Multi-level analysis of monk parakeet vocalisations shows emergent dialects between cities in the European invasive range

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Abstract

Geographic differences in vocal dialects have provided strong evidence for animal culture, with patterns likely arising from generations of social learning and transmission. The current knowledge on the evolution of vocal dialects has predominantly focused on fixed repertoire, territorial song. The study of vocal dialects in open-ended flexible learners and in contexts where vocalisations serve other functions is therefore necessary for a more comprehensive understanding of vocal dialect evolution. Parrots are open-ended vocal learners where vocalisations are used for social contact and coordination. Here, we recorded monk parakeets (*Myiopsitta monachus*) across multiple spatial and social scales in their European invasive range. We then compared calls using a multi-level Bayesian

model and sensitivity analysis, with this novel approach allowing us to explicitly compare dialects at multiple spatial scales, even in unmarked populations. We found support for founder effects and/or cultural drift at the city level, consistent with passive cultural processes leading to large scale dialect differences. We did not find a strong signal for dialect differences between groups within cities, suggesting groups did not actively converge on a group level signal, as expected under the group membership hypothesis. We demonstrate how our sensitivity analysis highlights the robustness of the results and offer an explanation that unifies the results of prior monk parakeet dialect studies.

Introduction

Differences in vocalisations between groups or populations have been identified across multiple animal species. Often termed 'dialects' (Marler and Tamura 1962), such geographic variation in vocalizations has provided some of the strongest evidence for vocal learning and animal culture (Catchpole and P. J. Slater 2003; Podos and Warren 2007; Aplin 2019). In particular, vocal dialects in songbirds have been the focus of decades of intensive research (P. Slater 2003). In songbirds, song is primarily used to defend territories and attract mates (Krebs and Kroodsma 1980; Kroodsma and Byers 1991; Catchpole and P. J. Slater 2003), and is often exclusively learned early in development before becoming crystallised. Coupled with vocal convergence and conformity (Robert F Lachlan, Ratmann, and Nowicki 2018), this early flexibility can result in highly stable and localised dialects. For example, male new world sparrows (*Passerllidae*) exhibit complex songs that form clear geographic dialects (Williams, Levin, et al. 2013; Robert F Lachlan, Ratmann, and Nowicki 2018). These dialects are maintained over long periods of time and may play an important function in species recognition and mate choice (Robert F Lachlan, Ratmann, and Nowicki 2018; P. Slater 2003). However, the study of dialects in open-ended vocal production learners outside the context of song is relatively understudied and the mechanisms leading to emergent dialect patterns in these cases are poorly understood (Wright and Dahlin 2018).

Open-ended vocal production learning refers to the ability to modify or change produced vocalizations throughout adulthood (Beecher and Brenowitz 2005; Janik and P. J. Slater 1997; Janik and Knörnschild 2021). Open-ended vocal production learning has evolved in several taxonomic groups including bats, cetaceans and three main groups of birds: hummingbirds (*Trochilidae*), passerines (i.e., *Corvidae*) and parrots (*Psittaformes*). Despite the flexibility in their vocal abilities, many parrot species show geographic variation in their contact calls (Wright 1996; Wright and Dahlin 2018). In addition, some parrots are able to actively converge or diverge their vocalizations both on short (i.e, within minutes) (Balsby and Bradbury 2009; Thomsen, Balsby, and Dabelsteen 2019) and long (across multiple weeks) time scales (Hile, Plummer, and Striedter 2000), leading to group-level or pair-specific vocal signatures (Dahlin et al. 2014).

