

1 Individual vocal signatures show reduced complexity following invasion

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18 **Abstract:** The manner in which vocal learning is used for social recognition may be sensitive
19 to the social environment. Biological invaders capable of vocal learning are useful for testing
20 this possibility, as invasion alters population size. If vocal learning is used for individual
21 recognition, then individual identity should be encoded in frequency modulation patterns of
22 acoustic signals. Furthermore, frequency modulation patterns should be more complex in
23 larger social groups, reflecting greater selection for individual distinctiveness. We compared
24 social group sizes and used supervised machine learning and frequency contours to compare
25 contact call structure between native range monk parakeets (*Myiopsitta monachus*) in
26 Uruguay and invasive range populations in the U.S. Invasive range sites exhibited fewer
27 nests and simpler frequency modulation patterns. Beecher's statistic revealed reduced
28 individual identity content and fewer possible unique individual signatures in invasive range
29 calls. Lower estimated social densities and simpler individual signatures are consistent with
30 relaxed selection on the complexity of calls learned for individual recognition in smaller social
31 groups. These findings run counter to the traditional view that vocal learning is used for
32 imitation, and suggest that vocal learning can be employed to produce individual vocal
33 signatures in a manner sensitive to local population size.

34

35 **Introduction:** One way in which vocal learning can be used is to signal group identity for
36 social recognition [1–3]. Patterns of acoustic convergence within social groups, consistent
37 with vocal learning being employed for group recognition, have been identified in cetaceans,
38 bats, songbirds, and parrots [3]. Vocal learning may also be used to create individually
39 distinctive acoustic signals, often termed “individual signatures”, as found in many of the
40 same taxonomic groups [1,4–6]. The manner in which different taxa use vocal learning to
41 recognize group members could be sensitive to population size and social dynamics.

42 In larger populations, greater social density results in more individuals for potential
43 receivers to discriminate, leading to increased uncertainty about signalers’ identities, and
44 increased selection on signalers to produce distinctive individual signatures [7]. In species
45 that employ vocal learning for individual vocal recognition, such selection to produce
46 individually distinctive signals should manifest in the acoustic structure of learned calls. For
47 instance, learning can be employed to produce individually distinctive frequency modulation
48 patterns in acoustic signals [4–6,8]. In such systems, frequency modulation patterns in
49 learned signals should be more complex in larger social groups, and simpler in smaller social
50 groups, leading to fewer potential unique individual signatures [9]. Biological invaders offer
51 useful models for addressing these ideas, as invasive populations often exhibit reduced
52 population sizes compared to the native range [10].

53 We asked whether the way in which vocal learning is employed for social recognition is
54 resilient or sensitive to changes in population size by evaluating contact calls of an invasive
55 parrot. Monk parakeets (*Myiopsitta monachus*) are native to South America, may use vocal
56 learning for individual recognition [11], and have established invasive populations across the
57 world through the pet trade [12]. We predicted that estimated social densities would be lower

58 following invasion, and frequency modulation patterns in invasive range contact calls would
59 be simpler compared to the native range.

60

61 **Methods**

62 *Contact call recording*

63 Native range contact calls were recorded in 2017 at nest sites in Uruguay, as previously
64 described [11]. Invasive range contact calls were recorded at nest sites across five states in
65 the U.S. over different years. When possible, we estimated the numbers of nests visible at
66 recording sites (Supplementary Table 1). We obtained previously published calls recorded in
67 2004 in Connecticut, Florida, Louisiana, and Texas [13]. Calls were also recorded in Texas
68 and New Orleans in 2011, Arizona in 2018, and Texas in 2019. We repeatedly sampled
69 contact calls from 8 native and 9 invasive birds, otherwise, a single contact call was obtained
70 per unmarked bird (Supplementary Tables 2 - 4). Most recording sessions were performed
71 with Marantz PMD661 MKII and PMD660 solid state recorders, Sennheiser ME67 long
72 shotgun microphones, and digitized at 44100 Hz sampling rate and 16 bit depth. Invasive
73 range 2004 sessions employed Marantz PMD670 or PMD690 recorders with Sennheiser
74 ME67/K6 shotgun microphones, digitized at 48000 Hz and 16 bits [13]. Invasive range calls
75 were selected using Raven version 1.4 [14], and pre-processing was performed with the
76 warbleR package in R to retain high quality calls [15,16].

