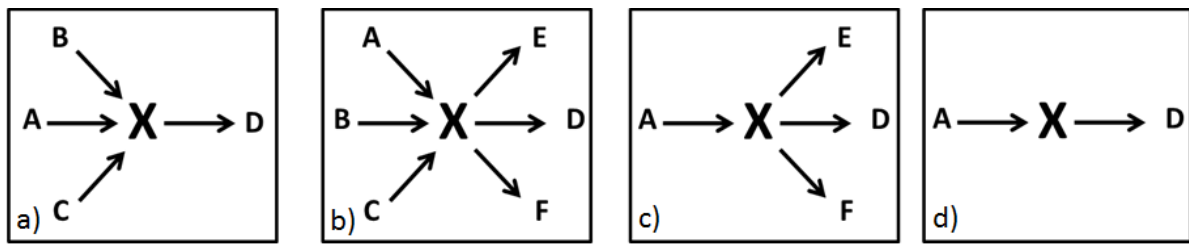
- 396 11. Cody ML, Stabler E, Sánchez Castellanos HM, Taylor CE. Structure, syntax and
397 “small-world” organization in the complex songs of California Thrashers (*Toxostoma*
398 *redivivum*). *Bioacoustics*. 2016;25(1):41-54.
- 399 12. Taylor CE, Cody ML. Bird song: a model complex adaptive system. *Artificial Life*
400 *and Robotics*. 2015;20(4):285-90.
- 401 13. Hedley RW. Composition and sequential organization of song repertoires in Cassin’s
402 Vireo (*Vireo cassinii*). *Journal of Ornithology*. 2016;157(1):13-22.
- 403 14. Watts DJ, Strogatz SH. Collective dynamics of ‘small-world’ networks. *nature*.
404 1998;393(6684):440-2.
- 405 15. Milo R, Shen-Orr S, Itzkovitz S, Kashtan N, Chklovskii D, Alon U. Network motifs:
406 simple building blocks of complex networks. *Science*. 2002;298(5594):824-7.
- 407 16. Zipf GK. *Human behavior and the principle of least effort: An introduction to human*
408 *ecology*: Ravenio Books; 1949.
- 409 17. Zipf GK. *The Psycho-Biology of Language: An Introduction to Dynamic Psychology*.
410 Cambridge: Addison-Wesley Press; 1968.
- 411 18. Hailman JP, Ficken MS, Ficken RW. The ‘chick-a-dee’ calls of *Parus atricapillus*: a
412 recombinant system of animal communication compared with written English. *Semiotica*.
413 1985;56(3-4):191-224.
- 414 19. Martins EP. Structural complexity in a lizard communication system: the *Sceloporus*
415 *graciosus* "push-up" display. *Copeia*. 1994:944-55.
- 416 20. Briefer E, Osiejuk TS, Rybak F, Aubin T. Are bird song complexity and song sharing
417 shaped by habitat structure? An information theory and statistical approach. *Journal of*
418 *theoretical biology*. 2010;262(1):151-64.
- 419 21. McCowan B, Doyle LR, Jenkins JM, Hanser SF. The appropriate use of Zipf’s law in
420 animal communication studies. *Animal Behaviour*. 2005;69(1):F1-F7.

- 421 22. Kopleinig A. Using the parameters of the Zipf–Mandelbrot law to measure diachronic
422 lexical, syntactical and stylistic changes—a large-scale corpus analysis. *Corpus Linguistics*
423 and *Linguistic Theory*. 2015.
- 424 23. Allen JA, Garland EC, Dunlop RA, Noad MJ. Cultural revolutions reduce complexity
425 in the songs of humpback whales. *Proceedings of the Royal Society B: Biological Sciences*.
426 2018;285(1891):20182088.
- 427 24. Murray A, Dunlop RA, Noad MJ, Goldizen AW. Stereotypic and complex phrase
428 types provide structural evidence for a multi-message display in humpback whales
429 (*Megaptera novaeangliae*). *The Journal of the Acoustical Society of America*.
430 2018;143(2):980-94.
- 431 25. Suzuki R, Buck JR, Tyack PL. Information entropy of humpback whale songs. *The*
432 *Journal of the Acoustical Society of America*. 2006;119(3):1849-66.
- 433 26. Miksis-Olds JL, Buck JR, Noad MJ, Cato DH, Dale Stokes M. Information theory
434 analysis of Australian humpback whale song. *The Journal of the Acoustical Society of*
435 *America*. 2008;124(4):2385-93.
- 436 27. Moore RK, Marxer R, Thill S. Vocal Interactivity in-and-between Humans, Animals,
437 and Robots. *Frontiers in Robotics and AI*. 2016;3.
- 438 28. Pinker S, Jackendoff R. The faculty of language: what's special about it? *Cognition*.
439 2005;95(2):201-36.
- 440 29. Allen JA, Garland EC, Murray A, Noad MJ, Dunlop R. Using self-organizing maps to
441 classify humpback whale song units and quantify their similarity. *Journal of the Acoustical*
442 *Society of America*. 2017;142(4):1943-52.
- 443 30. Garland EC, Lilley MS, Goldizen AW, Rekdahl ML, Garrigue C, Noad MJ. Improved
444 versions of the Levenshtein distance method for comparing sequence information in animals'
445 vocalisations: tests using humpback whale song. *Behaviour*. 2012;149(13-14):1413-41.