Several hypotheses have been proposed to explain the formation of vocal dialects in open-ended vocal production learners such as parrots. The *group membership hypothesis* posits that vocal dialects serve a functional purpose of increased recognition of group members and possibly foraging efficiency within social groups (Bradbury, Vehrencamp, et al. 1998; Sewall, Young, and Wright 2016). In support of this hypothesis, a wide range of studies have found that some parrot species (Wright and Dorin 2001; Vehrencamp et al. 2003; Dahlin et al. 2014), bats (Knörnschild et al. 2012) and dolphins (Janik and P. J. Slater 1998) appear to use calls to strengthen social bonds in groups. In terms of observable predictions, we would propose that this active process of group convergence should manifest as group signatures at small geographic scales, with this scale further depending on group size and social structure. Along the same lines, if populations demonstrate large degrees of

fission-fusion dynamics, this could possibly lead to a clinal gradient, where vocalizations produced in close geographic proximity sound more similar than those produced further apart (Bradbury, Cortopassi, et al. 2001).

The *cultural drift hypothesis* proposes that dialects form as the result of passive cultural processes, with either copying errors or innovations combined with neutral or directed cultural evolution that allows for groups to diverge (Williams, Levin, et al. 2013; Williams and Robert F Lachlan 2022; Payne 1978). Previous research suggests that sexual selection (Nowicki, Peters, and Podos 1998) and conformity (Robert F Lachlan, Ratmann, and Nowicki 2018) both represent likely selective pressures in songbird species. In open-ended learning species such as parrots, contact calls are likely not subject to sexual selection (Bradbury and Balsby 2016). Isolation and cultural drift combined with conformity therefore appears to be the most plausible explanation for many species. For example, yellow-napped amazons (*Amazona auropalliata*) (Wright 1996) and St. Lucia parrots (*Amazona versicolor*) (Martínez and Logue 2020) both demonstrate dialect boundaries that correspond with barriers to movement. Unlike the *group membership hypothesis*, the *cultural drift hypothesis* does not necessarily require active convergence at the group level. Under this scenario, we would expect to observe dialects across isolated geographic regions, likely at larger scales where boundaries exist that isolate populations.

In contrast to the *group membership hypothesis*, the *individual signature hypothesis* posits that individuals actively diverge their vocalisations to try and sound as distinct from one another as possible (Nowicki and Searcy 2014). In this scenario, we would not necessarily expect to observe vocal dialects, despite the social learning of vocalisations. This is because the drive for individual distinctiveness may lead to fully maximised variation within groups (Gillam and Chaverri 2012), making any effect of cultural drift between populations difficult to detect. This type of pattern has been observed in other open-ended learning species such as dolphins (Oswald et al. 2021), and parrot species such as green rumped parrotlets (*Forpus passerinus*) (Berg et al. 2011) and monk parakeets (Smith-Vidaurre, Araya-Salas, and Wright 2020). However, the *individual signature hypothesis* is not necessarily mutually exclusive with the *group membership hypothesis*. Indeed there is evidence that some species can maintain individual signatures while also maintaining strong group level signatures (Thomsen, Balsby, and Dabelsteen 2013). The precise trade-off between maintaining dialect signatures at the group level and obscuring them remains unclear.

Monk parakeets (*Myiopsitta monachus*) are an excellent study system to elucidate the processes that lead to vocal dialects in open-ended vocal learners. Monk parakeets have a large invasive range across Europe and North America (Forshaw and Cooper 1989), where populations are largely concentrated in cities, often with little movement between them (Postigo et al. 2019; Edelaar et al. 2015). Importantly, monk parakeets have various population substructures that allow for close study of dialect patterns at multiple scales. They nest in single or composite nests, the latter containing multiple nests, each with one or multiple chambers per pair. These nest structures occur in larger nesting colonies. In cities, these nesting colonies are often located within parks or other green areas, clearly delineated from other colonies, although with potential between-park movement and dispersal (Eberhard 1998). A recent study in the native range of monk parakeets found evidence that individual signatures obscured any emergent dialects (Smith-Vidaurre, Araya-Salas, and Wright 2020). Interestingly, regional dialects between cities have been observed in the invasive populations of monk parakeets in the United States (Buhrman-Deever, Rappaport, and Bradbury 2007).