77

78 *Acoustic structure analyses*

79 Differences in call structure between ranges were evaluated with supervised machine
80 learning models that classified calls back to each range. Models were built with 203
81 predictors, including 15 standard acoustic measurements and 188 features (Supplementary
82 Methods 2.1.1). Spectrum-based measurements were obtained using a Hanning window,

83 window length of 398, window overlap of 90 for Fourier transformations, and a bandpass filter
84 of 0.5 to 9kHz [11]. 1561 calls were split into training, validation, and prediction datasets. 548
85 calls used for prediction (230 native, 318 invasive) were visualized in two-dimensional
86 acoustic space by applying multidimensional scaling (MDS) to the proximity matrix of the final
87 random forests model. A Gaussian kernel density estimator was applied to MDS coordinates
88 to yield density in random forests acoustic space.

89 80 calls were subsampled to evaluate frequency modulation patterns between ranges.
90 10 sites were randomly selected per range, and 4 calls randomly chosen per site.
91 Fundamental frequencies were estimated at 100 timepoints per call, and used to manually
92 trace the second harmonic with warbleR [15]. 5 points were dropped from the start and end of
93 each frequency contour, and spline interpolation performed across the remaining 90 points
94 with smoothing. Smoothed contours were used to estimate frequency peaks and troughs per
95 call. We obtained means and standard error of the number of peaks per call, modulation rate
96 (number of peaks divided by the duration of call), and the maximum slope of frequency
97 modulation per call (largest negative slope between peaks and neighboring troughs). The
98 effect size of range was calculated as Cohen's d on the 3 frequency modulation
99 measurements, as well as 15 standard acoustic measurements. Acoustic measurements with
100 the largest effects of range were also compared among invasive calls sampled over time, to
101 assess whether the patterns identified held over 15 years of sampling in the invasive range.
102 Invasive range populations that grew over time could experience greater selection for more
103 distinctive individual signatures, confounding direct comparisons between ranges.

104

105 *Individual identity content*

106 Beecher's statistic (HS) was employed to quantify the amount of individual identity content in
107 calls of repeatedly sampled individuals per range [17]. We used 5 individuals per range,

108 recorded at a single site-year in the native range (site 1145 in 2017), or a single city-year
109 (Austin, TX in 2019) in the invasive range. These individuals showed similar patterns of
110 dispersion in acoustic space (Supplementary Figure 2). HS was calculated by principal
111 components analysis on Mel-frequency cepstral coefficients (MFCC) of all calls per individual,
112 or the second harmonic frequency contours for 5 randomly sampled calls per bird (or all calls
113 if 5 or less were recorded), with 5 points dropped on either end, and without spline
114 interpolation. The number of possible unique individual signatures given the amount of
115 individual identity content per range was estimated as 2^{HS} [9,17].

116

117 **Results**

118 *Lower nest density in invasive range*

119 We observed (mean \pm standard error) 36.35 ± 12.24 nests per site for the native range, and
120 5.94 ± 1.23 for the invasive range. The maximum number of nests observed at a given site
121 was an order of magnitude greater in the native range (Supplementary Table 1), and nest
122 estimates were significantly different between ranges (Mann-Whitney difference in location
123 with 95% CI: 14 (7, 26), $Z = 4.21$, $p < 0.0001$).