- 446 31. Garland EC, Rendell L, Lilley MS, Poole MM, Allen JA, Noad MJ. The devil is in the
447 detail: quantifying vocal variation in a complex, multileveled, and rapidly evolving display.
448 *Journal for the Acoustical Society of America*. 2017;142(1):460-72.
- 449 32. Sokal RR, Rohlf FJ. The comparison of dendrograms by objective methods. *Taxon*.
450 1962:33-40.
- 451 33. Sanchez H, Vallejo E, Taylor C, editors. PajaroLoco: a suite of programs to study the
452 grammatical structure of bird songs. Proceedings of the 20th international symposium on
453 artificial life and robotics (AROB 20th 2015), Beppu, Japan; 2015.
- 454 34. Wolfram Research Inc. PajaroLoco. Mathematica version 10.4. 10.4 ed: Wolfram
455 Research Inc, Champaign, IL; 2016.
- 456 35. Humphries MD, Gurney K. Network ‘small-world-ness’: a quantitative method for
457 determining canonical network equivalence. *PloS one*. 2008;3(4):e0002051.
- 458 36. Mandelbrot B. On the theory of word frequencies and on related Markovian models of
459 discourse. *Structure of language and its mathematical aspects*. 1961;12:190-219.
- 460 37. Grimsley JMS, Monaghan JJM, Wenstrup JJ. Development of Social Vocalizations in
461 Mice. *PloS ONE*. 2011;6(3):e17460.
- 462 38. Cancho R, Solé RV. The small world of human language. *Proceedings of the Royal
463 Society of London B: Biological Sciences*. 2001;268(1482):2261-5.
- 464 39. Ferrer i Cancho R, Solé RV. Least effort and the origins of scaling in human
465 language. *Proceedings of the National Academy of Sciences*. 2003;100(3):788-91.
- 466 40. Capitán JA, Borge-Holthoefer J, Gómez S, Martínez-Romo J, Araujo L, Cuesta JA, et
467 al. Local-based semantic navigation on a networked representation of information. *PloS one*.
468 2012;7(8):e43694.
- 469 41. Payne K, Payne R. Large scale changes over 19 years in songs of humpback whales in
470 Bermuda. *Ethology*. 1985;68(2):89-114.

- 471 42. Guinee LN, Payne KB. Rhyme-like Repetitions in Songs of Humpback Whales.
472 *Ethology*. 1988;79(4):295-306.
- 473 43. Payne K. The progressively changing songs of humpback whales: A window on the
474 creative process in a wild animal. *The origins of music*. 2000:135-50.
- 475 44. van Heijningen CA, De Visser J, Zuidema W, Ten Cate C. Simple rules can explain
476 discrimination of putative recursive syntactic structures by a songbird species. *Proceedings of*
477 *the National Academy of Sciences*. 2009;106(48):20538-43.
- 478 45. Feher O, Ljubicic I, Suzuki K, Okanoya K, Tchernichovski O. Statistical learning in
479 songbirds: From self-tutoring to song culture. *Phil Trans R Soc Lond B Biol Sci*.
480 2016;372:20160053.
- 481 46. Romberg A, Saffran J. *Statistical learning and language acquisition*. Wiley Interdiscip
482 *Rev Cogn Sci*. 2010;1:906-14.
- 483 47. Garland EC, Rendell L, Lamoni L, Poole MM, Noad M. Song hybridization events
484 during revolutionary song change provide insights into cultural transmission in humpback
485 whales. *Proceedings of the National Academy of Sciences*. 2017;114(30):7822-9.
486
487

