1   Cultural transmission in humpback whales: insights from song hybridization events

2   during revolutionary song change

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14   Classification: Biological sciences, Ecology

15   Short title: Hybridization in humpback whale songs

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26 **Abstract**

27 Cultural processes occur in a wide variety of animal taxa from insects to cetaceans.

28 The songs of humpback whales are one of the most striking examples of the

29 transmission of a cultural trait and social learning in any non-human animal. To

30 understand how songs are learnt, we investigate rare cases of song hybridization,

31 where parts of an existing song are spliced with a new one, likely prior to an

32 individual totally adopting the new song. Song unit sequences were extracted from

33 over 9,300 phrases recorded during two song revolutions across the South Pacific

34 Ocean, allowing fine-scale analysis of composition and sequencing. In hybrid songs

35 the current and new songs were spliced together in two specific ways: 1) singers

36 placed a single hybrid phrase, in which content from both songs were combined,

37 between the two song types when transitioning from one to the other, and/or 2)

38 singers spliced complete themes from the revolutionary song into the current song.

39 Sequence analysis indicated that both processes were governed by structural

40 similarity rules. Hybrid phrases or theme substitutions occurred at points in the songs

41 where both songs contained 'similar sounds arranged in a similar pattern'. Songs

42 appear to be learnt as segments (themes/phrase types), akin to birdsong and human

43 language acquisition, and these can be combined in predictable ways if the underlying

44 structural pattern is similar. These snapshots of song change provide new insights into

45 the mechanisms underlying song learning in humpback whales, and comparative

46 perspectives on the evolution of human language and culture.

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51   **Significance Statement**

52   Cetaceans show some of the most sophisticated and complex vocal and cultural

53   behavior outside of humans. Our shared mammalian heritage makes them profoundly

54   relevant in any comparative framework. Humpback whales sing a culturally evolving

55   song display; it is also one of the most striking examples of the transmission of a

56   cultural trait and social learning in any non-human animal. Here, by investigating the

57   rare cases of song hybridization, where parts of an existing song are spliced with a

58   novel, revolutionary song, we unearth a number of underlying structural rules

59   governing song change. These rules likely assist humpback whales in rapidly learning

60   their complex and ever-changing songs, and provide insights into the evolution of

61   human language and culture.

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64   **Introduction**

65   Cultural transmission has been shown in a wide variety of taxa spanning birds, fish,

66   insects, cetaceans and non-human primates (1, 2). We define culture in the broad

67   sense as shared information or behavior acquired through some form of social

68   learning from conspecifics (3–5). Each of these studies has provided examples

69   demonstrating a behavioral trait being passed from one individual to another, and on

70   occasion entire populations, through some form of social learning. Cetaceans show

71   some of the most sophisticated and complex vocal and cultural behavior outside of

72   humans (6, 7), including vocal learning, shared traditions and gene-culture

73   coevolution. For example, southern right whales (*Eubalaena australis*) demonstrate

74   strong migratory culture (8), while bottlenose dolphins (*Tursiops truncatus* and *T.*

75   *aduncus*) demonstrate the cultural transmission of tool-use (9, 10). Both sperm whales

76 (*Physeter macrocephalus*) and killer whales (*Orcinus orca*) have culturally

77 transmitted group vocalizations that are maintained over decades (11, 12), and also

78 appear to undergo gene-culture coevolution (13–15).

79 Humpback whales (*Megaptera novaeangliae*) possess multiple, independently

80 evolving cultural traditions including maternally directed site fidelity to breeding and

81 feeding grounds (16), socially learned feeding tactics (17), and song displays that are

82 subject to cultural evolution and revolution (18–20). Humpback whale song is one of

83 the most elaborate acoustic displays in the animal kingdom (21). The song is

84 produced solely by adult males (22) and is therefore considered a product of sexual

85 selection, even though the details of how it functions as a signal are still debated (23).

86 Song is organized in a nested hierarchy: single sounds are termed 'units', a

87 sequence of units is grouped into a 'phrase', phrases are repeated to form a 'theme',

88 and a number of different themes are usually sung in a set order to form the 'song'

89 (24). To move from one theme into another, a single 'transitional phrase' is

90 sometimes sung that contains content from the preceding and following themes (20).