124

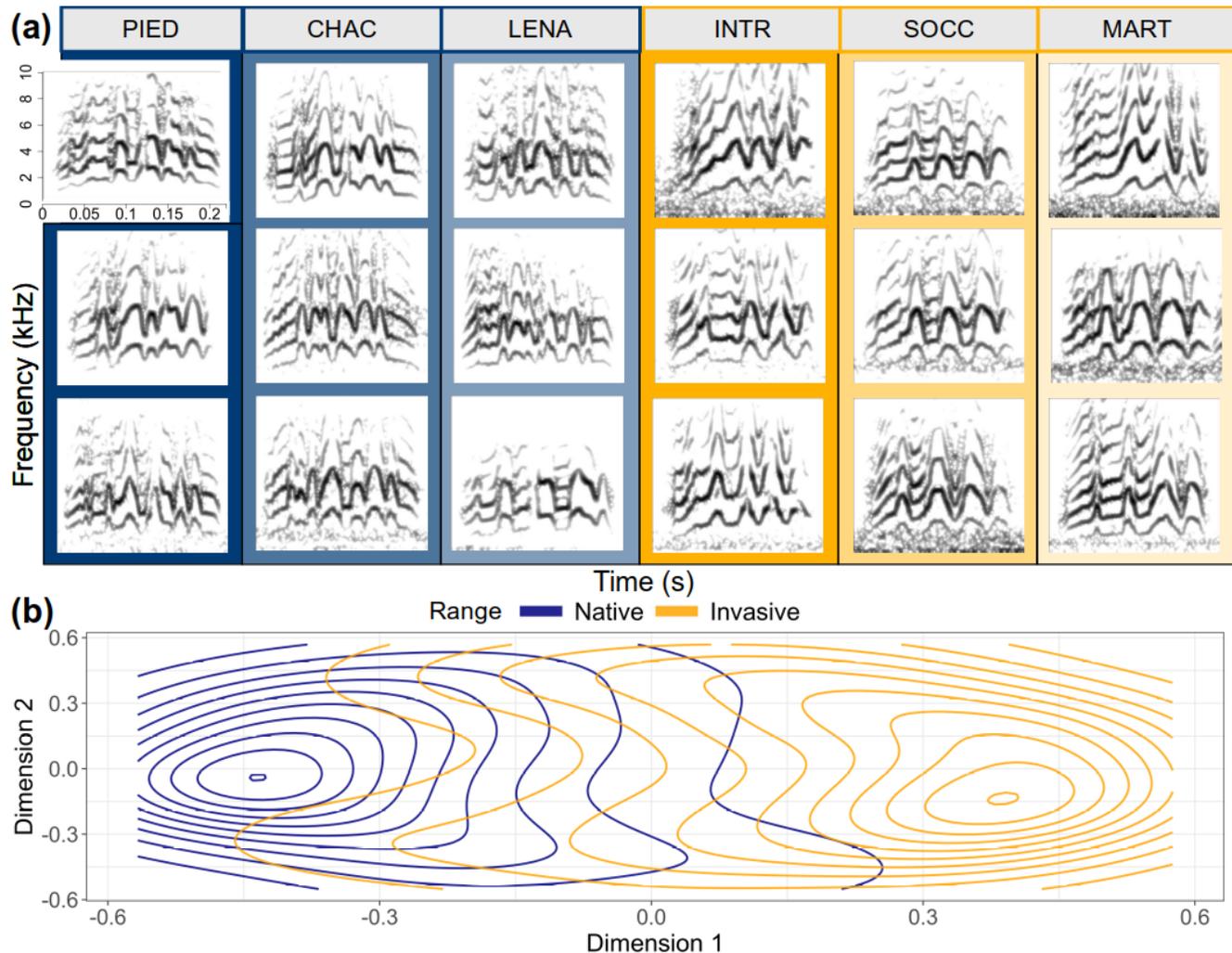
125 *Simpler frequency modulation patterns in invasive range calls*

126 Native and invasive range calls exhibited structural differences. Frequency modulation
127 patterns were visibly different between ranges (Figure 1a), consistent with high classification
128 accuracy by supervised random forests (Supplementary Table 5), and differentiation between
129 ranges in random forests acoustic space (Figure 1b). Frequency modulation patterns
130 contributed significantly to structural differences between ranges. Invasive range calls
131 exhibited fewer frequency modulation peaks, lower modulation rates, and shallower maximum
132 peak – trough slopes (Figure 2b). The effects of range on frequency modulation

133 measurements were large and significant (Supplementary Table 6), and these trends were
134 consistent over the 15 year sampling period in the invasive range (Supplementary Figure 1).

