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The effect of social structure on vocal flexibility in monk parakeets

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The social complexity hypothesis argues that communicative complexity arises as a result of social complexity, with this occurring through mechanisms including plasticity and selection. Most research to date has focused on ultimate drivers of repertoire size, for example finding that cooperative breeding species exhibit larger repertoires. Until this date, to our knowledge, no study has focused on individual-level drivers of vocal diversity. Here, we examine social networks and vocalizations in wild colonial-nesting monk parakeets (*Myiopsitta monachus*). We recorded social networks for 337 individuals, relatedness for 100 individuals and matched these with 5599 vocalizations from 229 individuals over 2 years. Overall, we found that all individuals exhibited high contact-call diversity; however, individual-level diversity increased with age in 2020 and with number of nest mates in 2021. Call similarity was not predicted by relatedness, but individuals with stronger affiliative bonds had more dissimilar calls, suggesting an active process to sound unique among close associates. Finally, females had more diverse repertoires, producing relatively fewer contact calls across years and individuals living in larger groups had more diverse repertoires in 2021. Our results demonstrate a multi-faceted social influence on call content, diversity and repertoire diversity, exhibiting how fine-scale variation in social structure can influence expressed vocal complexity.

1. Introduction

Animal species differ widely in the flexibility and complexity of their vocal communication systems. Some species exhibit relatively fixed and simple vocal repertoires, while other species share information about predator type [1], intent to move [2] and individual [3] or group identity [4]. The evolutionary drivers of this variation in vocal complexity have been of long-standing interest to researchers. Most notably, Freeberg [5] put forward the 'social complexity hypothesis', which states that communicative complexity arises as a result of a need to navigate social interactions and dilemmas in larger or more complex groups. Multiple studies have since used comparative analyses to examine the correlates between vocal repertoire size or diversity and various measures of sociality in taxonomic groups ranging from primates [6], bats [7] and birds [8]—for a summary see Peckre *et al*. [9]. This body of work has suggested a general pattern whereby cooperatively breeding species, or species living in larger groups, have more diverse vocalization types, often summarized as 'larger groups have more to talk about' [10, p. 1873].

Many species exhibit vocal learning, with songs and calls shaped by interactions with parents and peers, either in an early developmental period, or throughout life. In these species, individual or population-level vocal repertoire size and diversity can additionally be shaped by this learning process. For instance, even without active selection, copy error and innovation can lead to the appearance of novel variants of vocalizations [11–13]. Cultural evolutionary models such as the 'primary ratchet model' argue that social structure will then affect how new behaviours spread in the population and whether they are retained over generations, with larger or better connected populations holding a more diverse distribution of variants [14]. In line with this prediction, several recent studies have found a decline in song complexity in declining populations of songbird species [15,16]. Similarly, the social complexity hypothesis predicts that within flexible communication systems, individuals in larger groups will acquire or express more complex vocalizations [5]. In the best explored case study, Freeberg [5] first found that wild Carolina chickadees (*Poecile carolinensis*) interacting in larger groups had greater entropy in the note composition of the sequences they uttered. Chickadees were then caught and kept in aviaries under different group sizes. After several weeks, birds in larger groups produced social calls with the potential for greater information content than those in small groups, suggesting that communicative complexity was a facultative response to the social context. However, within-species tests of the social complexity hypothesis remain rare. Within a species, sociality can influence vocal behaviour in a different way as well. Individuals that are more closely associated can actively converge vocally to signal group identity and groups can vocally converge to signal the willingness to fuse during foraging [17–23] leading to the situation where closely associated individuals and groups spending time foraging together sound more similar.