91 Different versions of the display (containing different themes) are termed 'song types'

92 (18). Within each population, there is usually strong conformity to a single song type

93 at any point in time (25). However, the song is constantly changing (20), and all

94 males must continuously incorporate these alterations to maintain the observed

95 conformity. This slow and gradual change is a process of cultural evolution in which

96 subtle changes occur over time at a population scale (20, 26).

97 Populations within an ocean basin sing similar songs, but the similarity

98 depends on both geographic (27, 28) and temporal distances, as transmission of song

99 changes across a region may take several years (18, 29, 30). In the western and central

100 South Pacific region, song also undergoes dramatic cultural 'revolutions', where the

101   song type from a neighbouring population is rapidly adopted by all of the males in an

102   adjacent population (18, 19). We have previously described the rapid, repeated and

103   regular horizontal cultural transmission of multiple song types creating multiple song

104   revolutions across the western and central South Pacific region (18, 29, 30). Among

105   populations in any non-human animal, this is a very rare, possibly unique, example of

106   population-wide horizontal cultural transmission where behavioural variants are

107   transmitted rapidly and repeatedly (18). However, we know little regarding the

108   underlying vocal and sequence learning mechanisms governing this extraordinary

109   cultural phenomenon.

110   Mechanisms of vocal learning are far better understood for human language

111   acquisition and birdsong than for cetacean vocalizations (7). Humpback whales are

112   'vocal production learners' as they are able to modify the form of their own vocal

113   signals after experience with signals from other individuals (7). Vocal production

114   learning is not widespread; thus far only a few mammalian groups including

115   cetaceans, pinnipeds, bats, elephants and humans have been shown to be capable of it

116   (7). An important limitation when studying large cetacean species is the inability to

117   conduct controlled laboratory experiments. While learning and song production can

118   be mapped to different pathways in the brain for songbirds, mice and humans (to

119   name a few (31)), this is not yet possible with large, free-roaming cetaceans. However,

120   we can explore the learning mechanisms involved by examining the structure and

121   arrangement of the song displays in detail, and comparing any rules we uncover

122   governing the arrangement and learning of song to those currently known in human

123   language acquisition and birdsong learning.

124   Statistical learning, where patterns and structure are identified based on the

125   statistical information present in sensory stimuli, is a common human learning

126 mechanism present in all sensory modalities (32). From a very young age human

127 infants are able to detect, extract and generalize statistical regularities (*i.e.,* simple

128 algebraic rules) from their auditory environment (32, 33), and understanding how they

129 use this statistical information to learn language is a major research focus (32). The

130 ability to detect transition probabilities, the probability that a given sound or syllable

131 follows another one (32, 33), is important in understanding word segmentation or

132 grammar learning tasks. From a comparative perspective, recent work has

133 demonstrated that zebra finches (*Taeniopygia guttata*) generate phonological

134 categories that result in the song being easier for others to learn (34). Understanding

135 how humpback whales learn their extended song sequences is therefore of interest in

136 the comparative study of mechanisms for learning sequences and patterns in cultural

137 vocal signals.

138   Segmentation, the chunking of sequences into smaller components (phrases or

139 words) that can later be recombined, is another important mechanism in human

140 language acquisition (32, 33, 35, 36). Songbirds have been shown to segment when

141 learning their song displays (37–40). Segments are typically separated by longer

142 pauses (silence), and these pauses may provide an emphasis that aids in memorization

143 of segment chunks (39). In a recent review of human language and non-human animal

144 communication, Birchenall (33) suggests that the process of segmentation may also

145 be present in humpback whale song learning. Given the importance of segmentation

146 to language acquisition and the presence of this mechanism in the learning of

147 birdsong, this is a logical starting place to study humpback whale song learning.

148   Here, we present evidence that humpback whales use segmentation in song

149 learning by examining recordings made during the process of learning a new song in

150 the context of a song revolution event. Recording a whale in the act of changing his

151 song is challenging; they are highly mobile and one cannot simply record all of an

152 individual's song during a two to three month singing season and >6,000 km

153 migration. We therefore investigate some rare cases of song hybridization recorded

154 during song revolution events to understand how individual whales transition between

155 two different songs. These hybrid songs, which contain themes and elements from

156 both the previous song and the new, revolutionary song, presumably represent a

157 transition phase in the process by which singers change their song display to a new,

158 completely different arrangement. We aim to identify if there are any underlying