488 **Figure Legends**

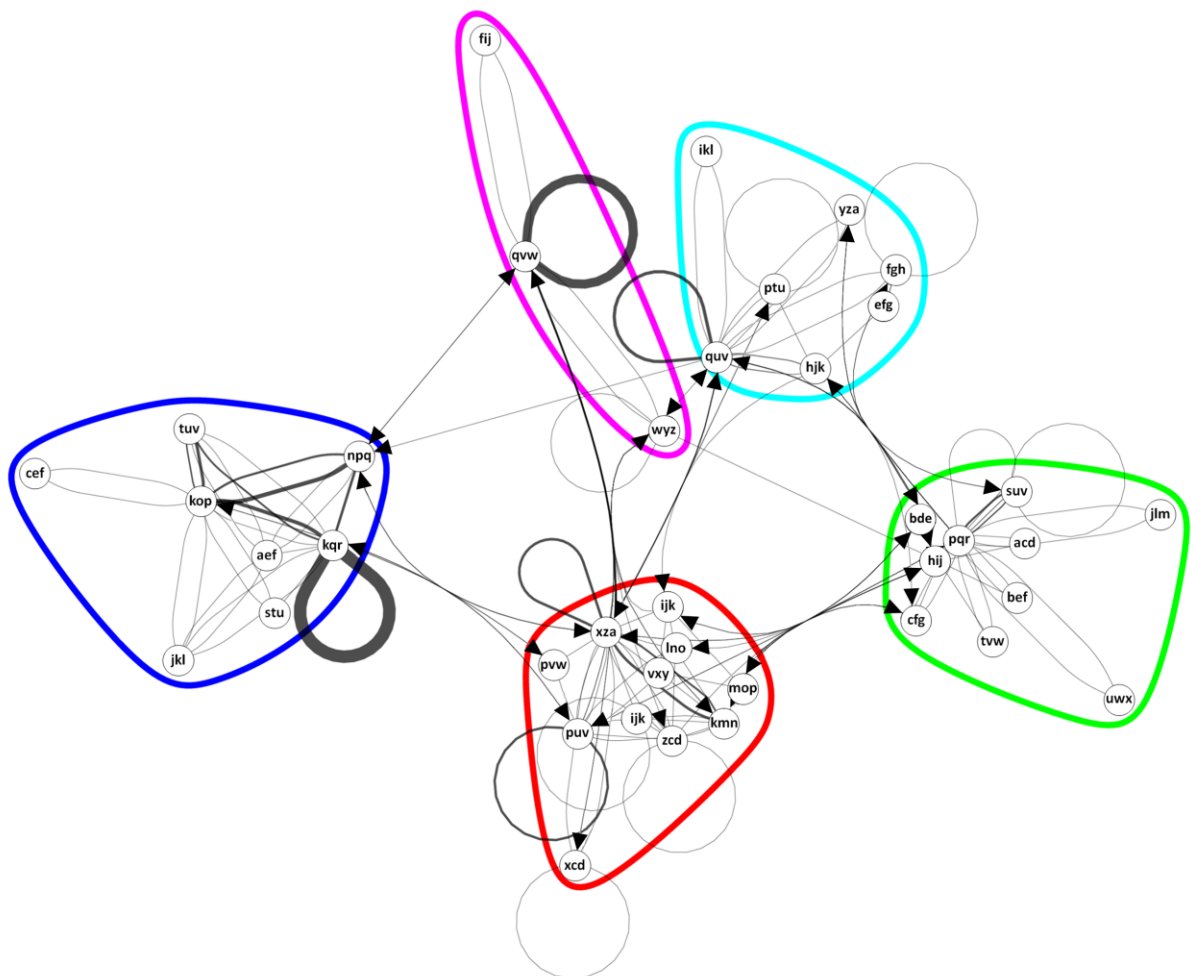


489

490 **Figure 1** Diagrams representing the four types of transition motifs, adapted from Sasahara *et*

491 *al.* (8): a) Bottleneck, b) Hourglass, c) Branch, and d) One-way.