The vast majority of previous work has focused on ultimate questions of the coevolution of vocal diversity and social complexity using comparative analyses [9]. We therefore still lack tests of these hypotheses at the individual level (but see Deecke *et al*. [24]). Such close examination in known individuals gives the opportunity to go beyond measures of group size to interrogate what types of social relationships and social structures are most likely to impact vocal diversity in vocal-learning species. Yet, vocalizations often perform multiple functions across different contexts; therefore, individual-level vocal diversity and repertoires may be influenced by different types of social relationships. Social network analysis enables a detailed description of social structure that spans from the individual to the population [25]. In particular, recent developments in multiplex networks allow for multiple types of associations (e.g. foraging, aggression and spatial proximity) to be separately recorded, with metrics computed across all social networks. The resulting social measures have been shown to be qualitatively different from aggregate scores on monoplex networks in a number of studies [26–28]. From the social network, multiple useful metrics can be computed. Degree is an expression for how many conspecifics an individual interacts with, betweenness an expression for how important an individual is for information flow through the network and eigenvector centrality an expression for how influential an individual is in the network. From a multiplex network, versatility is a measure similar to degree, but includes connections across network types.

Here, we explore the correlation between contact call and repertoire diversity and social networks in a wild population of monk parakeets (*Myiopsitta monachus*) in Barcelona, Spain. The monk parakeet is a medium-sized parrot originally from central South America that has invaded and established large populations in southern Europe since the 1960s [29]. Uniquely among parrots, monk parakeets build communal nests from sticks, where multiple breeding pairs or cooperatively breeding trios expand on the same nest structure. Nests exist in aggregated colonies and are maintained and roosted in year round [30,31]. In European cities, monk parakeets forage in fission–fusion flocks around nesting colonies [32], with foraging flocks ranging between 1 and 50 or more individuals, and with contact calls and other call types being uttered regularly. Parrot species have repertoires ranging from a handful of call types [33] to dozens [34,35] and can vocally learn throughout their lives [18]. Earlier work on monk parakeet vocalizations has described 11 distinct call types [36] but only the contact call has been extensively studied [37–40. Previous work has suggested that these contact calls are individually distinct [37–39] but with high within-individual variability [39]. Unlike other studied parrot species, there is no evidence for active convergence on group-level vocal signatures [37,41]. However, previous work has also found information content to be lower in the American invasive range compared to the native range [38], suggesting either a decline in call complexity with lower population sizes or a historical bottleneck.

In our study, we recorded vocalizations from 229 individually marked monk parakeets in Promenade Passeig de Lluís Companys and Parc de la Ciutadella, Barcelona, Spain for two months over a 2-year period. We classified vocalizations into 11 call types and measured repertoire diversity, diversity in the contact call for each individual, information content in the contact call, as well as a matrix of contact-call similarity between all individuals. We combined this with a description of the social lives of individuals, where we measured foraging associations, aggressive interactions, affiliative interactions and co-nesting associations, while controlling for relatedness. We then used these data to test three predictions based on the primary ratchet model and the social complexity hypothesis: (i) we predicted individuals more central in the social network to have more diverse contact calls and to have a dominant contact call variant with greater information content. Given the multi-faceted nature of monk parakeet social structure, we hypothesized that this centrality could occur either in the nesting or foraging network, or across both and did not make any predictions as to which was more likely; (ii) we predicted that individuals with greater unweighted degree, betweenness and eigenvector centrality to have a more diverse vocal repertoire (greater entropy), either because they have opportunities to learn new call types (acquisition) or because they might encounter more social interaction types (production); and (iii) previous results from parrots have shown that individuals exhibit vocal convergence with group members and mates [34,42,43], with a potentially important role of convergence in pair bonding [44]. Despite the lack of group-level signatures in monk parakeets across parks, we predicted contact calls from closely associated individuals to be more similar across all social networks within the park. Alternatively, if contact calls are largely learnt and crystallized in the nest (perhaps functioning for kin recognition), we would expect a closer relationship between vocal similarity and relatedness [45]. Finally, if contact calls purely represent individual identity and are not socially learned, there should be no effect of social relationship. See table 1 for all predictions and how these were modelled.