159 structural rules governing song change (*e.g.,* segmentation, transition probabilities)

160 that can provide insight into how new songs can be learned so rapidly. We

161 hypothesize that new songs will be learned as segments if segmentation is a taxon-

162 general mechanism (hypothesis 1). Identifying the level in the song hierarchy (phrase,

163 theme or song) that comprises a segment will provide important information as to

164 how the song is memorized. Alternatively, parts of both song types may be spliced

165 together in a random arrangement of new and old units. This would indicate that the

166 structural arrangement of an individual's song disintegrates to a babbling/subsong

167 phase (41) before learning the new song arrangement, and that segmentation is not

168 occurring. Additionally, we hypothesize that if segmentation occurs, then the

169 combination of these segments from both song types by an individual will not be

170 random (hypothesis 2). That is, the insertion of new song segments into the existing

171 song will be at locations in the existing song where there is some structural similarity

172 in the sound units, phrases or themes of the old and new songs, rather than at random

173 positions. This 'similar sounds in similar arrangements' mechanism would be akin to

174 word substitutions in humans such as malapropisms, where an incorrect word with a

175 similar sound is used in place of the correct word (42). To test these hypotheses, we

176   first investigated how each singer displaying a hybrid song transitioned between song

177   types, and secondly we quantified the similarity in arrangement between the themes

178   from each song using sequence analysis metrics. We analyzed four hybrid songs

179   recorded during two different song revolutions from two geographic locations

180   (eastern Australia and French Polynesia). Thus far, these are the only examples of

181   hybrid songs[*] in over 20 years of fieldwork from five populations where song

182   revolutions are known to occur regularly, and from which approximately 1,500 song

183   sequences representing at least 100,000 phrases have been analyzed.

184

185   **Results**

186   Three separate datasets were included in the analysis as each contained one or more

187   hybrid songs. These spanned two geographic locations: Peregian Beach, eastern

188   Australia (1996-97 and 2002-03), and Mo'orea, French Polynesia (2005); and two

189   song revolutions: from Pink to Black (Australia 1996-97), the 'original' song

190   revolution (19), and from Blue to Dark Red (which occurred in Australia in 2002-03,

191   and French Polynesia in 2005 (20)). Over 46 hours of song from 50 singers and four

192   song types (each given an arbitrary color label – Blue, Dark Red, Pink and Black, to

193   be consistent with published analyses of these song types) were analyzed from French

194   Polynesia (2005: 18 singers, 1 hybrid) and eastern Australia (1996-97: 2 singers each

195   based on the highest quality singer for each song type from 249 singers presented in

196   (19), 2 hybrids; and 2002-03: 26 singers, 1 hybrid).

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[*]A fifth hybrid song has been identified. This recording is of a very poor quality (low signal-to-noise ratio). Themes can be sporadically identified but the clear transitions between themes required for the current analysis is lacking. We therefore excluded this recording from analysis. The recording was from eastern Australia in 1997 as part of the Pink-Black song revolution presented in (19).

197   To identify if new songs were learned as segments (hypothesis 1), we first

198   needed to classify each potential segment. As there are multiple levels in the

199   humpback song hierarchy, each being a potential basis for segmentation, we analyzed

200   each level. First, individual sounds were classified into categories (*i.e.,* unit types;

201   Tables S1-S2, SI Methods). Then the stereotyped sequences of units that made

202   phrases were established and further grouped into themes (see SI Methods and Table

203   S1). Themes from each song type were labeled 1 through 37 (Table 1; also see SI

204   Methods and Table S1) following previous classification of these song types (18, 19,

205   29, 43, 44). The song type of origin (Pink or Black) for theme 11 was uncertain and

206   thus remained unresolved, as it was not heard in any non-hybrid songs (Fig. 1, Table

207   1 and Table S1). The sequence of themes for each hybrid singer was established

208   (Table 1). It is immediately obvious that the hybrid songs examined here comprised

209   complete themes from the two different song types combined into a single song –

210   segmentation occurred at the theme level.

211   Given that hybrid songs contained theme segments from each song type, we

212   investigated if there were any patterns to the arrangement of themes (hypothesis 2).

213   To do this we a) established the location of hybrid transitions in the song, b)

214   investigated how each singer transitioned between the song types, and c) quantified

215   the similarity of theme content using sequence analysis metrics to understand why a

216   singer might switch at that particular location in the song.

