

1 Multi-level Bayesian analysis of monk parakeet contact calls
2 shows dialects between European cities

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20 cation, culture

21 **Abstract**

22 Geographic differences in vocalisations provide strong evidence for animal culture, with patterns
23 likely arising from generations of social learning and transmission. The current knowledge on the
24 evolution of vocal variation has predominantly focused on fixed repertoire, territorial song in passer-
25 ine birds. The study of vocal communication in open-ended learners and in contexts where vocali-
26 sations serve other functions is therefore necessary for a more comprehensive understanding of vocal
27 dialect evolution. Parrots are open-ended vocal production learners that use vocalisations for social
28 contact and coordination. Geographic variation in parrot vocalisations typically take the form of
29 either distinct regional variations known as dialects or graded variation based on geographic distance
30 known as clinal variation. In this study, we recorded monk parakeets (*Myiopsitta monachus*) across
31 multiple spatial scales (i.e. parks and cities) in their European invasive range. We then compared

32 calls using a multi-level Bayesian model and sensitivity analysis, with this novel approach allowing
33 us to explicitly compare vocalisations at multiple spatial scales. We found support for founder effects
34 and/or cultural drift at the city level, consistent with passive cultural processes leading to large scale
35 dialect differences. We did not find a strong signal for dialect or clinal differences between parks
36 within cities, suggesting that birds did not actively converge on a group level signal, as expected
37 under the group membership hypothesis. We demonstrate the robustness of our findings and offer
38 an explanation that unifies the results of prior monk parakeet vocalisation studies.

39 Introduction

40 Differences in vocalisations between groups or populations have been identified across multiple animal
41 species. Such geographic variation in vocalisations has provided some of the strongest evidence
42 for vocal learning and animal culture (Marler and Tamura 1962; Catchpole and Slater 2003; Podos
43 and Warren 2007; Aplin 2019). In particular, patterns of vocal variation in songbirds have been the
44 focus of decades of intensive research (Slater 2003). In songbirds, song is primarily used to defend
45 territories and attract mates (Krebs and Kroodsma 1980; Kroodsma and Byers 1991; Catchpole and
46 Slater 2003), and is often exclusively learned early in development. Coupled with vocal convergence
47 and conformity (Lachlan, Ratmann, and Nowicki 2018), this early flexibility can result in highly
48 stable and localised dialects. For example, male new world sparrows (*Passerellidae*) produce complex
49 songs that form clear geographic dialects (Williams, Levin, et al. 2013; Lachlan, Ratmann, and
50 Nowicki 2018). These dialects are maintained over long periods of time and may play an important
51 function in species recognition and mate choice (Lachlan, Ratmann, and Nowicki 2018; Slater 2003).
52 Furthermore, the way dialects are structured can depend heavily on behavior and social structure.
53 This is supported by examples of species that have limited migration and dispersal between populations,
54 which show a gradual change in vocal differentiation across a geographical clinal gradient
55 (D. E. Irwin, Thimban, and J. H. Irwin 2008). However, the study of vocal variation in open-ended
56 vocal production learners outside the context of bird-song is relatively understudied and the mechanisms
57 leading to emergent dialect or clinal patterns in these cases are poorly understood (Wright
58 and Dahlin 2018).

59 Open-ended vocal production learning refers to the ability to modify or change produced vocalisations
60 throughout adulthood (Beecher and Brenowitz 2005; Janik and Slater 1997; Janik and Knörnschild
61 2021). Open-ended vocal production learning has evolved in several taxonomic groups including bats,
62 cetaceans and three main groups of birds: hummingbirds (*Trochilidae*), passerines (i.e.,
63 *Corvidae*, *Fringillidae*, *Sturnidae*) and parrots (*Psittiformes*). Many parrot species show geographic
64 variation in their contact calls (Wright 1996; Wright and Dahlin 2018), and, in captive
65 studies, are able to actively converge their vocalisations across long (multiple weeks) time scales
66 (Hile, Plummer, and Striedter 2000). This observation of group convergence has been hypothesized
67 to lead to group-level vocal signatures (Dahlin et al. 2014). In addition to long time scales, parrots
68 can also rapidly modify their calls (i.e., within seconds) (Balsby and Bradbury 2009; Thomsen,
69 Balsby, and Dabelsteen 2019; Scarl and Bradbury 2009; Vehrencamp et al. 2003) depending on
70 specific social context (for example, addressing flock members (Balsby, Momberg, and Dabelsteen
71 2012)). This extreme rapid flexibility could be another possible mechanism leading to overarching
72 geographic variation (Barker et al. 2021).

73 Several hypotheses have been proposed to explain patterns of geographic vocal variation in open-
74 ended vocal production learners such as parrots. The *group membership hypothesis* posits that vocal
75 dialects serve a functional purpose of increased recognition of group members and possibly foraging

76 efficiency within social groups (Bradbury, Vehrencamp, et al. 1998; Sewall, Young, and Wright 2016).
77 In support of this hypothesis, a wide range of studies have found that some parrot species (Wright
78 and Dorin 2001; Vehrencamp et al. 2003; Dahlin et al. 2014), bats (Knörnschild et al. 2012) and
79 dolphins (Janik and Slater 1998) appear to use calls to strengthen social bonds in groups. Under this
80 framework, particular call types, and/or dialects could undergo social selection, allowing for stable
81 call types (Wright 1996). In terms of observable predictions, we would propose that this active
82 process of group convergence should manifest as group signatures at small geographic scales, with
83 this scale further depending on group size and social structure. Along the same lines, if populations
84 demonstrate large degrees of fission-fusion dynamics, this could possibly lead to a clinal gradient,
85 where vocalisations produced in close geographic proximity sound more similar than those produced
86 further apart (Bradbury, Cortopassi, et al. 2001).

87 The *cultural drift hypothesis* proposes that vocal variation forms as the result of passive cultural
88 processes, with either copying errors or innovations combined with neutral or directional cultural
89 evolution that allows for groups to diverge (Williams, Levin, et al. 2013; Williams and Lachlan
90 2022; Payne 1978). Previous research suggests that sexual (Nowicki, Peters, and Podos 1998) and
91 social selection (Lachlan, Ratmann, and Nowicki 2018) both represent likely selective pressures in
92 songbird species. In open-ended learning species such as parrots, contact calls are likely not subject
93 to sexual selection (Bradbury and Balsby 2016). Isolation and cultural drift combined with social
94 selection, therefore appears to be the most plausible explanation for many species. For example,
95 crimson rosella (*Platycercus elegans*) (Ribot et al. 2012) and St. Lucia parrots (*Amazona versicolor*)
96 (Martínez and Logue 2020) both demonstrate dialect boundaries that correspond with barriers to
97 movement. Unlike the *group membership hypothesis*, the *cultural drift hypothesis* does not necessarily
98 require selection for convergence at the group level. Under this scenario, we would expect to observe
99 dialects across isolated geographic regions, likely at larger scales where boundaries exist that isolate
100 populations.

101 In contrast to the *group membership hypothesis*, the *individual signature hypothesis* posits that
102 individuals actively modify their vocalisations to try and sound as distinct from one another as
103 possible (Nowicki and Searcy 2014). In this scenario, we would not necessarily expect to observe
104 geographic vocal variation, despite the social learning of vocalisations. This is because the drive
105 for individual distinctiveness may lead to fully maximised variation within groups (Gillam and
106 Chaverri 2012), making any effect of cultural drift between populations difficult to detect. This
107 type of pattern has been observed in other open-ended learning species such as dolphins (Oswald
108 et al. 2021), and parrot species such as green rumped parrotlets (*Forpus passerinus*) (Berg, Delgado,
109 Okawa, et al. 2011) and monk parakeets (Smith-Vidaurre, Araya-Salas, and Wright 2020). However,
110 the *individual signature hypothesis* is not necessarily mutually exclusive with the *group membership*
111 *hypothesis*. Indeed there is evidence that some species can maintain individual signatures while also
112 maintaining strong group level signatures (Wright 1996; Thomsen, Balsby, and Dabelsteen 2013;
113 Wright 1996). The precise mechanism that causes individual signatures to outweigh dialects versus
114 having strong individual signatures in concert with strong dialect boundaries remains unclear.