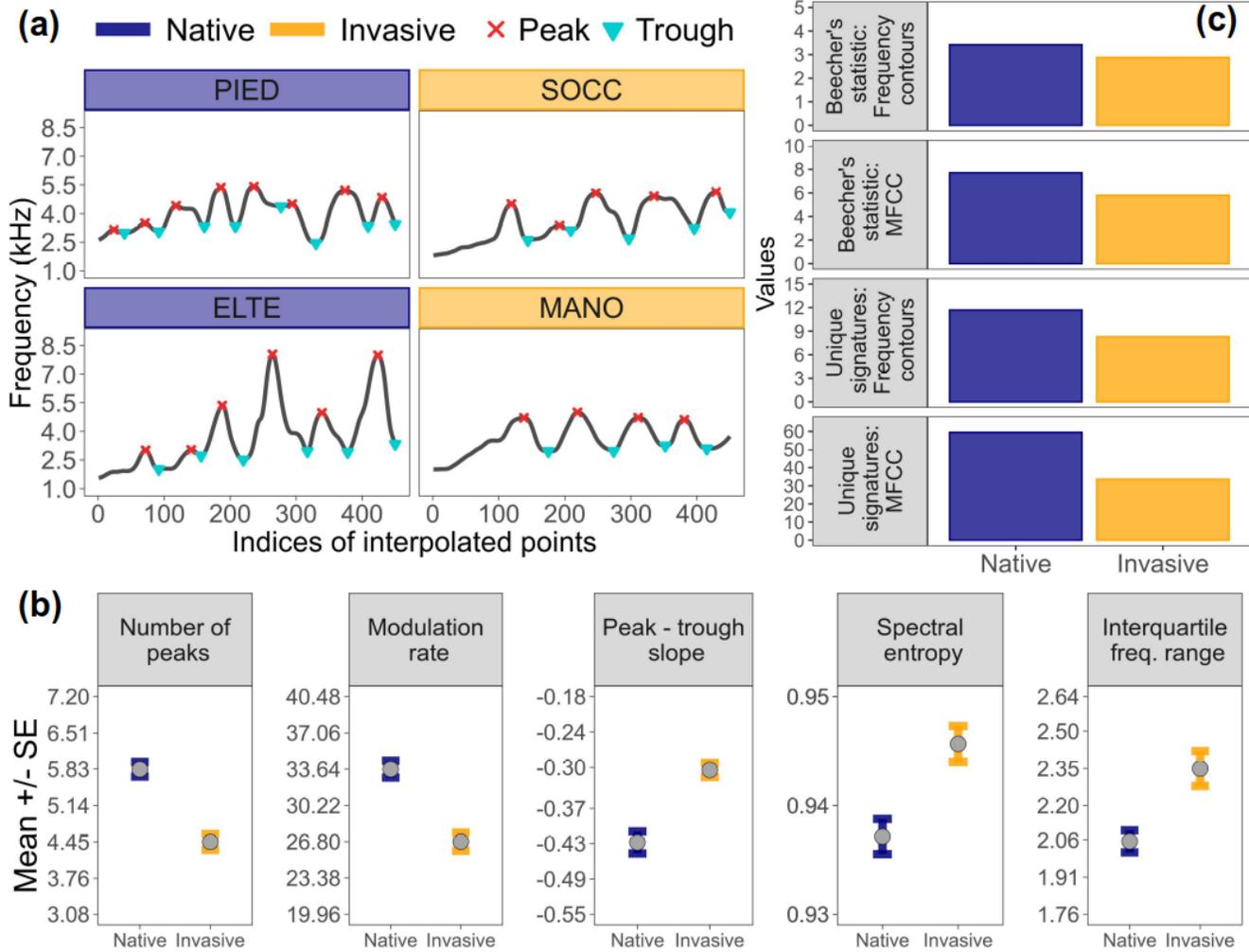
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136 Figure 1:



137 Figure 1 Legend: Differentiation in contact call structure between ranges. (a) Example lexicon
138 with spectrograms of 3 randomly selected calls from 3 sites per range, each call represents a
139 different unmarked individual. Calls were sampled over similar areas per range. Native and
140 invasive range calls shown were recorded in 2017 and 2019, respectively. (b) Estimated
141 kernel density contours in random forests acoustic space for the prediction dataset. Contours
142 delineate bins of density values, with each bin representing 1/10th of the density per range.
143 Dimension 1 coordinates were flipped to place native range contours on the left-hand side.