In the current study, we aim to untangle these competing hypotheses by examining patterns of vocalisations across nesting colonies (i.e., parks) and cities in the invasive range of monk parakeets

in Europe. Because most European populations of monk parakeets have comparable genetic compositions (Edelaar et al. 2015), it allows us to consider the influence of cultural patterns rather than potential genetic differences between the populations. Our populations contain many subpopulations (i.e., parks) making it possible to conduct a two-level comparison with many replicates. If dialects are found at the colony (park) level, selection for call sharing with other group members is likely at play, lending credence to vocal convergence via the *group membership hypothesis*. If dialects exist only at the city level, it would suggest social learning with neutral selection via a cultural founder effect and/or cultural drift, similar to that often observed in songbirds (Robert F Lachlan, Ratmann, and Nowicki 2018; A. J. Baker and Jenkins 1987). Lastly, if no dialects are found between cities, it could suggest that active divergence occurs at the individual level and that selection for individual signatures obscures population level patterns (Smith-Vidaurre, Araya-Salas, and Wright 2020).

Methods

Study System

Monk parakeets are a medium sized colonially-nesting parrot. While native to South America, they have been transported by the pet trade across the world and have established large invasive populations in several European countries including Spain, France, Belgium, Italy and Greece. These populations are usually clustered in cities and towns, often with relatively little dispersal between them (Dawson Pell et al. 2021). Monk parakeets in Europe breed from March to August and roost in their nests year-round senar2019reproductive. Nests are often highly spatially clustered, with several nest chambers per nest, several nests per tree and trees often clustered together (Eberhard 1998). Population sizes vary within and between cities and parks, with estimates ranging between one nest chamber in Thisio park, Athens to 99 in Gendarmerie School Park, Athens.

Data Collection

We collected vocalisations from monk parakeets in 39 parks across eight cities in four countries: Athens, Barcelona, Bergamo, Brussels, Legnago, Madrid, Pavia and Verona in November 2019 (see Table 1 for sampling effort per park). Vocalisations were opportunistically recorded between sunrise and sunset with a Sennheiser K6 + ME67 microphone and either a Sony PCM M10 or Sony PCM D100 recorder. Recordings were made at a distance between one and 20 meters and lasted 20 minutes or until the bird moved away. If calls could be assigned with certainty to a focal bird this was verbally annotated. Behaviours observed during or just before vocalisation were also verbally annotated.

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

Data Processing

Raw recordings were first imported to Raven Lite (K. Lisa Yang Center for Conservation Bioacoustics 2016). We manually selected the start and end times of all vocalisations with reasonable signal to noise ratio and annotated the caller ID and behaviour if available. Using a custom script in R (R Core Team 2021), all selected calls from Raven were clipped and high quality spectrograms were created (see Data availability statement). All spectrograms were then manually inspected and calls that were considered to be poor quality were removed.

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

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

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

We used dynamic time warping (DTW) to measure dissimilarity between all pairs of contact calls. This algorithm takes two time series and measures the optimal similarity between them (Bellman and Kalaba 1959). We used the function *dtw* from the package *dtw* (Giorgino 2009) to run DTW on the fundamental frequency traces. We normalised and log transformed the resulting distance matrix. To obtain a two dimensional representation of all calls we ran a principle coordinate analysis (PCO) using the function *pcoa* from the package *ape* (Paradis and Schliep 2019). To verify the robustness of our methods across different techniques, we also obtained a distance matrix using spectrographic cross correlation. We used both uniform manifold approximation (UMAP) and principle component analysis (PCA) for dimension reduction (see Supplemental Materials). All approaches gave similar results.

Statistical Analysis

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

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

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

Results

In total we traced 3630 contact calls using Luscinia. This encompassed 1-4 days of recording effort and 2-756 recorded calls at each park, with a median of 48.5 calls (n=28). At the city level between 100 (Verona) and 701 calls (Brussels) were recorded, with a median of 459 calls (n=8). See Table 1 for full sample effort per city and park.