217   To understand the location of theme transitions the full sequence of themes

218   from all singers was used to construct a first-order Markov model based on the

219   frequencies of transition between phrases (Fig. 2). Transitions occurred between the

220   Pink and Black song types at multiple locations in the song (Fig. 2*A* and Table 1) but,

221   in contrast, transitions between the Blue and Dark Red song types occurred only at

222   two locations in the song (Fig. 1 and Fig. 2*B*). At these transition locations, singers

223   often placed a transitional phrase between the two song types to mediate the transition

224   (Tables 1-2). This single phrase combined the starting units from the preceding phrase

225   with units from the following phrase (typically the ending units; Fig. 1, Table 2 and

226   S1).

227   We characterized the structural similarity, that is the similarity in the sequence

228   of units that comprised each theme/phrase type (laid out in Table S1), between each

229   pair of songs (*e.g.,* Blue *vs.* Dark Red) using the Levenshtein distance, a common

230   similarity metric in linguistic and humpback song comparisons (29, 43, 45, 46). In

231   songs from the 2005 French Polynesia Blue-Dark Red revolution, hierarchical

232   clustering of themes showed a single location on the dendrogram where themes from

233   both song types grouped together on a branch (Fig. 3*A*). This was where the singer of

234   the hybrid song in the French Polynesian dataset switched between song types (Fig. 2

235   and Tables 1-2). In songs from the eastern Australia 2002 revolution involving the

236   same song types, this pattern was not as clear since theme transitions did not occur at

237   the most similar themes (Fig. 3*B*). Instead, theme transitions were mediated by a

238   transitional phrase (Tables 1-2). Finally, in songs from the 1996 eastern Australia

239   Pink-Black revolution, the dendrogram showed a single location where themes from

240   both song types grouped together on a branch (Fig. 3*C* and SI Results). This was

241   where the majority of transitions in hybrid songs occurred between the song types

242   (Table 2). The hybrid singers replaced the next theme in the song sequence with a

243   similarly arranged theme from the other song type (Fig. 1 and Table 2). The

244   remaining theme transitions were either mediated by a transitional phrase or the

245   mechanism of transition between the song types was unclear (Tables 1-2). Regardless,

246   in addition to transitional phrases this final analysis strongly indicates that transitions

247 between song types are not random and occur more often at locations where theme

248 content is most similar.

249

250 **Discussion**

251 Hybrid songs are recorded extremely rarely but are of interest because they capture

252 some part of the process by which singers change their song display from an older

253 version (type) to a new, completely different arrangement. The hybrid songs

254 presented here were all captured during song revolution events, when singers using

255 both the old and new song types were in the same population. It is clear that new

256 songs are learnt as segments, confirming hypothesis 1 (see also (33)), indicating that

257 segmentation is a learning mechanism found in the cetacean lineage. The way singers

258 move between song types during singing bouts suggests that these displays are

259 unlikely to be learnt as a whole. Instead, songs are split into theme segments, and the

260 fact that transitions between song types occur at specific points in the theme sequence

261 suggests that each theme is learnt as a separate entity. Segmentation or chunking of

262 sequences is an important mechanism in human language acquisition (35), where a

263 stream of utterances is segmented into smaller components (phrases or words) and

264 later recombined (36). Songbirds have also been shown to segment their song displays

265 (37–40) and statistically learn sound categories (34). Juvenile male songbirds may

266 learn their song from one or more tutors as a sequence of syllable segments, which

267 they recombine to form their own song (37–40). In humpback whales, our results

268 suggest that a male learns the new song as theme segments which he combines with

269 older themes as he progressively learns the new song. The novelty-threshold

270 hypothesis suggests that novelties in the song are adopted by singers once reaching a

271 threshold prevalence (47), and therefore an individual male would need to hear a new

272   song from multiple individuals before adopting the change. He therefore has multiple

273   potential models for each theme and a general overview of the 'correct' sequence of

274   the themes. The highly stereotyped nature of theme and phrase sequences, both of

275   which we quantified as transition probabilities (*e.g.,* Fig. 2 and also by (48)), strongly

276   suggests humpback whales, like songbirds, use statistical learning in learning their

277   song display (34).