492



493

494 **Figure 2** Example of a directed network representation of units for the song sequences for 2002

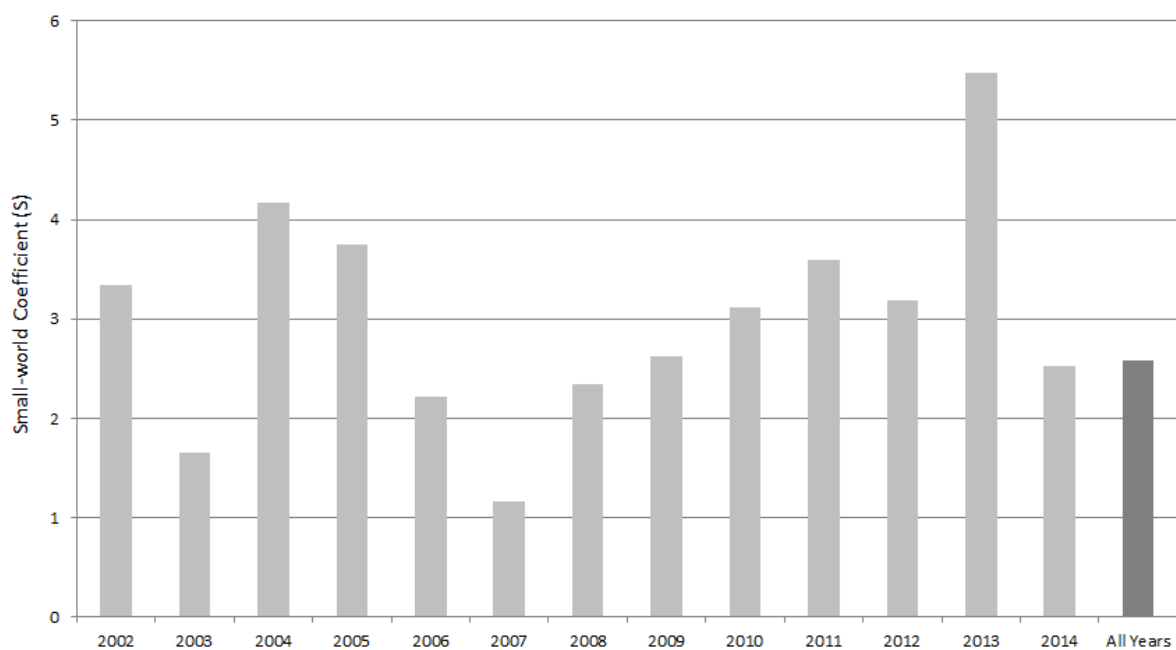
495 ($S=3.3$, $N=36$) with an average amount of small-world structure (average $S=3.0$). Units served

496 as the vertices and the transitions between units served as the directed edges (or connections)

497 between vertices. Arrows indicate transition direction between units, and line thickness

498 indicates the frequency of the transitions. There are high amounts of clustering between certain
499 groups of units ('network communities') circled in different colours. Units within network
500 communities have more transitions between each other than with units outside their own
501 community. Only a few transitions connect units between separate network communities.
502 Network representations for each year (2002-2014) and for all years combined can be found in
503 Supplementary information Figs. S1-S14.