2. Methods

2.1. Study system

The study was conducted on wild monk parakeets in Parc de la Ciutadella and surrounding areas in Barcelona, Spain between 27 October–19 November 2020 and 31 October–30 November 2021 (55 days total, see [39] for more details). This time frame was chosen because it does not overlap with the breeding season, juveniles are largely independent and opportunities to observe interactions between unrelated individuals are greatest. December and January were not included because the birds are less active, with temperature and light limiting the hours available for behavioural observation.

Monk parakeets have been reported as an invasive species in Barcelona since the late 1970s [46]. From May 2002, individuals have been regularly captured and ringed using a walk-in trap on Museu de Ciències Naturals de Barcelona and captured directly on their nest as fledglings [47]. As a result, approximately 50% of birds were marked during the 2020 data collection period. Before the 2021 data collection period, this was supplemented with additional intensive night trapping at nests over a one week period, resulting in approximately 60–80% of the local population being marked. Individuals were ringed with stainless steel leg-bands and plastic neck-collars with a small metal medallion displaying a unique identification (ID) [47]. All birds were ringed with special permission EPI 7/2015 (01529/1498/2015) from Direcció General del Medi Natural i Biodiversitat, Generalitat de Catalunya.

During capture birds were aged as nestling, juvenile (<1 year) or adult. A small blood sample was taken from either the brachial or jugular vein of each individual, stored in 98% ethanol and kept at −20°C. Samples were then molecularly sexed by Vetgenomics at the Universitat Autònoma de Barcelona using

Table 1. Hypotheses, models, predictions and results. (Models are abbreviated versions of the full Bayesian multilevel models specified in the electronic supplementary material. All variables were included as varying effects. S = contact call similarity, M = mate network, R = relatedness, F = foraging network, N = nesting network, T = tolerance network, D = contact call diversity, A = age, Se = sex, C = chamber size, Tr = tree size, I = contact call information content and De = degree)

response variable	predictor variable	model	expectation	result
contact call similarity	mate network	$S \sim M + R + F + N + T$	more similar	none
	foraging network	$S \sim M + R + F + N + T$	more similar	none
	nest network	$S \sim M + R + F + N + T$	more similar	more similar
	tolerance network	$S \sim M + R + F + N + T$	more similar	less similar
	relatedness	$S \sim M + R + T$	more similar	none
contact call diversity/	network position	$D \sim N + A + Se + T + Tr$	more diverse	none
repertoire diversity	age	$D \sim A + N + C + S$	less diverse	more diverse
	sex	$D \sim N + A + Se + C + Tr$	none	females more diverse
	chamber size	$D \sim C + A + Se$	more diverse	more diverse
	tree size	$D \sim N + A + Se + C + Tr$	more diverse	none
contact information	degree	$I \sim De + A + Tr$	more information	none
content	tree size	$I \sim De + A + Tr$	more information	none
	age	$I \sim De + A + Tr$	none	none

the P2 and P8 primers (Griffiths *et al*. [48] P2 labelled with 6-carboxyfluorescein). Additional sexings were obtained from Dawson Pell *et al*. [49]. Relatedness was then determined for 100 individuals using 21 microsatellites that were previously described by Dawson Pell *et al*. [31].

2.2. Social data collection

To quantify foraging associations, we walked random routes through Parc de la Ciutadella, where the starting point and route were randomized for each session. Data were collected for at least 6 hours of data collection between sunrise and sunset each day. Effort was distributed randomly throughout the day. When we encountered a single individual or group foraging or perched in any location other than a nesting tree we recorded the identity of all marked individuals. If birds were being actively provisioned by people or foraging on bread or rice we did not include the recording, because such aggregations might not represent active social association choices. We then conducted ad libitum observations in groups of displacements, fights, allopreening and close tolerance until all individuals had left or 20 minutes had passed (for details of behavioural definitions see the electronic supplementary material).