278   In songbirds, segments are typically separated by longer pauses (silence), and

279   these pauses may provide an emphasis that aids in memorization of segment chunks

280   (39). This feature of pauses between segments of zebra finch song is also a feature of

281   humpback whale song as a phrase is delineated from the start of another phrase by a

282   longer pause (24, 49). Given that a single humpback whale song can last anywhere

283   from five to 30 minutes (24), any aid in memorization of such a long display would be

284   under strong selection. The repetition of phrases within themes introduces redundancy

285   in the song, and likely aids memorization through repetition and reduced content.

286   Further, rhyme-like patterns in humpback song (50) appear similar to rhyme patterns

287   in human poems or prose, which also aid recall (51). The question of how humpback

288   whales remember their song display (they rarely sing the wrong thing) is still open.

289   From playback studies we know humpback whales react more strongly to novel songs

290   than to the song of the current year (see (52)). They can identify 'same' from

291   'different'. It would be interesting to explore how long their song memory lasts, as

292   bottlenose dolphins have been shown to remember vocalizations (signature whistles

293   of conspecifics) for over 20 years (53). Such a song memory could drive the

294   directional change in song revolutions (to stop whales reverting back to the previous

295   song type), leading to the broad-scale cultural phenomenon we observe (18).

296   Hybrid songs from both song revolutions contained themes from one song

297   type that were spliced into the middle of the other song type (Table 1). There are

298   multiple examples of such hybrid song production in songbirds at the boundary of two

299   song dialect areas or the boundary between two closely related species (41). For

300   example, orange-tufted sunbirds (*Nectarinia osea*) have sharp dialect boundaries but a

301   small number of birds along these boundaries sing songs from both dialects (*i.e.,*

302   hybrids) (54). Similarly, in the village indigobird (*Vidua chalybeata*), a species that

303   undergoes continuous population-wide song evolution in some ways similar to

304   humpback whale songs, males along dialect boundaries have been recorded singing

305   hybrid songs that combined songs from each dialect (55). In yellow-rumped caciques

306   (*Cacicus cela vitellinus*), another species with continuous population-wide song

307   evolution, males in a colony may occasionally incorporate a foreign song type as part

308   of their yearly population dialect if the two colonies are closely situated (56). In

309   another example, at the range interface of black-capped chickadees (*Poecile*

310   *atricapillus*) and Carolina chickadees (*P. carolinensis*), birds from both species

311   displayed bilingual or atypical repertoires (57). Clearly segmentation is an important

312   general mechanism in vocal learning present in multiple independent lineages.

313   Transitions between humpback whale song types were often mediated by a

314   transitional phrase containing individual sound units from the previous and following

315   phrases that were common to both song types (Tables 1-2 and Figs. 1-2). Transitional

316   phrases are a neglected component of the song in general as they are often excluded

317   from analyses focused on delineating song types (49). The variable structure of

318   transitional phrases can make them difficult to categorize, particularly if they are not

319   routinely used in all transitions between themes. Nevertheless, it is clear this normal

320   component of song organization is important to allow an ordered progression from

321   one theme into another, regardless of the song types.

322   Transitions between song types were partially governed by structural

323   similarity, based on the Markov model and sequence analysis (Figs. 2-3), rejecting

324   random combinations of segments (hypothesis 2). The sequence analysis indicated

325   that transitions or theme substitutions occurred more often in locations that contained

326   'similar sounds arranged in a similar pattern' in old and new songs (Fig. 3). Themes

327   either progressed into a similarly sounding theme of the other song type or replaced

328   that similarly sounding theme altogether (Table 2). In addition to segmenting, song

329   learning and change are partially governed by structural similarity rules where

330   transitions or theme substitutions occur in locations that contain similar sounds

331   arranged in a similar pattern (*i.e.,* a 'switch when similar' rule). Word substitutions in

332   humans such as malapropisms, the use of an incorrect word in place of a word with a

333   similar sound (42), is highly suggestive for a general mechanism. These transition

334   points based on similarity could act as a point of reference or cue allowing the singer

335   to switch from the old into the new song at this position in the song. Such anchors are

336   present in human vocal performances (*e.g.,* oral traditions (51)), and single sounds or

337   words and similar note arrangements are used to transition among songs in human

338   music performances. Finally, the ability to jump from one song into another is also a

339   feature of birdsong, for example, counter-singing allows a male to select a matching

340   song of a rival male and switch to singing that song in an aggressive context (41).