There was a clear clustering by city (see Figure 1a) with distinct differences based on PC1. In particular, Bergamo, Legnago and Pavia exhibited distinct dialects compared to other cities (Figure 1c). For the second principle coordinate, the results demonstrated differences in Brussels, Legnago and Bergamo, with Athens in the middle (see Figure 1b). In general, there was considerable variation between cities (mean σ_{ciy} PC 1: 0.40, 89% PI: 0.19-0.67, mean σ_{city} PC 2: 0.58, 89% PI: 0.34-0.92), and less variation between parks (mean σ_{park} PC 1: 0.21, 89% PI: 0.12-0.34, mean σ_{park} PC 2: 0.29, 89% PI: 0.19-0.42). These results were consistent across methods (see Supplemental Materials).

In contrast, few differences were detected between parks within cities. Differences were only observed in a few cases. Lago Casa del Campo and Parque de el Ritero were clearly different from other parks in Madrid. Likewise, Gendarmerie School Park and the National Garden were different from other parks in Athens. It is important to mention that those observed park level differences could potentially be a result of incorrect pooling (i.e, assigning unique IDs to vocalisations from the same individual or assigning one ID to vocalisations from different individuals), as the standard deviation across parks was well within the values found in the sensitivity analysis (see Supplemental Materials, Figure S3). Park level means can appear very different under incorrect pooling, even when no signal exists in the simulated data (see Figure S1, Supplemental Materials). The city level signal

city	park	number of days	number of calls	number of nest holes
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.

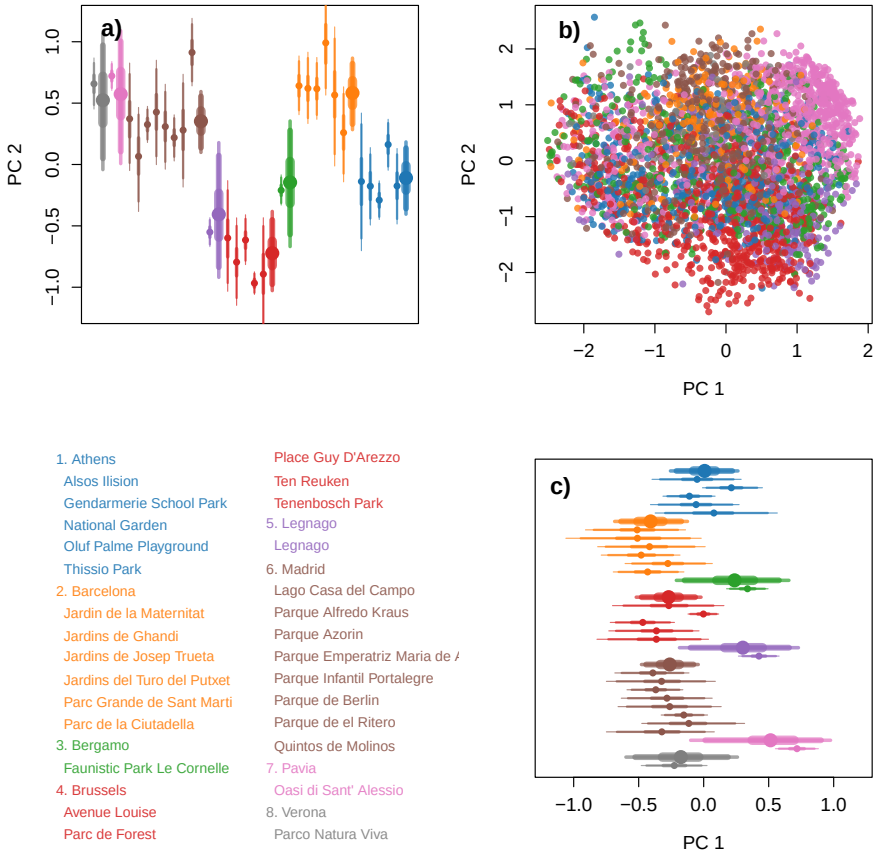

Figure 1: Result for PCO. Colour represents city (see legend). a) City (thick) and park (thin) averages (dots) and 50, 90 and 95% intervals for PC 1. b) Scatter-plot of all calls included in the model. c) City (thick) and park (thin) averages (dots) and 50, 90 and 95% intervals for PC 2.