115 Monk parakeets (*Myiopsitta monachus*) are an excellent study system to elucidate the processes
116 that lead to geographic vocal variation in open-ended vocal learners. Monk parakeets have a large
117 invasive range across Europe and North America (Forshaw and Cooper 1989), where populations
118 are largely concentrated in cities, often with little movement between them (Postigo et al. 2019;
119 Edelaar et al. 2015). Importantly, monk parakeets have various population substructures that allow
120 for close study of geographic vocal variation patterns at multiple scales. They nest in single or

121 compound nests, the latter containing multiple nests, each with one or multiple chambers per pair
122 (SQS personal observation). Nest openings correspond to nest chambers, which can serve as a proxy
123 for population size. These nest structures occur in larger nesting colonies. The term colony is
124 often defined as one or more nest structures located within 200m of each other (see (Reed et al.
125 2014)). In cities and invasive populations, these nesting colonies are often located within parks or
126 other green areas, clearly delineated from other colonies (Eberhard 1998), although with potential
127 between-park movement and dispersal (Bucher, Martin, et al. 1990). A recent study in the native
128 range of monk parakeets found evidence that individual signatures outweighed any emergent dialects
129 (Smith-Vidaurre, Araya-Salas, and Wright 2020). Interestingly, regional dialects between cities have
130 been observed in the invasive populations of monk parakeets in the United States (Buhrman-Deever,
131 Rappaport, and Bradbury 2007).

132 In the current study, we aim to assess these competing hypotheses by examining patterns of
133 vocalisations across parks and cities in the invasive range of monk parakeets in Europe. Because
134 most European populations of monk parakeets have comparable genetic compositions (Edelaar et
135 al. 2015), it allows us to consider the influence of cultural processes rather than potential genetic
136 differences between the populations. Our populations contain many sub-populations (i.e., parks)
137 making it possible to conduct a two-level comparison with many replicates. If dialects or clinal
138 variation are found at the park level, selection for call sharing with other group members is likely
139 at play, lending credence to vocal convergence via the *group membership hypothesis*. Of course, if
140 movement between parks is low, one could not rule out the possibility of cultural drift also occurring.
141 If dialects exist only at the city level, it would suggest a cultural founder effect and/or cultural drift,
142 similar to that often observed in songbirds (Lachlan, Ratmann, and Nowicki 2018; A. J. Baker and
143 Jenkins 1987). Lastly, if no dialects are found between cities, several testable hypotheses, such as
144 founder effects and selection for distinctive calls at the individual level (Smith-Vidaurre, Araya-Salas,
145 and Wright 2020) could be considered.

146 **Methods**

147 **Study System**

148 Monk parakeets are a medium sized colonially-nesting parrot. While native to South America,
149 they have been transported by the pet trade across the world and have established large invasive
150 populations in several European countries including Spain, France, Belgium, Italy and Greece. These
151 populations are usually clustered in cities and towns, often with relatively little dispersal between
152 them (Dawson Pell et al. 2021). Monk parakeets in Europe breed from March to August and
153 roost in their nests year-round (Senar, Carrillo-Ortiz, et al. 2019). Nests are often highly spatially
154 clustered, with several nest chambers per nest, several nests per tree and trees often clustered
155 together (Eberhard 1998). Population sizes vary within and between cities and parks, with estimates
156 ranging between one nest chamber in Thisio park, Athens to 99 in Gendarmerie School Park, Athens.

157 **Data Collection**

158 We collected vocalisations from monk parakeets in 39 parks across eight cities in four countries:
159 Athens, Barcelona, Bergamo, Brussels, Legnago, Madrid, Pavia and Verona in November 2019 (see
160 Table 1 for sampling effort per park, see Figure 1 for sampling area, and see supplemental materials
161 for maps of parks within cities). Vocalisations were opportunistically recorded between sunrise and

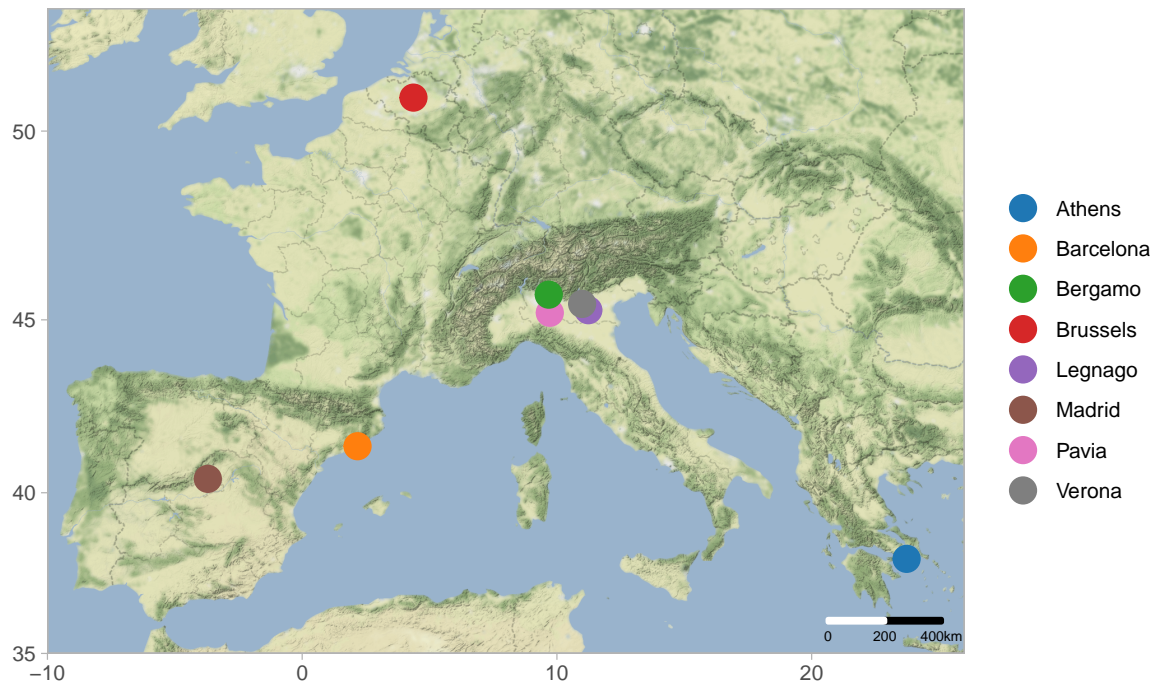


Figure 1: Map of study locations. Map created using ggmap (Kahle and Wickham 2013), ggrepel (Slowikowski 2021), and ggsn (Santos Baquero 2019). Map tiles by Stamen Design, under CC BY 3.0. Data by OpenStreetMap, under ODbL.

162 sunset with a Sennheiser K6 + ME67 microphone and either a Sony PCM M10 or Sony PCM D100
163 recorder. Recordings were made at a distance between one and 20 meters and lasted 20 minutes or
164 until the bird moved away. If calls could be assigned with certainty to a focal bird this was verbally
165 annotated.

166 Although individuals were not identifiable across recordings, whenever possible we recorded the
167 vocalising individual with a unique ID within a recording. We also included recordings when the
168 vocalising individual was not assigned a unique ID. In order to avoid assigning a unique ID to
169 each vocalisation made by an unidentified individual, we grouped them by five minute intervals of
170 recording, assuming recordings during that time span came from one individual. Some recordings
171 were also videotaped with a Philips HC-V777EG-K to allow assignment of calls during processing.
172 We tested how this incorrect pooling might have affected the results in a sensitivity analysis (see
173 Supplemental Materials).