341   This strongly suggests the presence of an underlying mechanism allowing plasticity in

342   vocal output shared among vocal learning species.

343   We suggest the 'switch when similar' rule may be stronger and thus more

344   important in one direction (*i.e.,* old to new themes; Table 2) assisting singers in

345   learning new themes sequentially and in the 'correct' order. The whale is attempting

346   to learn the new display; this is very directional. The location in the song where 'old'

347   themes encroach back into the song display may be less important and is unlikely to

348   be governed by this similarity rule (explaining the majority of un-similar transitions

349   backwards). These new to old song transitions appear to be mediated more often by

350   transitional phrases (Table 2).

351   The process of vocal production learning (7) of a completely new song type

352   could occur through a number of structural changes to the song as new themes must

353   be learnt and old themes removed. Multiple studies indicate that male humpback

354   whales adhere to the current arrangement of the song (*e.g.,* (20, 25)). Importantly,

355   once a new song is recorded in a population, all males switch to this new song (18,

356   19). Clearly, the song is learnt as theme segments to aid in the learning of this

357   complex display. In male village indigobirds immigrant males add song types from

358   their new dialect and then drop their 'old', foreign song types within a year (55). We

359   suggest humpback whales may undertake a similar process by adding in new themes

360   starting at 'similar locations' and then progressively deleting the old themes. Intense

361   cultural conformity is likely influencing these vocal displays, which are in turn also

362   driven by sexual selection. The presence of an innate template likely governs the

363   underlying processes and rules of song learning (58), overlaid with a more flexible

364   cultural component that governs what variant of the song display to sing, regardless of

365   the species. The details of how songs change when there is a general conformity to a

366   population song, and how this process interacts with sexual selection which underlies

367   the humpback song display, are important questions for future research.

368

369   **Conclusions.** Humpback whales provide a unique perspective for understanding of

370   animal culture. Their mammalian heritage also makes them particularly important to

371   our understanding of structurally-arranged vocal communication and the potential

372   origins of human language. Here, by investigating rare cases of song hybridization,

373   where parts of an existing song are spliced with a novel, revolutionary song, we have

374   unearthed a number of underlying structural rules governing song change including

375   segmentation and transition/substitution of themes based on the similarity in sound

376   sequences. These rules likely assist humpback whales in rapidly learning their

377   complex and ever-changing songs, and provide insights into the evolution of human

378   language and culture.

379

380   **Methods**

381   **Song recordings.** All recordings covered the frequency range of humpback whale

382   song (see SI Methods for detailed recording settings). The units in each recording

383   were transcribed by a human classifier (ECG or LL), and a subset of units measured

384   for a suite of acoustic parameters to ensure consistent naming (45). As humpback

385   whale song is highly stereotyped (24), units were grouped into phrases, phrases into

386   themes, and themes into song types. Previous studies have identified and quantified

387   these four song types (Pink, Black, Blue and Dark Red), the themes (labeled 1-37)

388   and unit types within each, and their cultural transmission across the western and

389   central South Pacific (18, 19, 29, 43, 59).

390

391   **Theme transitions to understand song sequences.** For each recording, the

392   sequences of themes, including phrase repetitions, transitional phrases and hybrid

393   phrases, were noted. Transition tables were calculated and a first-order Markov model

394   of phrase transition probabilities was constructed for each song revolution using these

395   data: Pink to Black, and Blue to Dark Red. The 2002-03 eastern Australian and 2005

396   French Polynesian data were combined given they represented the same song types

397   (18, 29), and the aim of this higher-level analysis was to identify position(s) within a

398   song where a singer may transition between two song types.

399

400   **Structural similarity of themes.** The Levenshtein distance (LD) or string edit

401   distance is a powerful metric for comparing humpback whale song sequences, which

402   we and others have used extensively to understand song similarity at all levels within

403   the song hierarchy (29, 43, 45, 46, 59–61). The LD similarity index produces a

404   measure of similarity (between 0 and 1) among multiple sequences of varying lengths,

405   and provides an overall understanding of the similarity of all sequences (see (45)).