144 **Figure 2:**



146 **Figure 2 Legend:** Simpler frequency modulation patterns in the invasive range. (a) Smoothed
 147 second harmonic frequency contours, marked with estimated peaks and troughs. (b) Mean
 148 and standard error of acoustic measurements with the largest effects of range, in decreasing
 149 order of absolute effect size magnitude (left to right). (c) Beecher's statistic and the number of
 150 possible unique individual signatures, calculated with frequency contours as well as Mel-
 151 frequency cepstral coefficients.

152 *Less individual identity content in invasive range calls*

153 Beecher's statistic was lower for invasive range calls. This reduced individual identity content
154 yielded fewer distinctive individual signatures compared to native range calls, and trends were
155 similar between MFCC and frequency contours (Figure 2c, Supplementary Table 7). MFCC
156 includes frequency modulation patterns as well as other aspects of acoustic structure,
157 including timbre and absolute frequency, that may arise from individual differences in vocal
158 morphology.

159

160 **Discussion:** Social group sizes and contact calls of native and invasive range monk
161 parakeets were compared to ask whether the use of vocal learning for individual recognition
162 could be sensitive to changes in the social environment following invasion. We found smaller
163 social groups at invasive range sites, and frequency modulation patterns, which can be
164 altered by learning and used for individual vocal recognition [4–6,8], were significantly simpler
165 and contained less individual identity content in invasive range calls. Our results suggest that
166 monk parakeets use vocal learning for individual recognition, and that this use of vocal
167 learning for social recognition is sensitive to social changes associated with invasion.

168 Simpler frequency modulation patterns in the invasive range may be due to lower
169 social densities and hence relaxed selection for individual vocal distinctiveness. Smaller
170 invasive population sizes are a well-documented outcome of invasion [10]. Indeed, we
171 observed fewer nests at invasive range sites, indicative of reduced local social densities
172 compared to the native range. We do not know whether social dynamics are also altered
173 following invasion, but this seems plausible given reduced population sizes as well as
174 increased population isolation compared to the population contiguity observed in the native
175 range (Smith-Vidaurre, pers. obs.).

176 Alternatively, the structural changes we identified could be due to a withdrawal of
177 learning founder effect [18–20], if invasive populations were established by juvenile and/or
178 captive birds that lacked adult tutors and thus developed atypical calls. We consider this
179 alternative less likely, because changes in acoustic structure were concentrated on aspects of
180 frequency modulation rather than distributed across all acoustic measurements. Furthermore,
181 these changes were seen across multiple, presumably independent, invasions in 5 different
182 states. Another possibility is that structural change could be due to genetic bottlenecks,
183 another common outcome of biological invasions [21,22]. If structural variation in contact calls
184 had a strong genetic component, acoustic variation should have decreased in concert with the
185 reduced neutral genetic variation previously reported in the U.S. [23], yielding high overlap
186 among individuals in acoustic space over short geographic distances. Instead, we identified
187 similarly high levels of acoustic variation among individuals in the invasive range as
188 previously found in the native range, indicating that although invasive range calls contain less
189 individual identity information, individuals in both ranges are using learning to diverge in
190 acoustic space (Smith-Vidaurre et al., unpublished data).

191 Reduced individual identity content in invasive range calls is consistent with relaxed
192 selection for individual recognition in smaller populations. Beecher’s statistic (HS) calculated
193 with Mel-frequency cepstral coefficients (MFCC) estimated 59 unique individual signatures for
194 the native range versus 33 for the invasive range, while HS from frequency contours
195 estimated 11 versus 8 unique signatures. Future work should manipulate social group size as
196 well as social dynamics to ask whether vocal learning facilitates altering individual signatures
197 to match changes in social group complexity over short timescales. Monk parakeets exhibit
198 high fission-fusion fluidity [24], but how social dynamics influence individual recognition
199 remains an open question.