174 Data Processing

175 Raw recordings were first imported to Raven Lite (Cornell Lab of Ornithology, NY 2016). We
176 manually selected the start and end times of all vocalisations with reasonable signal to noise ratio
177 and annotated the caller ID and behaviour if available. Using a custom script in R (R Core Team

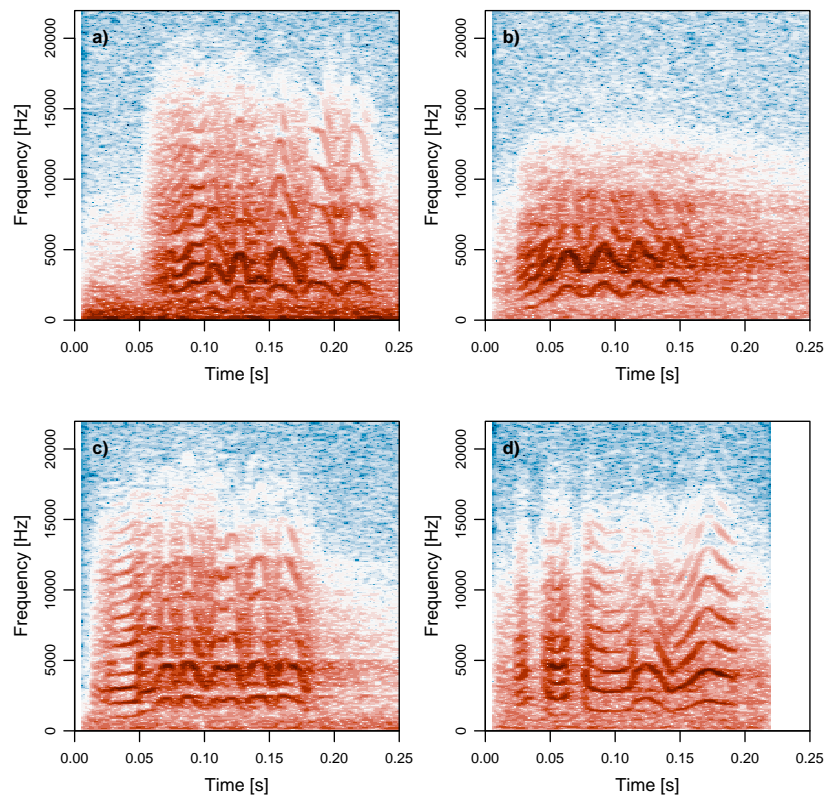


Figure 2: Examples of four contact call variants. a) typical, b) four triangle, c) ladder start, d) mix alarm.

178 2021), all selected calls from Raven were clipped and high quality spectrograms were created (see
179 Data availability statement). All spectrograms were then manually inspected and calls that were
180 considered to be poor quality were removed.

181 The remaining calls were categorised as contact calls (tonal calls with at least three peaks in their
182 frequency modulation) and other calls. Contact calls were further manually sorted into six variants:
183 *typical* (stereotyped call with four rounded frequency modulated components), *four triangle* (stereo-
184 typed call with four triangular shaped frequency modulated components), *ladder start* (call with
185 low frequency harmonic in the first component), *ladder middle* (call with low frequency harmonic
186 in the middle of the call), *ladder multiple* (call with multiple low frequency harmonic components)
187 and *mix alarm* (call with frequency modulated components mixed with amplitude modulated com-
188 ponents). For examples of four of the variants see Figure 2. We choose to use a structural definition
189 to designate call types rather than a behavioural one, since most recordings where behaviours were
190 available were of single perched individuals (Smith-Vidaurre, Araya-Salas, and Wright 2020).

191 To assess whether our categorizations of call variants were reproducible, we created a randomized
192 sample of 1000 calls from our dataset, including both contact and non-contact calls. We then asked
193 an independent observer to classify the calls. We assessed both how the observer’s classifications
194 of contact calls vs. non-contact calls, and how the observer’s classifications of contact call variants
195 compared to our own. The agreement between our own observations of contact vs. non-contact
196 calls and the independent observers’ observations was very strong (Kappa statistic, $k = 0.83$, $Z =$
197 26.2 , %-agree = 91.6). The agreement between our classifications of contact call variants and the
198 independent observers’ classifications was moderately strong (Kappa statistic, $k = 0.59$, $Z = 35.6$,
199 %-agree = 74.3).

200 All good quality contact calls were saved as separate sound files and imported to Luscinia (Lach-
201 lan 2007). Using Luscinia’s algorithm we traced the fundamental frequency semi-manually. Some
202 calls could not be traced well and were excluded (28%). The fundamental frequency traces were
203 imported to R and smoothed in two steps to get rid of small errors. First, gaps where Luscinia could
204 not detect the fundamental frequency were filled with a straight line from the last detected point
205 to the first detected point after the gap. Then `smooth.spline (stats)` was used with `spar = 0.4` to
206 remove outliers. Traces were visually inspected to ensure proper fit.

207 We used dynamic time warping (DTW) to measure similarity between all pairs of contact calls.
208 This algorithm takes two time series and measures the optimal similarity between them (Bellman and
209 Kalaba 1959). We used the function `dtw` from the package `dtw` (Giorgino 2009) to run DTW on the
210 fundamental frequency traces. We normalised and log transformed the resulting distance matrix. To
211 represent each call as a single point in two-dimensional space we ran a principal coordinate analysis
212 (PCO) using the function `pcoa` from the package `ape` (Paradis and Schliep 2019). To verify the
213 robustness of our DTW-PCO analysis, we also obtained a distance matrix using spectrographic cross
214 correlation using the entire spectrogram. We used both uniform manifold approximation (UMAP)
215 and principal component analysis (PCA) for dimension reduction (see Supplemental Materials). All
216 approaches gave similar results.

217 Statistical Analysis

218 We used a Bayesian multilevel model to test how much variation in PC1 and PC2 was explained
219 by the two geographic levels of interest, park and city. Both were included as varying effects. To
220 control for pseudo replication we included the verbally annotated IDs whenever possible as varying
221 effects as well. When IDs were not available, we grouped all calls occurring in the same five minute
222 interval as one individual. We conducted a sensitivity analysis to test how well this approach could
223 mitigate the effects of pseudo replication (see Supplemental Materials). The full model structure for
224 PC1 (standardised) is as follows:

$$\begin{aligned} \text{PC1} &\sim \text{normal}(\mu_{\text{obs}}, \sigma_{\text{obs}}) \\ \mu_{\text{obs}[i]} &= \alpha_{\text{city}[i]} + \alpha_{\text{park}[i]} + \alpha_{\text{ind}[i]} \\ \alpha_{\text{city}} &\sim \text{normal}(\mu_{\text{city}}, \sigma_{\text{city}}) \\ \alpha_{\text{park}} &\sim \text{normal}(0, \sigma_{\text{park}}) \\ \alpha_{\text{ind}} &\sim \text{normal}(0, \sigma_{\text{ind}}) \\ \mu_{\text{city}} &\sim \text{normal}(0, 1) \\ \sigma_{\text{city}}, \sigma_{\text{park}}, \sigma_{\text{ind}} &\sim \text{exponential}(2) \end{aligned}$$

city	park	number of days	number of calls	number of nest openings
Athens	Oluf Palme Playground	3	35	9
Athens	National Garden	4	287	49
Athens	Alsos Ilision	2	52	10
Athens	Gendarmerie School Park	3	86	99
Athens	Thissio Park	1	2	1
Barcelona	Parc de la Ciutadella	3	85	33
Barcelona	Jardins del Turo del Putxet	1	98	1
Barcelona	Jardins de Ghandi	1	2	4
Barcelona	Jardins de Josep Trueta	1	20	7
Barcelona	Parc Grande de Sant Marti	1	44	54
Barcelona	Jardin de la Maternitat	1	19	11
Bergamo	Faunistic Park Le Cornelle	2	456	26
Brussels	Parc de Forest	4	559	96
Brussels	Ten Reuken	2	19	NA
Brussels	Avenue Louise	1	6	7
Brussels	Tenenbosch Park	1	10	1
Brussels	Place Guy D'Arezzo	2	107	13
Legnago	Legnago	2	345	10
Madrid	Parque de el Ritero	1	13	NA
Madrid	Parque de Berlin	3	218	65
Madrid	Lago Casa del Campo	2	91	18
Madrid	Parque Azorin	2	141	55
Madrid	Parque Emperatriz Maria de Austria	1	45	NA
Madrid	Parque Infantil Portalegre	1	9	6
Madrid	Quintos de Molinos	1	10	2
Madrid	Parque Alfredo Kraus	1	5	10
Pavia	Oasi di Sant' Alessio	1	756	34
Verona	Parco Natura Viva	1	110	37

Table 1: Recording effort per city and park. Number of days represents how many days the parks were visited. Not all recording sessions were entire days. Number of calls represents how many calls were included in the final analysis.