406   Here, we compared the sequence of units (*i.e.,* a phrase) to establish the most

407   representative phrase for each theme based on the similarity in the sequence of units

408   (see SI Methods for further information and Table S1 (29, 43, 45, 46)). These

409   representative phrases for each theme (laid out in Table S1) were then compared

410   between the two song types (Pink *vs.* Black, or Blue *vs.* Dark Red) to quantify the

411   structural similarity among themes in an attempt to identify any underlying structural

412   rules for the transitions highlighted in the Markov models. Similarity scores were

413   hierarchically clustered and bootstrapped in R using the *hclust*, *pvclust* and *pvrect*

414   packages to ensure the resulting structure was stable and likely to occur (43, 45, 62).

415   Branches with high bootstrap values (AU significance p>95% and BP significance

416   p>70%) are strongly supported by the data while lower values suggest variability in

417   their division (45). As a further test of how well each dendrogram represented the data,

418   the Cophenetic Correlation Coefficient (CCC) was also calculated. A CCC score of

419   over 0.8 is considered a good representation of the associations within the data (63).

420

438

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605

606 **Figure Legends**

607 **Fig. 1.** Example spectrograms of hybrid transitional phrases, corresponding parent

608 themes and substituted themes from the Blue and Dark Red song types (top panels),

609 and the Pink and Black song types (bottom panels). The top panel shows the theme

610 progression (from left to right) of the transition from Blue theme 24, through the

611 hybrid 24/37*a* phrase into Dark Red theme 37*a* and then theme 37*b* (singer HYB1;

612 Table 1). Panel 2 shows the theme progression from Dark Red theme 31*a* to Blue

613 theme 27 mediated by hybrid transition phrases 27/31*a* and 31*a*/27 (note the

614 difference in arrangement depending on the direction of transition (singer HYB2)).

615 Panel 3 shows the theme progression (left to right) from Pink theme 1, through hybrid

616 phrase 1/7*a* into Black theme 7*a* (singers HYB3 and HYB4; Table 1), and the

617 substituted Pink theme 2. The bottom panel shows the theme progression (left to

618   right) from Black theme 9*b*, through hybrid phrase 9*b*/4 into Pink theme 4 (singers

619   HYB3 and HYB4; Table 1). It also shows Pink theme 3 and the unresolved theme 11.

620   Spectrograms were 2048 point fast Fourier transform (FFT), Hanning window and

621   75% overlap, generated in RAVEN PRO 1.4. (Corresponding audio files are provided

622   online).

623

624   **Fig. 2.** First-order Markov model of theme transitions to understand hybridization

625   between (*A*) Pink-Black song types (N=2,222 phrase transitions, N=4 individuals),

626   and (*B*) Blue-Dark Red song types (N=8,852 phrase transitions, N=46 individuals).

627   Each node represents a theme or 'phrase type', color-coded by song type. White

628   nodes represent transitional phrases and dashed lines indicate transitions between

629   song types. Arrows represent the direction of movement and thicker lines indicate

630   higher transition probabilities. Transitions between the Pink and Black song types (*A*)

631   occurred at multiple locations (theme 1 to 7*b*, 9*b* to 4, 10*a* to 1, 4 to 10*a*, 10*a* to 5*b*, 8*b*

632   to 4, and 8*a* to 5*b*). In contrast, transitions between the Blue and Dark Red song types

633   (*B*) occurred only at two specific locations in the song: Blue theme 27 - Dark Red

634   theme 31*a* (both directions), and Blue theme 24 - Dark Red theme 37*a* (one-way).

635   Phrase repetitions are removed from the figure for ease of display.

636

637   **Fig. 3.** Dendrogram of bootstrapped (1000) similarity matrices of average-linkage

638   hierarchical clustered median unit sequences for each theme for (*A*) French Polynesia

639   2005 Blue and Dark Red song types (Cophenetic Correlation Coefficient = 0.93), (*B*)

640   eastern Australia 2002-2003 Blue and Dark Red song types (Cophenetic Correlation

641   Coefficient = 0.88), and (*C*) eastern Australia 1996-1997 Pink and Black song types

642   (Cophenetic Correlation Coefficient = 0.95). Multi-scale bootstrap resampling (AU,

643   left, red dot indicates p > 95%) and normal bootstrap probabilities (BP, right, green

644   dot indicates p > 70%) are displayed. Branches with high AU values are strongly

645   supported by the data. Dashed boxes indicate where themes from different song types

646   appear together on a branch.