200 Simpler individual signatures may be favored due to cognitive costs, or may arise from
201 developmental constraints. In larger social groups, receivers incur the cognitive costs of
202 discriminating among more individuals while simultaneously processing more complex
203 individual signatures against a noisier background. Signalers should also experience costs of
204 learning to encode more distinctive individual signatures through fine-scale structural
205 variation. Monk parakeets both produce and recognize contact calls, therefore all individuals
206 should experience costs of both receiver perception and vocal production [3]. As the
207 perception and production of complex individual signatures impose greater cognitive burdens,
208 simpler individual signatures should be present in smaller groups in which accurate
209 recognition is possible without such complexity. Simpler or less informative signaler traits
210 should also be favored when the costs of errors in individual recognition are lower [25]. Both
211 factors could be working in the smaller populations found in the invasive range to yield
212 simpler signatures. Finally, simpler individual signatures may reflect developmental
213 constraints in receiver perception. Although parrots are considered open-ended vocal learners
214 [26], we do not know whether auditory perception remains sensitive throughout adulthood
215 [27]. In monk parakeets, perception of individual signatures may be constrained by local
216 social densities experienced during sensitive developmental periods. The findings we present
217 here on complexity of individual signatures produced by an invasive parrot add to a
218 foundation for future work on how vocal learning is employed for individual recognition in
219 dynamic social groups.

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235 **References:**

- 236 1. Janik VM, Slater PJB. 2000 The different roles of social learning in vocal
237 communication. *Anim. Behav.* **60**, 1–11. (doi:10.1006/anbe.2000.1410)
- 238 2. Nowicki S, Searcy W. 2014 The evolution of vocal learning. *Curr. Opin. Neurobiol.* **28**,
239 48–53. (doi:10.1016/j.conb.2014.06.007)
- 240 3. Sewall KB, Young AM, Wright TF. 2016 Social calls provide novel insights into the
241 evolution of vocal learning. *Anim. Behav.* **120**, 163–172.
242 (doi:10.1016/j.anbehav.2016.07.031)
- 243 4. Fripp D, Owen C, Quintana-Rizzo E, Shapiro A, Buckstaff K, Jankowski K, Wells R,
244 Tyack P. 2005 Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their
245 signature whistles on the signature whistles of community members. *Anim. Cogn.* **8**,
246 17–26. (doi:10.1007/s10071-004-0225-z)

- 247 5. Berg KS, Delgado S, Cortopassi KA, Beissinger SR, Bradbury JW. 2012 Vertical
248 transmission of learned signatures in a wild parrot. *Proc. R. Soc. B Biol. Sci.* **279**, 585–
249 591. (doi:10.1098/rspb.2011.0932)
- 250 6. Berg KS, Delgado S, Okawa R, Beissinger SR, Bradbury JW. 2011 Contact calls are
251 used for individual mate recognition in free-ranging green-rumped parrotlets, *Forpus*
252 *passerinus*. *Anim. Behav.* **81**, 241–248. (doi:10.1016/j.anbehav.2010.10.012)
- 253 7. Tibbetts EA, Dale J. 2007 Individual recognition: it is good to be different. *Trends Ecol.*
254 *Evol.* **22**, 529–537. (doi:10.1016/j.tree.2007.09.001)
- 255 8. Janik VM, Sayigh LS, Wells RS. 2006 Signature whistle shape conveys identity
256 information to bottlenose dolphins. *Proc. Natl. Acad. Sci. U. S. A.* **103**, 8293–8297.
257 (doi:10.1073/pnas.0509918103)
- 258 9. Beecher M. 1989 Signaling systems for individual recognition: an information theory
259 approach. *Anim. Behav.* **38**, 248–261. (doi:10.1016/S0003-3472(89)80087-9)
- 260 10. Lockwood JL, Cassey P, Blackburn T. 2005 The role of propagule pressure in explaining
261 species invasions. *Trends Ecol. Evol.* **20**, 223–228. (doi:10.1016/j.tree.2005.02.004)
- 262 11. Smith-Vidaurre G, Araya-Salas M, Wright TF. 2020 Individual signatures outweigh social
263 group identity in contact calls of a communally nesting parrot. *Behav. Ecol.* **31**, 448–
264 458. (doi:10.1093/beheco/arz202)
- 265 12. Russello MA, Avery ML, Wright TF. 2008 Genetic evidence links invasive monk
266 parakeet populations in the United States to the international pet trade. *BMC Evol. Biol.*
267 **8**, 217. (doi:10.1186/1471-2148-8-217)
- 268 13. Buhrman-Deever SC, Rappaport AR, Bradbury JW. 2007 Geographic variation in
269 contact calls of feral North American populations of the monk parakeet. *Condor* **109**,
270 389–398. (doi:10.1525/boom.2013.3.4.67.B)
- 271 14. Bioacoustics Research Program. 2014 Raven Pro: Interactive Sound Analysis Software.
- 272 15. Araya-Salas M, Smith-Vidaurre G. 2017 warbleR: an R package to streamline analysis
273 of animal acoustic signals. *Methods Ecol. Evol.* **8**, 184–191. (doi:10.1111/2041-
274 210X.12624)
- 275 16. R Core Team. 2018 R: A Language and Environment for Statistical Computing.
- 276 17. Linhart P, Osiejuk TS, Budka M, Salek M, Spinka M, Policht R, Syrova M, Blumstein DT.
277 2019 Measuring individual identity information in animal signals: overview and
278 performance of available identity metrics. *Methods Ecol. Evol.* **2019**, 1558–1570.
279 (doi:10.1111/2041-210X.13238)