225 The model was fitted using the No U-turn Sampler, an improved version of the Hamiltonian
226 Monte Carlo algorithm in Stan (Gelman, Lee, and Guo 2015). A similar model was run for PC2.

227 Results

228 In total we traced 3630 contact calls using *Luscinia*. This encompassed 1-4 days of recording effort
229 and 2-756 recorded calls at each park, with a median of 48.5 calls (n=28 parks). At the city level
230 between 100 (Verona) and 701 calls (Brussels) were recorded, with a median of 459 calls (n=8 cities).
231 See Table 1 for additional sampling details.

232 There was clustering by city (see Figure 3b) with distinct differences based on PC1 (see Figure 4c).
233 In particular, Bergamo, Legnago and Pavia were different from the other cities (Figure 4c). For the

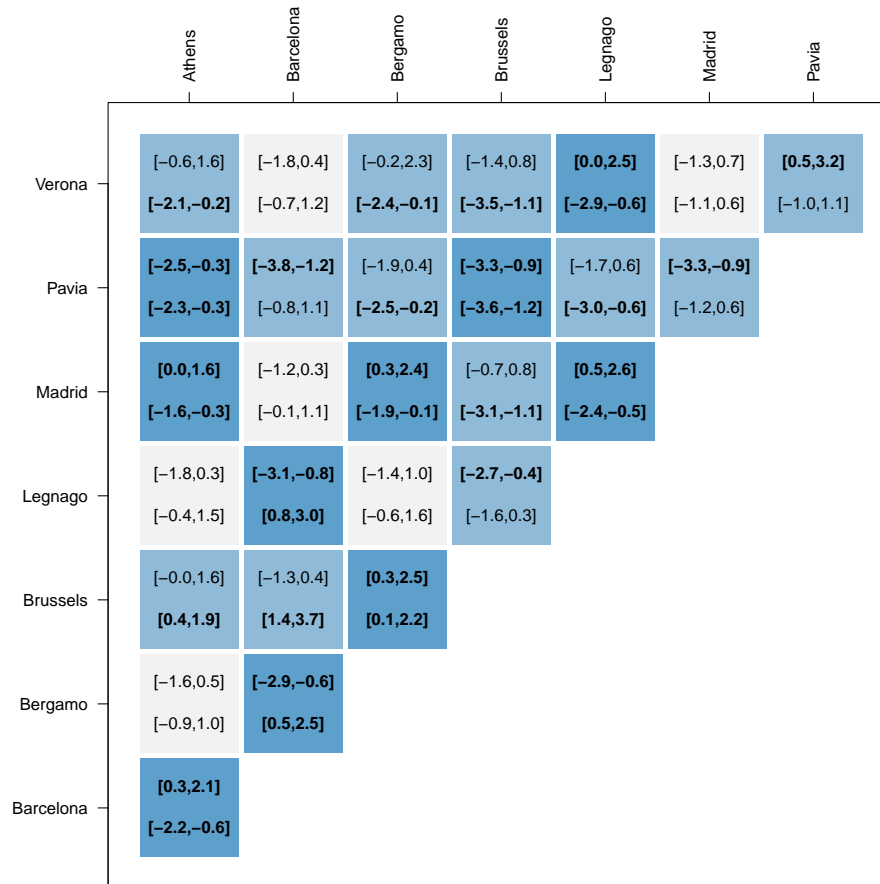


Figure 3: Pairwise contrasts between city means. Number in brackets give the 89% posterior interval for principal coordinate 1 (top) and 2 (bottom) for all city pairs. Intervals are in bold if they do not overlap 0. Squares are coloured dark if either one or both of the intervals do not overlap 0.

234 second principal coordinate, the results demonstrated high levels of differentiated dialects between
 235 the majority of different cities (see Figure 4a). In general, there was considerable evidence that
 236 vocalisations varied between cities (mean σ_{city} PC 1: 0.40, 89% PI: 0.19-0.67, mean σ_{city} PC 2:
 237 0.58, 89% PI: 0.34-0.92), and varied less between parks (mean σ_{park} PC 1: 0.21, 89% PI: 0.12-0.34,
 238 mean σ_{park} PC 2: 0.29, 89% PI: 0.19-0.42) as demonstrated by the sigma parameters and pair-wise
 239 contrasts (see Figure 3). These results were consistent across methods (see Supplemental Materials).

240 In contrast, there was little evidence for widespread differences between parks within cities.
 241 Differences were only observed in a few cases. Lago Casa del Campo and Parque de el Ritero were
 242 clearly different from other parks in Madrid. Likewise, Gendarmerie School Park and the National
 243 Garden were different from other parks in Athens. It is important to mention that those observed
 244 park level differences could potentially be a result of incorrect pooling (i.e, assigning unique IDs to
 245 vocalisations from the same individual or assigning one ID to vocalisations from different individuals),
 246 as the standard deviation across parks was well within the values found in the sensitivity analysis

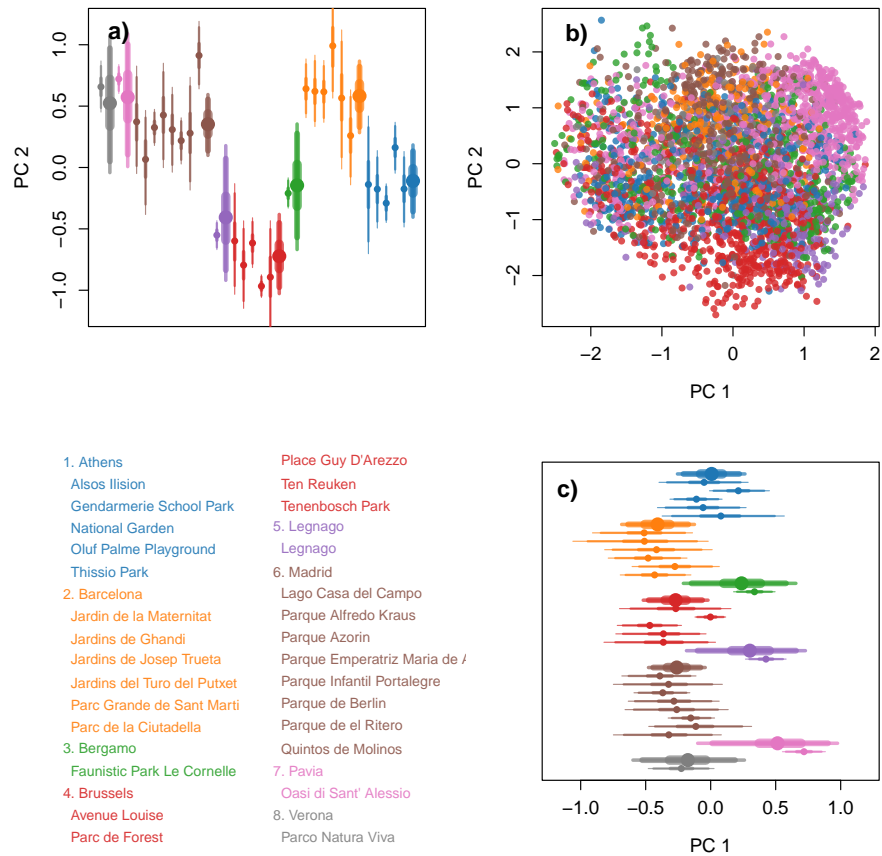


Figure 4: Result for PCO. Colour represents city (see legend). a) City (thick) and park (thin) averages (dots) and 50, 90 and 95% intervals for PC 2. b) Scatter-plot of all calls included in the model. c) City (thick) and park (thin) averages (dots) and 50, 90 and 95% intervals for PC 1.