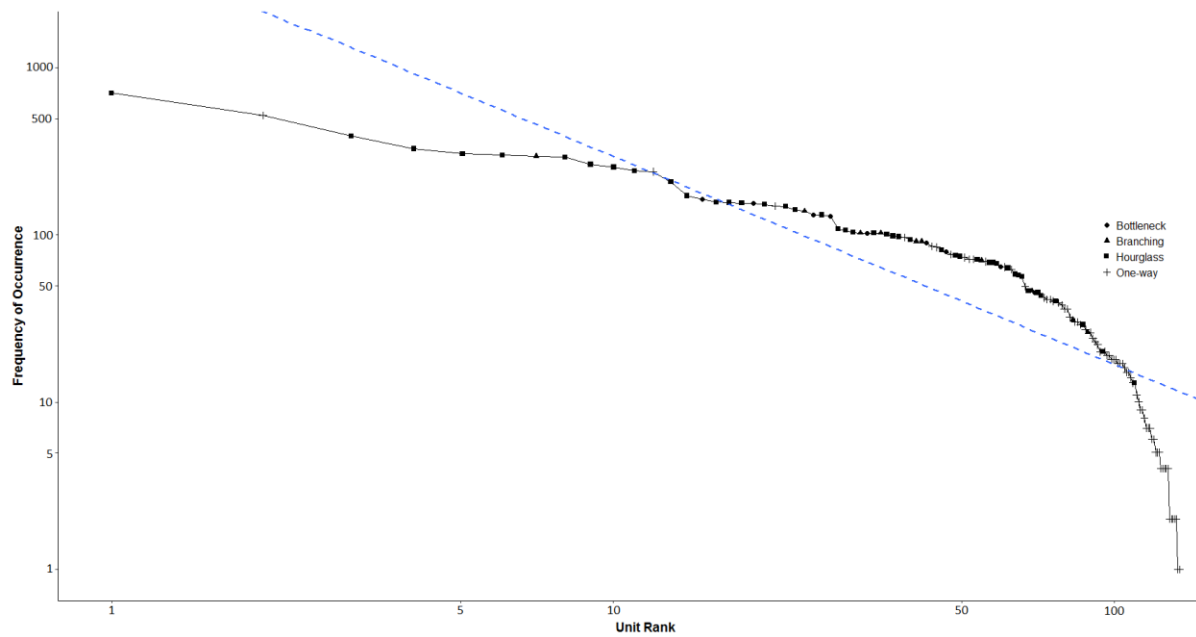
504



505

506 **Figure 3** Small-world coefficient (S) values. S-values are shown for each year (average
507 $S=3.01$) based on all of the song cycles for that year ($N=12$ in 2006, $N=4$, in 2007, $N=36$ per
508 year 2002-2005 and 2008-2014; light grey bars), as well as the coefficient for all of the song
509 cycles (412 for 2002-2014) in all years combined (dark grey bar). The black line marks the
510 threshold for small-world topography ($S=1.0$).

511



512

513 **Figure 4** Unit usage distribution for all years combined. The logarithmic distribution of rank
 514 of unit use (x-axis) is modelled as a function of the frequency of occurrence (y-axis) for all
 515 units used across every song type in every year (N=412 song cycles). The dashed line
 516 represents a linear regression line of best fit. Each data point is labelled according to which
 517 transition motif (hourglass, branching, bottleneck, one-way) that unit was categorized as during
 518 analysis. Distributions for each year can be found in the Supplementary Information Figs. S1-
 519 S14.

520

521 **Table Legends**

522 **Table 1** Network features for each year and all years combined. Features include song type
 523 (whether a song resulted from incremental evolutionary (E) or rapid revolutionary (R) changes
 524 identified in Allen et al. (23)), the small-world coefficient (S), average path length (L),
 525 clustering coefficient (C), number of network communities (NC), unit repertoire size (Rep),
 526 slope of unit usage (Slope), percentage of deterministic motifs (DM), and percentage of non-
 527 deterministic motifs (NDM).

528

Year	Type	S	L	C	Rep	NC	Slope	DM	NDM
2002	E	3.3	2.4	0.5	39	5	-2.2	70%	30%
2003	R	1.7	2.1	0.4	28	5	-2.2	57%	43%
2004	E	4.2	2.2	0.6	57	7	-1.9	63%	37%
2005	E	3.8	2.4	0.6	56	5	-2.1	55%	45%
2006	R	2.2	2.1	0.5	40	5	-1.6	50%	50%
2007	R	1.2	2.3	0.3	21	5	-1.1	62%	38%
2008	E	2.4	2.1	0.4	55	4	-2.1	58%	42%
2009	R	2.6	1.8	0.7	44	5	-2.1	57%	43%
2010	E	3.1	2.2	0.6	65	5	-1.9	57%	43%
2011	R	3.6	2.2	0.6	67	3	-1.9	61%	39%
2012	E	3.2	2.1	0.6	73	4	-1.8	53%	47%
2013	R	5.1	2.0	0.7	48	4	-2.2	71%	29%
2014	R	2.5	2.0	0.5	41	4	-2.1	54%	46%
All Years	N/A	2.6	1.9	0.6	142	12	-1.5	56%	44%

529

530 **Table 2** Network features in seven bird song displays compared with humpback whale song
531 (current study, averaged over all 13 study years). S = small-world coefficients are given, as
532 well as each of the four transition motifs (one-way, hourglass, bottleneck, branch). All
533 transitions are presented as percentages of the total number of transitions found in those
534 displays. ¹Taylor and Cody, 2015; ²Cody *et al.*, 2016; ³Weiss *et al.*, 2014.

Species	S	Deterministic		Non-Deterministic	
		One-way	Bottlenecks	Hourglass	Branches
Western tanager ¹	2.10	57%	0%	43%	0%
Cassin's vireo ¹	4.70	38%	21%	26%	15%
Black-headed grosbeak ¹	2.70	34%	18%	25%	23%
Redthroat ¹	4.10	55%	7%	32%	5%
Sage thrasher ¹	2.86	62%	10%	20%	9%
California thrasher ¹	2.60	51%	3%	27%	19%
California thrasher ²	1.69	50%	7%	32%	11%
Nightingale ³	4.29	35%	15%	35%	14%
Humpback whale	3.00	51%	8%	30%	11%

535