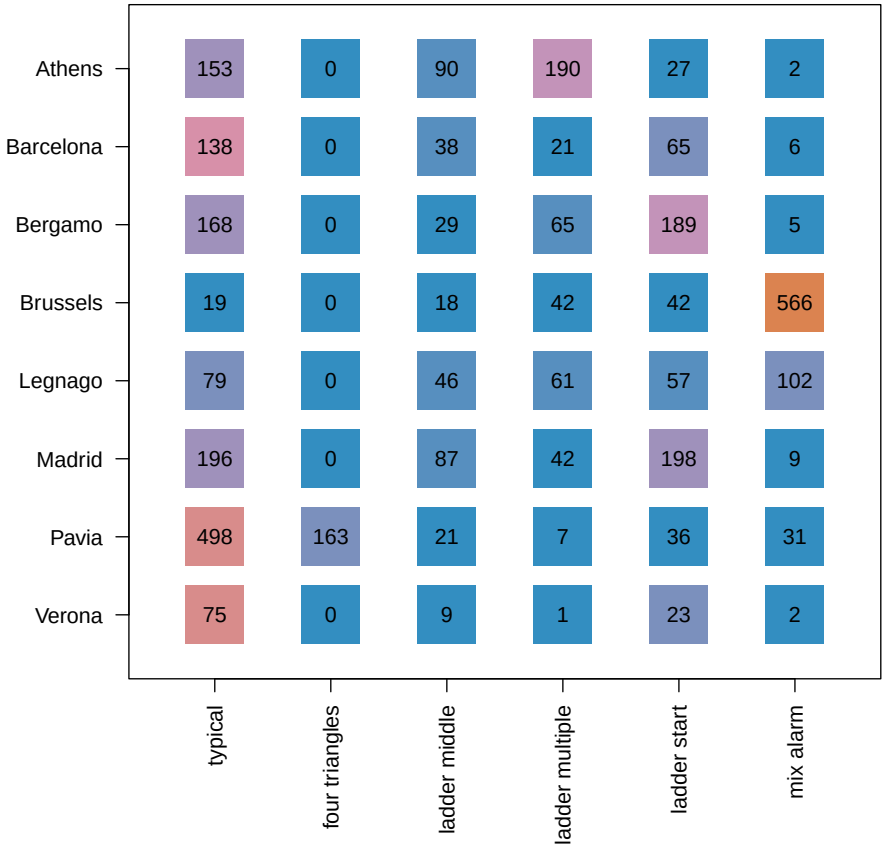

Figure 2: Distribution of variants across cities. Numbers are represented in black, colours represent the percentage of the given variant within the given city and range from 0% (blue) to 100% (orange).

we detected is much stronger than the simulated results due to incorrect pooling (see Supplemental Materials, Figure S2). This lends strong support for dialect differences between cities, while there is no support for this at the park level given the few differences observed.

In addition to observing overall differences between parks and cities, we examined the proportion of call type variants that were observed across the different cities (see Figure 2). The results clearly demonstrated an overall spread of contact calls across cities, however, some cities also had predominately unique variants. Most cities had *typical* contact calls (see Figure 3a). Multiple cities had a large proportion of contact calls that started with a low frequency component - *ladder start* (see Figure 3c). Pavia was characterized by the *four triangle* contact call with four triangular frequency modulations (see Figure 3b). Brussels stood out from the rest with the *mix alarm* contact call, containing multiple alarm-like notes (see Figure 3d).