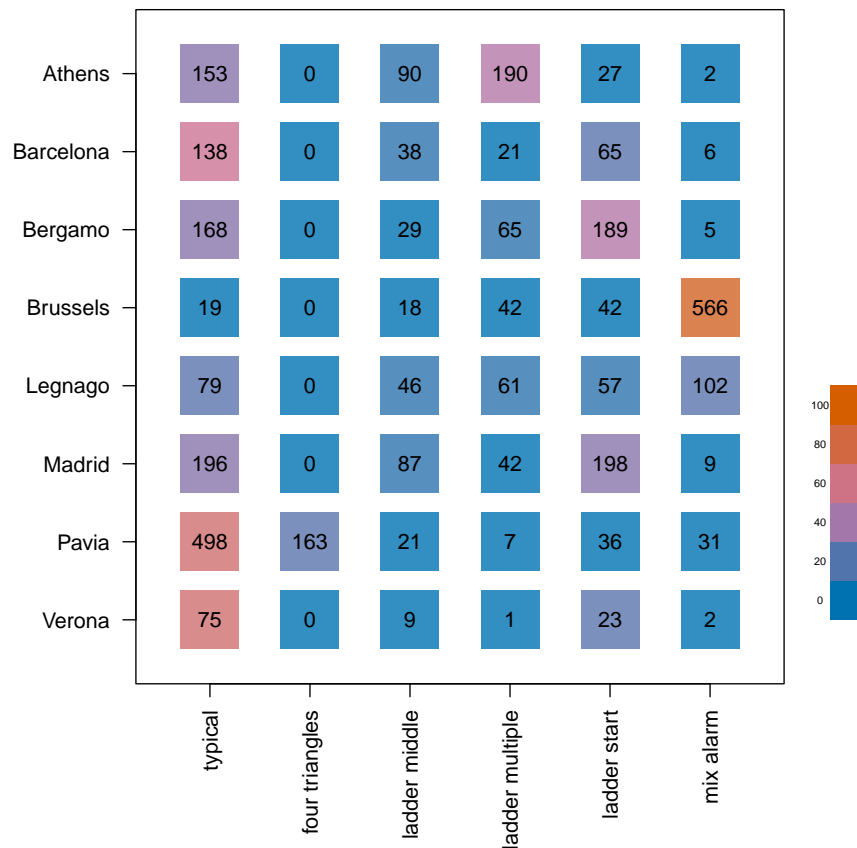


Figure 5: Distribution of variants across cities. Numbers are represented in black, colours represent the percentage of the given variant within the given city and range from 0% (blue) to 100% (orange) - see colour scale bar.

247 (see Supplemental Materials, Figure S3). Park level means can appear very different under incorrect
 248 pooling, even when no signal exists in the simulated data (see Figure S1, Supplemental Materials).
 249 The city level signal we detected is much stronger than the simulated results due to incorrect pooling
 250 (see Supplemental Materials, Figure S2). This lends strong support for dialect differences between
 251 cities, while there is no support for this at the park level given the few differences observed.

252 In addition to assessing overall differences between parks and cities, we examined the proportion
 253 of contact call variants that were observed across the different cities (see Figure 5). We found that in
 254 most cities, the *typical* variant was predominant (see Figure 2a), and 4-5 other variants were usually
 255 present at intermediate to low frequencies. Multiple cities had a large proportion of contact calls that
 256 started with a low frequency component - *ladder start* (see Figure 2c). Pavia was characterized by
 257 the *four triangle* contact call with four triangular frequency modulations (see Figure 2b). Brussels
 258 stood out from the rest with the *mix alarm* contact call, containing multiple alarm-like notes (see
 259 Figure 2d).

260 Discussion

261 Our results provide strong evidence that monk parakeet contact calls differ between multiple cities
262 across their European range. Vocal differences between the parks within cities were also detected,
263 however, these differences were less consistent compared to the dialect pattern we observed at the
264 city level and appeared to be only present in a few parks (see Figure 4). Overall, our results
265 provide support for the *cultural drift hypothesis*, while finding no support for the *group membership*
266 *hypothesis*. If vocal convergence was occurring at the group level, we would expect a stronger signal
267 for dialects or clinal variation at the park level compared to city level, because movement between
268 parks is likely very limited (Senar, Moyà, et al. 2021). Instead, our results demonstrate strong dialect
269 differences at the city level. This result suggests that passive cultural processes are at play (Podos
270 and Warren 2007; Sewall, Young, and Wright 2016; Bradbury and Balsby 2016). Finally, while we
271 cannot directly test this hypothesis in our framework, the lack of consistent evidence for park level
272 differences is a pattern in line with other monk parakeet research (Smith-Vidaurre, Araya-Salas, and
273 Wright 2020) that found strong support for the *individual signature hypothesis*. We should note that
274 this is not mutually exclusive with the *cultural drift hypothesis*. It could be that both are operating
275 simultaneously at different spatial scales (Thomsen, Balsby, and Dabelsteen 2013), highlighting the
276 importance of spatial scale in dialect studies.

277 Detecting the spatial scale at which geographic vocal variation emerges can be difficult, especially
278 in a largely untagged population. For example, (Smith-Vidaurre, Araya-Salas, and Wright 2020)
279 used partial Mantel tests and detected a signal at all scales of their analysis. However, they were not
280 able to directly compare this to the individual signal, as sample sizes differed and Mantel tests do not
281 provide a comparable statistic. A Bayesian multilevel model does provide such a statistic (σ_{park} and
282 σ_{city}) and allows one to test the influence of incorrect pooling in a largely untagged population (see
283 sensitivity analysis - Supplemental Materials). We can therefore say with a high degree of confidence
284 that the city level signal outweighs the park level signal and is well above any spurious signal that
285 might be due to incorrect pooling.

286 Previous studies in other parrot species have often argued that dialects arise at the group level
287 because of selective pressures to conform to local variants (Wright and Dahlin 2018; Eberhard et al.
288 2022), including an active signalling of group membership. However, because we observed little
289 evidence for dialects among parks, we do not think it likely that monk parakeets conform to local
290 dialect types as a mechanism to identify group members. Instead, we find it more likely that the
291 observed dialects among cities result from either random errors and conformity as described in the
292 *cultural drift hypothesis*, or from an influence of the original founding populations (Ju et al. 2019).
293 This supports other work in parrots that has also found dialects all be it at smaller geographical
294 scales (Wright 1996; Buhrman-Deever, Rappaport, and Bradbury 2007; Martínez and Logue 2020;
295 M. C. Baker 2003; Kleeman and Gilardi 2005).

296 Given the limited dispersal between European populations of monk parrots, another possibility
297 is that there is vocal and genetic concordance, as is observed in crimson rosellas (Ribot et al. 2012)
298 and palm cockatoos (Keighley et al. 2020). However, we find this unlikely in our study system.
299 A previous study found that genetic differences between populations of monk parakeets in Europe
300 are minimal, and that most areas were likely sourced from the same founding populations (Edelaar
301 et al. 2015). Thus, genetic differences appear to be a less likely explanation for city level vocal
302 differences than cultural processes, with the source groups determining the starting vocal dialect of
303 each population. Even though previous work combined with our results suggest that monk parakeet

304 contact calls are at least partially socially learned, the exact process is not fully resolved and the
305 ontogeny of vocal learning needs more attention. It is well known that call structure of individuals
306 is influenced by vertical transmission and the family environment (Berg, Delgado, Cortopassi, et al.
307 2012; Berg, Beissinger, and Bradbury 2013; Arellano et al. 2022). Prior research suggests that
308 dispersing juveniles are the ones most likely to modify their calls after dispersal while adults do not
309 (Wright and Dorin 2001). However, we did not observe clear dialects at the park level, to which
310 juveniles could converge.