- 280 18. Parker KA, Anderson MJ, Jenkins PF, Brunton DH. 2012 The effects of translocation-
281 induced isolation and fragmentation on the cultural evolution of bird song. *Ecol. Lett.* **15**,
282 778–785. (doi:10.1111/j.1461-0248.2012.01797.x)
- 283 19. Lachlan RF, Verzijden MN, Bernard CS, Jonker PP, Koese B, Jaarsma S, Spoor W,
284 Slater PJB, ten Cate C. 2013 The progressive loss of syntactical structure in bird song
285 along an island colonization chain. *Curr. Biol.* **23**, 1896–1901.
286 (doi:10.1016/j.cub.2013.07.057)
- 287 20. Thielcke G. 1973 On the origin of divergence of learned signals (songs) in isolated
288 populations. *Ibis (Lond. 1859)*. **115**, 511–516. (doi:10.1111/j.1474-919X.1973.tb01989.x)
- 289 21. Bock DG, Caseys C, Cousens RD, Hahn MA, Heredia SM, Hubner S, Turner KG,
290 Whitney KD, Rieseberg LH. 2015 What we still don't know about invasion genetics.
291 *Mol. Ecol.* **24**, 2277–2297. (doi:10.1111/mec.13032)
- 292 22. Dlugosch KM, Parker IM. 2008 Founding events in species invasions: genetic variation,
293 adaptive evolution, and the role of multiple introductions. *Mol. Ecol.* **17**, 431–449.
294 (doi:10.1111/j.1365-294X.2007.03538.x)
- 295 23. Edelaar P *et al.* 2015 Shared genetic diversity across the global invasive range of the
296 monk parakeet suggests a common restricted geographic origin and the possibility of
297 convergent selection. *Mol. Ecol.* **24**, 2164–2176. (doi:10.1111/mec.13157)
- 298 24. Hobson EA, Avery ML, Wright TF. 2014 The socioecology of monk parakeets: insights
299 into parrot social complexity. *Auk* **131**, 756–775. (doi:10.1642/AUK-14-14.1)
- 300 25. Tibbetts EA, Liu M, Laub EC, Shen SF. 2020 Complex signals alter recognition
301 accuracy and conspecific acceptance thresholds. *Philos. Trans. R. Soc. B Biol. Sci.*
302 **375**, 20190482. (doi:10.1098/rstb.2019.0482)
- 303 26. Bradbury JW, Balsby TJS. 2016 The functions of vocal learning in parrots. *Behav. Ecol.*
304 *Sociobiol.* **70**, 293–312. (doi:10.1007/s00265-016-2068-4)
- 305 27. Dooling RJ, Leek MR, Gleich O, Dent ML. 2002 Auditory temporal resolution in birds:
306 discrimination of harmonic complexes. *J. Acoust. Soc. Am.* **112**, 748–759.
307 (doi:10.1121/1.1494447)