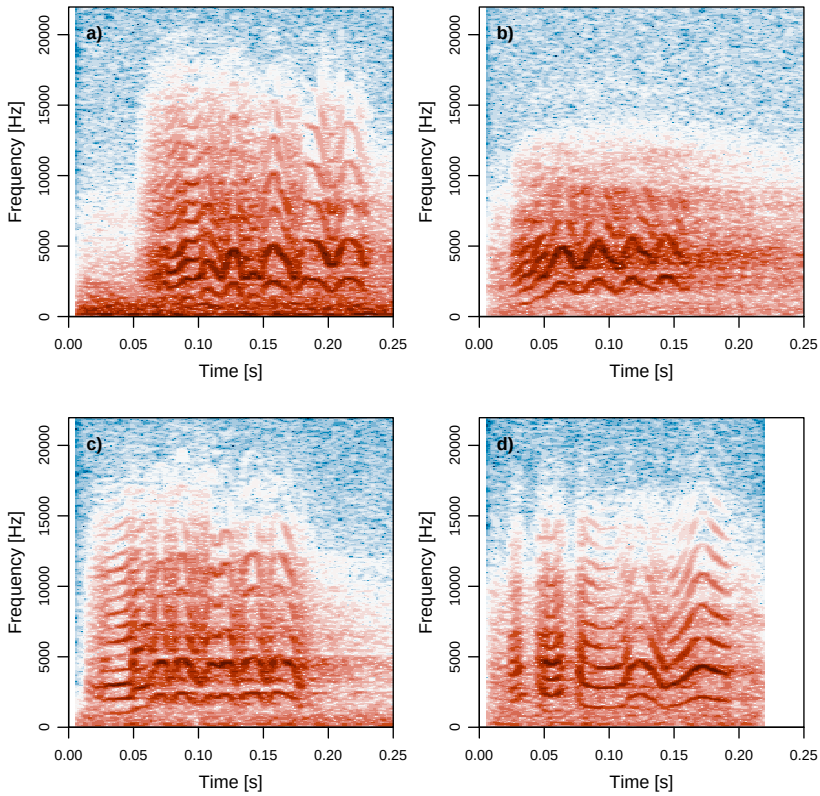

Figure 3: Examples of four contact call variants. a) typical, b) four triangle, c) ladder start, d) mix alarm.

Discussion

Our results provide strong evidence that monk parakeet contact calls differ between multiple cities across their European range. Vocal differences between the parks within cities were also detected, however, these differences were less reliable compared to the dialect pattern we observed at the city level and appeared to be strongly driven by particular outlier parks (see Figure 1). Overall, our results provide strong support for the *cultural drift hypothesis*, while finding no support for the *group membership hypothesis*. If vocal convergence was occurring at the group level, we would expect a stronger signal for dialects at the park level compared to city level. Instead, our results demonstrate strong dialect differences at the city level. This result suggests that passive cultural processes are at play (Podos and Warren 2007; Sewall, Young, and Wright 2016; Bradbury and Balsby 2016). Finally, the lack of strong evidence for park level differences provides some support for the *individual signature hypothesis*. This is not mutually exclusive with the *cultural drift hypothesis*. It could be that both are operating simultaneously at different spatial scales (Thomsen, Balsby, and Dabelsteen 2013), highlighting the importance of spatial scale in dialect studies.

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

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

Given the limited dispersal between European populations of monk parrots, another possibility is that there is vocal and genetic concordance, as is observed in crimson rosellas (Ribot et al. 2012) and palm cockatoos (Keighley et al. 2020). However, we find this unlikely in our study system. Most populations of monk parakeets in Europe were sourced from the same founding populations and genetic differences between populations are minimal (Edelaar et al. 2015). Thus, genetic differences appear to be a less likely explanation for city level vocal differences than cultural processes, with the source groups determining the starting vocal dialect of each population. Such cultural founder effects in dialect have been identified in passerine birds such as chaffinches (ROBERT F Lachlan and P. Slater 2003) and greenish warblers (D. Irwin, Thimgan, and J. Irwin 2008). Whether cultural drift or founder effects are responsible for the city level differences we observed, cultural transmission is required for the maintenance of the observed differences (Podos and Warren 2007).