311 Interestingly, previous research on invasive monk parakeets suggests that dispersal between both
312 parks and cities is very limited (Dawson Pell et al. 2021). Hence, we might expect cultural drift to
313 also lead to dialects at the park level, yet we see the opposite pattern. Interestingly, we also found no
314 support for clinal variation between parks (see further analysis in supplemental materials, where we
315 tested the effect of distance on park-level vocal similarity). One possible explanation for why we do
316 not observe dialects or geographic variation at the park level is provided by the *individual signature*
317 *hypothesis*. Here, the lack of a clear park signature could be explained by divergence in order to stand
318 out in acoustic space (Berg, Delgado, Okawa, et al. 2011). However, unlike the results from (Smith-
319 Vidaurre, Araya-Salas, and Wright 2020), which suggest that selection for individually distinctive
320 calls outweighs any selection for call convergence at the group level, we found very clear evidence
321 for dialects between cities. A possible explanation for this discrepancy is that the study undertaken
322 by Smith-Vidaurre, Araya-Salas, and Wright (2020) was undertaken in the native distribution of
323 monk parakeets, while our results were obtained in a large invasive range where populations are
324 fragmented and dispersal between populations (i.e., cities) is very unlikely (Dawson Pell et al. 2021;
325 Bucher, Martin, et al. 1990). In contrast, although dispersal patterns have not been fully described
326 in the native range, the habitat is more continuous, with increases in Eucalyptus trees allowing for
327 long distance dispersal across the entire range (Bucher and Aramburú 2014; Da Silva et al. 2010).
328 Furthermore, monk parakeets are considered an agricultural pest and are heavily persecuted in their
329 native range (Castro, Sáez, and Molina-Morales 2021). The effect of persecution is often increased
330 dispersal and between-group movement (Payo-Payo et al. 2018) leading to increased intermixing
331 between sub-populations that could potentially obscure any dialect patterns. Such differences in
332 dispersal might partially explain why dialects were also detected in populations of invasive monk
333 parakeets in the United States (Buhrman-Deever, Rappaport, and Bradbury 2007).

334 While we did not find evidence for strong convergence towards a group level signature in contact
335 calls, it could be the case that group signatures exist in other call types, or within very specific
336 variants of contact calls. In accordance to our call type analysis, (see Figure 5), most variants were
337 present in all cities, but some showed higher proportions than others. While we cannot be certain
338 that these variants drive the dialect differences between cities, or lack of in parks, they raise an
339 important point. Explicit experiments that strive to determine the function of these can help us
340 understand where and when to expect the stronger variation between them. Further complicating
341 this, is that as vocal learners, it is possible that certain populations learn to use different variants
342 in different contexts. The ontogeny of these variants, as well as the contextual mechanisms will
343 help further the study of dialect mechanisms in not only Monk Parakeets, but all Psitticine species.
344 In (Wright and Dorin 2001), it was found that juvenile birds more readily modified their contact
345 calls after translocation than adult birds. Given that our populations started from invasive released
346 birds, it could be a critical piece of information to know what the population dynamics were at the
347 beginning of invasion, and the dynamics of subsequent invasion.

348 An alternative explanation for the lack of strong park signals could be that group signatures
349 exist at a smaller scale. Monk parakeets nest in complex nest structures and previous work has

350 shown that birds from the same nest tree are more closely related than expected by chance and
351 tend to forage together (Dawson Pell et al. 2021). This might suggest that either passive or active
352 processes could instead result in a nest level, rather than park level, signature. Future studies should
353 focus on a single population and estimate the strength of the individual and group level signatures
354 across multiple scales. This should preferentially be done in an individually-marked population,
355 such that the temporal stability of vocalisations can also be estimated. Lastly, we recommend that
356 playback studies be conducted on monk parakeet across populations at both the park and city level
357 to indeed experimentally test whether birds can detect subtle variations in group signatures, not
358 picked up by our analyses. For example, tests could examine whether birds recognize calls from
359 their own versus distant colonies, as well as other cities. Furthermore, playback tests could be used
360 to test different substructures of the park (i.e., family unit, specific tree) to see if the park scale is
361 an appropriate scale to measure vocal variation. This type of research is needed before dismissing
362 the *group membership hypothesis* as a possible mechanism.

363 Geographic vocal variation is one of the primary forms of evidence for vocal learning (Lemon 1975;
364 Marler and Tamura 1962). However, our understanding of the processes that lead to this variation
365 at different scales and levels of population structure is lacking. A thorough understanding of these
366 processes is critical to elucidating the underlying mechanisms that drive vocal learning and dialect
367 formation. Monk parakeets and other parrot species are particularly useful model species to study
368 social dynamics and vocal learning because of their flexible learning and complex social system. By
369 continuing to apply novel techniques to the study of vocal patterns at different scales, we can uncover
370 more detailed mechanisms of how communication systems evolve in natural populations. Our study
371 demonstrates the existence of distinct dialects in European populations of monk parakeets, lending
372 support to the *cultural drift hypothesis* while simultaneously showing patterns inconsistent with the
373 *group membership hypothesis*. In addition to cultural drift, we also found evidence consistent with
374 the *individual signature hypothesis* at the park level. While further experimental study is needed
375 to confirm or refute these hypotheses, our extensive dataset, broad geographic scope and two-level
376 comparison provide critical and robust information that enhances our understanding of the important
377 role vocal learning plays in generating dialect differences among populations of Psittacine species.

378 **Ethics**

379 All data was collected without disturbing the animals and, therefore, this study did not require
380 any permits.

381 **Data, code and materials**

382 All small data files and code are publicly available on [https://github.com/simeonqs/Multi-level_](https://github.com/simeonqs/Multi-level_Bayesian_analysis_of_monk_parakeet_contact_calls_shows_dialects_between_European_cities)
383 [Bayesian_analysis_of_monk_parakeet_contact_calls_shows_dialects_between_European_cities](https://github.com/simeonqs/Multi-level_Bayesian_analysis_of_monk_parakeet_contact_calls_shows_dialects_between_European_cities).
384 Large data files are available to reviewers upon request. All data and code will be stored permanently
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403 **Author contributions**

404 Conceptualization: SQS, SAT, LMA, MBM; Data curation: SQS, SAT; Formal analysis: SQS,
405 SAT; Funding acquisition: LMA, MBM; Investigation: SQS, SAT; Methodology: SQS, SAT; Project
406 administration: SQS, SAT; Resources: LMA, MBM; Software: SQS, SAT; Supervision: LMA, MBM;
407 Validation: SQS, SAT; Visualization: SQS; Writing – original draft: SQS, SAT; Writing – review &
408 editing: SQS, SAT, LMA, MBM.

409 **Competing interests**

410 All authors declare to have no competing interests.

411 **References**

- 412 Aplin, Lucy M (2019). “Culture and cultural evolution in birds: a review of the evidence”. In: *Animal*
413 *Behaviour* 147, pp. 179–187.
- 414 Arellano, Caleb MM et al. (2022). “Allo-preening is linked to vocal signature development in a wild
415 parrot”. In: *Behavioral Ecology* 33.1, pp. 202–212.
- 416 Baker, Allan J and Peter F Jenkins (1987). “Founder effect and cultural evolution of songs in
417 an isolated population of chaffinches, *Fringilla coelebs*, in the Chatham Islands”. In: *Animal*
418 *Behaviour* 35.6, pp. 1793–1803.
- 419 Baker, Myron C (2003). “Local similarity and geographic differences in a contact call of the Galah
420 (*Cacatua roseicapilla assimilis*) in Western Australia”. In: *Emu* 103.3, pp. 233–237.
- 421 Balsby, Thorsten JS and Jack W Bradbury (2009). “Vocal matching by orange-fronted conures
422 (*Aratinga canicularis*)”. In: *Behavioural processes* 82.2, pp. 133–139.
- 423 Balsby, Thorsten JS, Jane Vestergaard Momberg, and Torben Dabelsteen (2012). “Vocal imitation
424 in parrots allows addressing of specific individuals in a dynamic communication network”. In:
425 *PLoS One* 7.11, e49747.
- 426 Barker, Alison J et al. (2021). “Cultural transmission of vocal dialect in the naked mole-rat”. In:
427 *Science* 371.6528, pp. 503–507.
- 428 Beecher, Michael D and Eliot A Brenowitz (2005). “Functional aspects of song learning in songbirds”.
429 In: *Trends in ecology & evolution* 20.3, pp. 143–149.

- 430 Bellman, R. and R. Kalaba (1959). “On adaptive control processes”. In: *IRE Transactions on Au-*
431 *tomatic Control* 4.2, pp. 1–9.
- 432 Berg, Karl S, Steven R Beissinger, and Jack W Bradbury (2013). “Factors shaping the ontogeny of
433 vocal signals in a wild parrot”. In: *Journal of Experimental Biology* 216.2, pp. 338–345.
- 434 Berg, Karl S, Soraya Delgado, Kathryn A Cortopassi, et al. (2012). “Vertical transmission of learned
435 signatures in a wild parrot”. In: *Proceedings of the Royal Society B: Biological Sciences* 279.1728,
436 pp. 585–591.
- 437 Berg, Karl S, Soraya Delgado, Rae Okawa, et al. (2011). “Contact calls are used for individual mate
438 recognition in free-ranging green-rumped parrotlets, *Forpus passerinus*”. In: *Animal Behaviour*
439 81.1, pp. 241–248.
- 440 Bradbury, Jack W and Thorsten JS Balsby (2016). “The functions of vocal learning in parrots”. In:
441 *Behavioral Ecology and Sociobiology* 70.3, pp. 293–312.
- 442 Bradbury, Jack W, Kathryn A Cortopassi, et al. (2001). “Geographical variation in the contact calls
443 of orange-fronted parakeets”. In: *The Auk* 118.4, pp. 958–972.
- 444 Bradbury, Jack W, Sandra L Vehrencamp, et al. (1998). “Principles of animal communication”. In:
445 Bucher, Enrique H and Rosana M Aramburú (2014). “Land-use changes and monk parakeet ex-
446 pansion in the Pampas grasslands of Argentina”. In: *Journal of Biogeography* 41.6, pp. 1160–
447 1170.
- 448 Bucher, Enrique H, Liliana F Martin, et al. (1990). “Social behaviour and population dynamics of
449 the Monk Parakeet”. In: *Proc. Int. Ornithol. Congr.* Vol. 20, pp. 681–689.
- 450 Buhrman-Deever, Susannah C, Amy R Rappaport, and Jack W Bradbury (2007). “Geographic
451 variation in contact calls of feral North American populations of the Monk Parakeet”. In: *The*
452 *Condor* 109.2, pp. 389–398.
- 453 Castro, Jorge, Carmen Sáez, and Mercedes Molina-Morales (2021). “The monk parakeet (*Myiop-*
454 *sitta monachus*) as a potential pest for agriculture in the Mediterranean basin”. In: *Biological*
455 *Invasions*, pp. 1–9.
- 456 Catchpole, Clive K and Peter JB Slater (2003). *Bird song: biological themes and variations*. Cam-
457 bridge university press.
- 458 Cornell Lab of Ornithology, NY (2016). *Raven Lite: Interactive Sound Analysis Software*. Ver-
459 sion 2.0.1. URL: <https://ravensoundsoftware.com>.
- 460 Da Silva, Anders Gonçalves et al. (2010). “Genetic evidence for high propagule pressure and long-
461 distance dispersal in monk parakeet (*Myiopsitta monachus*) invasive populations”. In: *Molecular*
462 *Ecology* 19.16, pp. 3336–3350.
- 463 Dahlin, Christine R et al. (2014). “A test of multiple hypotheses for the function of call sharing
464 in female budgerigars, *Melopsittacus undulatus*”. In: *Behavioral ecology and sociobiology* 68.1,
465 pp. 145–161.
- 466 Dawson Pell, Francesca SE et al. (2021). “Fine-scale genetic structure reflects limited and coor-
467 dinated dispersal in the colonial monk parakeet, *Myiopsitta monachus*”. In: *Molecular Ecology*
468 30.6, pp. 1531–1544.
- 469 Eberhard, Jessica R (1998). “Breeding biology of the Monk Parakeet”. In: *The Wilson Bulletin*,
470 pp. 463–473.
- 471 Eberhard, Jessica R et al. (2022). “Contact calls of island Brown-throated Parakeets exhibit both
472 character and variance shifts compared to calls of their mainland relatives”. In: *The Auk* 139.1,
473 ukab076.
- 474 Edelaar, Pim et al. (2015). “Shared genetic diversity across the global invasive range of the monk
475 parakeet suggests a common restricted geographic origin and the possibility of convergent selec-
476 tion”. In: *Molecular Ecology* 24.9, pp. 2164–2176.
- 477 Forshaw, Joseph Michael and William T Cooper (1989). *Parrots of the world*. JSTOR.

- 478 Gelman, Andrew, Daniel Lee, and Jiqiang Guo (2015). “Stan: A probabilistic programming language
479 for Bayesian inference and optimization”. In: *Journal of Educational and Behavioral Statistics*
480 40.5, pp. 530–543.
- 481 Gillam, Erin H and Gloriana Chaverri (2012). “Strong individual signatures and weaker group sig-
482 natures in contact calls of Spix’s disc-winged bat, *Thyroptera tricolor*”. In: *Animal Behaviour*
483 83.1, pp. 269–276.
- 484 Giorgino, Toni (2009). “Computing and visualizing dynamic time warping alignments in R: the dtw
485 package”. In: *Journal of statistical Software* 31, pp. 1–24.
- 486 Hile, Arla G, Thane K Plummer, and Georg F Striedter (2000). “Male vocal imitation produces call
487 convergence during pair bonding in budgerigars, *Melopsittacus undulatus*”. In: *Animal Behaviour*
488 59.6, pp. 1209–1218.
- 489 Irwin, Darren E, Matthew P Thimgan, and Jessica H Irwin (2008). “Call divergence is correlated
490 with geographic and genetic distance in greenish warblers (*Phylloscopus trochiloides*): a strong
491 role for stochasticity in signal evolution?” In: *Journal of evolutionary biology* 21.2, pp. 435–448.
- 492 Janik, Vincent M and Mirjam Knörnschild (2021). “Vocal production learning in mammals revis-
493 ited”. In: *Philosophical Transactions of the Royal Society B* 376.1836, p. 20200244.
- 494 Janik, Vincent M and Peter JB Slater (1997). “Vocal learning in mammals”. In: *Advances in the*
495 *Study of Behaviour* 26.1, pp. 59–100.
- 496 — (1998). “Context-specific use suggests that bottlenose dolphin signature whistles are cohesion
497 calls”. In: *Animal behaviour* 56.4, pp. 829–838.
- 498 Ju, Chenghui et al. (2019). “Four decades of cultural evolution in House Finch songs”. In: *The Auk:*
499 *Ornithological Advances* 136.1, uky012.
- 500 Kahle, David and Hadley Wickham (2013). “ggmap: Spatial Visualization with ggplot2”. In: *The R*
501 *Journal* 5.1, pp. 144–161. URL: [https://journal.r-project.org/archive/2013-1/kahle-](https://journal.r-project.org/archive/2013-1/kahle-wickham.pdf)
502 [wickham.pdf](https://journal.r-project.org/archive/2013-1/kahle-wickham.pdf).
- 503 Keighley, Miles V et al. (2020). “Modelling dispersal in a large parrot: a comparison of landscape
504 resistance models with population genetics and vocal dialect patterns”. In: *Landscape ecology*
505 35.1, pp. 129–144.
- 506 Kleeman, Patrick M. and James D. Gilardi (Feb. 2005). “Geographical Variation of St. Lucia Parrot
507 Flight Vocalizations”. In: *The Condor* 107.1, pp. 62–68. ISSN: 1938-5129. DOI: 10.1093/condor/
508 107.1.62. eprint: [https://academic.oup.com/condor/article-pdf/107/1/62/29714658/](https://academic.oup.com/condor/article-pdf/107/1/62/29714658/condor0062.pdf)
509 [condor0062.pdf](https://academic.oup.com/condor/article-pdf/107/1/62/29714658/condor0062.pdf). URL: <https://doi.org/10.1093/condor/107.1.62>.
- 510 Knörnschild, Mirjam et al. (2012). “Learned vocal group signatures in the polygynous bat *Sac-*
511 *copteryx bilineata*”. In: *Animal Behaviour* 84.4, pp. 761–769.
- 512 Krebs, John R and Donald E Kroodsma (1980). “Repertoires and geographical variation in bird
513 song”. In: *Advances in the Study of Behavior*. Vol. 11. Elsevier, pp. 143–177.
- 514 Kroodsma, Donald E and Bruce E Byers (1991). “The function (s) of bird song”. In: *American*
515 *Zoologist* 31.2, pp. 318–328.
- 516 Lachlan, Robert F (2007). “Luscinia: a bioacoustics analysis computer program”. In: *See luscinia.*
517 *sourceforge.net.[Google Scholar]*.
- 518 Lachlan, Robert F, Oliver Ratmann, and Stephen Nowicki (2018). “Cultural conformity generates
519 extremely stable traditions in bird song”. In: *Nature communications* 9.1, pp. 1–9.
- 520 Lemon, Robert E (1975). “How birds develop song dialects”. In: *The Condor* 77.4, pp. 385–406.
- 521 Marler, Peter and Miwako Tamura (1962). “Song” dialects” in three populations of White-crowned
522 Sparrows”. In: *The Condor* 64.5, pp. 368–377.
- 523 Martínez, Tanya M and David M Logue (2020). “Conservation practices and the formation of vocal
524 dialects in the endangered Puerto Rican parrot, *Amazona vittata*”. In: *Animal Behaviour* 166,
525 pp. 261–271.