Interestingly, previous research on invasive monk parakeets suggests that dispersal between both parks and cities is very limited (Dawson Pell et al. 2021). Thus, we might expect cultural drift to also lead to dialects at the park level, yet we see the opposite pattern. One possible explanation for why we do not observe dialects at the park level is provided by the *individual signature hypothesis*. Here, the lack of a clear park signature could be explained by divergence in order to stand out in acoustic space (Berg et al. 2011). However, unlike the results from (Smith-Vidaurre, Araya-Salas, and Wright 2020), which found that individual signatures outweigh group signatures at multiple scales, we found very clear evidence for dialects between cities. A possible explanation for this discrepancy is that (Smith-Vidaurre, Araya-Salas, and Wright 2020) was undertaken in the native distribution of monk parakeets (Smith-Vidaurre, Araya-Salas, and Wright 2020), while our results were obtained in a large invasive range where populations are fragmented and dispersal between populations (i.e., cities) is very unlikely (Dawson Pell et al. 2021; Bucher, Martin, et al. 1990). In contrast, although dispersal patterns have not been fully described in the native range, the habitat is more continuous, with increases in Eucalyptus trees allowing for long distance dispersal across the entire range (Bucher and Aramburú 2014; Da Silva et al. 2010). Furthermore, monk parakeets are considered an agricultural pest and are heavily persecuted in their native range (Castro, Sáez, and Molina-Morales 2021). The effect of persecution is often increased dispersal and between-group movement (Payo-Payo et al. 2018) leading to increased intermixing between subpopulations that could potentially obscure any dialect patterns. Such differences in dispersal might partially explain why dialects were also detected in populations of invasive monk parakeets in the United States (Buhrman-Deever, Rappaport, and Bradbury 2007).

There are several processes that remain understudied in monk parakeets and parrots in general. First, even though previous work combined with our results suggest that monk parakeet contact calls are at least partially socially learned, the exact process is not fully resolved and the ontogeny of vocal learning needs more attention. Second, while we did not find evidence for strong convergence towards a group level signature in contact calls, it could very well be that group signatures exist in other call types. Finally, it could also be that group signatures exist at a much smaller scale. Monk parakeets nest in complex nest structures and previous work has shown that birds from the same nest tree are more closely related than expected by chance and tend to forage together (Dawson Pell et al. 2021). This might suggest that either passive or active processes could instead result in a nest level, rather than park level, signature. Future studies should focus on a single population and estimate the strength of the individual and group level signatures across multiple scales. This should preferentially be done in an individually-marked population, such that the temporal stability of vocalisations can also be estimated.

Dialects are one of the primary forms of evidence for vocal learning (Lemon 1975; Marler and Tamura 1962). However, our understanding of the processes that lead to dialects at different scales and levels of population structure is lacking. A thorough understanding of these processes is critical to elucidating the underlying mechanisms that drive vocal learning and dialect formation. Monk parakeets and other parakeets are particularly useful model species to study social dynamics and vocal learning because of their flexible learning and complex social system. By continuing to apply novel techniques to the study of dialect patterns at different scales, we can uncover more detailed mechanisms of how communication systems evolve in natural populations. Our study demonstrates the existence of distinct dialects in European populations of monk parakeets, lending support to the *cultural drift hypothesis* while simultaneously providing evidence against the *group membership hypothesis*. In addition to cultural drift, we also found evidence consistent with the *individual signature hypothesis* at the park level. Our extensive dataset, broad geographic scope and two-level comparison provide critical and robust information that enhances our understanding of the

important role vocal learning plays in generating dialect differences among populations of Psittacine species.

Ethics

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

Data, code and materials

All small data files and code are publicly available on `https://github.com/simeonqs/Multi-level_analysis_of_monk_parakeet_vocalisations_shows_emergent_dialects_between_cities_in_the_Eu`. Large data files are available to reviewers upon request. All data and code will be stored permanently on Edmond upon acceptance.

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Author contributions

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

Competing interests

All authors declare to have no competing interests.

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