- 526 Nowicki, Stephen, Susan Peters, and Jeffrey Podos (1998). “Song learning, early nutrition and sexual
527 selection in songbirds”. In: *American Zoologist* 38.1, pp. 179–190.
- 528 Nowicki, Stephen and William A Searcy (2014). “The evolution of vocal learning”. In: *Current
529 opinion in neurobiology* 28, pp. 48–53.
- 530 Oswald, Julie N et al. (2021). “Species information in whistle frequency modulation patterns of
531 common dolphins”. In: *Philosophical Transactions of the Royal Society B* 376.1836, p. 20210046.
- 532 Paradis, Emmanuel and Klaus Schliep (2019). “ape 5.0: an environment for modern phylogenetics
533 and evolutionary analyses in R”. In: *Bioinformatics* 35, pp. 526–528.
- 534 Payne, Robert B (1978). *Population structure and social behavior: models for testing the ecological
535 significance of song dialects in birds*. Museum of Zoology, University of Michigan.
- 536 Payo-Payo, Ana et al. (2018). “Predator arrival elicits differential dispersal, change in age structure
537 and reproductive performance in a prey population”. In: *Scientific reports* 8.1, pp. 1–7.
- 538 Podos, Jeffrey and Paige S Warren (2007). “The evolution of geographic variation in birdsong”. In:
539 *Advances in the Study of Behavior* 37, pp. 403–458.
- 540 Postigo, Jose-Luis et al. (2019). “Mediterranean versus Atlantic monk parakeets *Myiopsitta monachus*:
541 towards differentiated management at the European scale”. In: *Pest Management Science* 75.4,
542 pp. 915–922.
- 543 R Core Team (2021). *R: A Language and Environment for Statistical Computing*. R Foundation for
544 Statistical Computing. Vienna, Austria. URL: <https://www.R-project.org/>.
- 545 Reed, Janet E et al. (2014). “Monk parakeet nest-site selection of electric utility structures in Texas”.
546 In: *Landscape and Urban Planning* 129, pp. 65–72.
- 547 Ribot, Raoul FH et al. (2012). “Learned vocal variation is associated with abrupt cryptic genetic
548 change in a parrot species complex”. In: *PloS one* 7.12, e50484.
- 549 Santos Baquero, Oswaldo (2019). *ggsn: North Symbols and Scale Bars for Maps Created with 'ggplot2'
550 or 'ggmap'*. R package version 0.5.3. URL: <https://github.com/oswaldosantos/ggsn>.
- 551 Scarl, Judith C and Jack W Bradbury (2009). “Rapid vocal convergence in an Australian cockatoo,
552 the galah *Eolophus roseicapillus*”. In: *Animal Behaviour* 77.5, pp. 1019–1026.
- 553 Senar, Juan Carlos, JG Carrillo-Ortiz, et al. (2019). “The reproductive capacity of Monk Parakeets
554 *Myiopsitta monachus* is higher in their invasive range”. In: *Bird Study* 66.1, pp. 136–140.
- 555 Senar, Juan Carlos, Aura Moyà, et al. (2021). “Sex and age effects on monk parakeet home-range
556 variation in the urban habitat”. In: *Diversity* 13.12, p. 648.
- 557 Sewall, Kendra B, Anna M Young, and Timothy F Wright (2016). “Social calls provide novel insights
558 into the evolution of vocal learning”. In: *Animal Behaviour* 120, pp. 163–172.
- 559 Slater, Peter JB (2003). “Fifty years of bird song research: a case study in animal behaviour”. In:
560 *Essays in Animal Behaviour: Celebrating 50 Years of Animal Behaviour*, pp. 301–313.
- 561 Slowikowski, Kamil (2021). *ggrepel: Automatically Position Non-Overlapping Text Labels with 'gg-
562 plot2'*. R package version 0.9.1. URL: <https://CRAN.R-project.org/package=ggrepel>.
- 563 Smith-Vidaurre, Grace, Marcelo Araya-Salas, and Timothy F Wright (2020). “Individual signatures
564 outweigh social group identity in contact calls of a communally nesting parrot”. In: *Behavioral
565 Ecology* 31.2, pp. 448–458.
- 566 Thomsen, Heidi M, Thorsten JS Balsby, and Torben Dabelsteen (2013). “Individual variation in the
567 contact calls of the monomorphic peach-fronted conure, *Aratinga aurea*, and its potential role in
568 communication”. In: *Bioacoustics* 22.3, pp. 215–227.
- 569 — (2019). “The imitation dilemma: can parrots maintain their vocal individuality when imitating
570 conspecifics?” In: *Behaviour* 156.5-8, pp. 787–814.
- 571 Vehrencamp, Sandra L et al. (2003). “Responses to playback of local vs. distant contact calls in the
572 orange-fronted conure, *Aratinga canicularis*”. In: *Ethology* 109.1, pp. 37–54.

- 573 Williams, Heather and Robert F Lachlan (2022). “Evidence for cumulative cultural evolution in bird
574 song”. In: *Philosophical Transactions of the Royal Society B* 377.1843, p. 20200322.
- 575 Williams, Heather, Iris I Levin, et al. (2013). “Three decades of cultural evolution in Savannah
576 sparrow songs”. In: *Animal Behaviour* 85.1, pp. 213–223.
- 577 Wright, Timothy F (1996). “Regional dialects in the contact call of a parrot”. In: *Proceedings of the
578 Royal Society of London. Series B: Biological Sciences* 263.1372, pp. 867–872.
- 579 Wright, Timothy F and Christine R Dahlin (2018). “Vocal dialects in parrots: patterns and processes
580 of cultural evolution”. In: *Emu-Austral Ornithology* 118.1, pp. 50–66.
- 581 Wright, Timothy F and Melinda Dorin (2001). “Pair duets in the yellow-naped amazon (Psittaci-
582 formes: *Amazona auropalliata*): responses to playbacks of different dialects”. In: *Ethology* 107.2,
583 pp. 111–124.