To quantify nesting associations, we mapped the location of all nesting structures in both years in in Parc de la Ciutadella, Promenade Passeig de Lluís Companys and Zoo de Barcelona (see the electronic supplementary material, S7 and S8). For each structure, we assigned a tree ID, nest ID and entry ID. Each entry was considered indicative of a single nest, even though nesting chambers can have multiple entries, a single entry usually only leads to one chamber. Once nest locations were mapped, we monitored all nest entries opportunistically throughout the field season, or until we had at least three sightings of at least two individuals for a nest entry (for details see the electronic supplementary material). Each individual was then assigned to the nest entry where it was observed most frequently. The nest network consisted of the physical distance between nesting locations for all individuals. Observations of social interactions at nest sites (e.g. allopreening) were also recorded opportunistically at nest sites.

2.3. Social network analysis

From the observations away and at the nests (see the electronic supplementary material for details), we generated five social networks for each data collection period: (i) the *nest network* consisted of the distance between nest locations for all individuals (0–966 m), where two nests in the same tree would

Table 2. Glossary. Definitions are based on Wey *et al*. [50] and Powell [51].

term	definition
node	an individuals in the network
edge	the connection between individuals in the network, e.g. if they share a nest
edge weight	the strengtht of the edge, e.g. based on the fraction of times individuals wereobserved together versus alone
degree	the number of edges attached to a node
eigenvector centrality	a measure of influence of a node in the network
betweenness centrality	the number of shortest paths between dyads on which the focal individual lies
multiplex network	a network consisting of multiple other networks where nodes present in multiple networks are connected
nest chamber size	number of individuals living within the same nest chamber, ranging from 1 to 4
tree size	number of individuals living within the same tree, ranging from 1 to 20
DAG	directed acyclic graph, representation of variables and their causal paths
back-door path	a non-causal path between two variables, represented by an arrow pointing towards the explanatory variable
indirect path	a causal path where one variable affects a second and the second affects
	a third variable, whereby an effect of the first on the third is observed
fork	a variable that has an effect on two other variables and can introduce a spurious correlation between the two
collider	a variable where to arrows enter, when included in the model this opens up a back-door path

be scored as 0. Values were normalized (0–1) before analysis. In addition, we recorded *tree group size* for each nesting tree, with this calculated as the number of conspecifics observed using the same nesting tree; (ii) the *mate network* consisted of a binary network where all individuals sharing the same nest chamber shared an edge (for definitions of terms see table 2). Preliminary analysis suggested that the vast majority of allopreening interactions were within mated pairs, and so observations of individuals allopreening were also incorporated into this network. In addition to this, we also recorded *chamber group size*, measured as the number of individuals assigned to a given nest entry; (iii) the *foraging network* was generated from foraging observations using a *gambit of the group* approach [52–54] where two individuals were given an edge if observed foraging in the same group. Edges were then scaled between 0 (never observed foraging together) and 1 (always observed foraging together) using the simple ratio index [25,55–57]; (iv) the *aggression network* was constructed from observations of displacements or fights observed either during foraging transects or at the nest. Given the relatively scarce data, we collated these data into a undirected binary network, where any two individuals that were involved in an aggressive interaction were scored as one and all other zero; and finally, the (v) *affiliative network* was similar, but constructed using all observations of close tolerance behaviour and allopreening.

We constructed a *multiplex network* that included four networks: (i) the *foraging network*, (ii) the *mate network*, (iii) the *aggression network*, and (iv) the *affiliative network*. The nesting network was not included owing to its close similarity with the *mate network*.

From the *foraging network*, we computed the social metrics of unweighted degree, betweeness and eigenvector centrality for each individual using the packages *sna* [58] and *igraph* [59]. These metrics respectively measure for each individual: (a) the number of foraging associates, (b) how much they move between groups, and (c) the number of foraging associates of their associates (a measure of indirect centrality). From the *multiplex network*, we calculated *degree versatility*, using a custom function that summed the unweighted degree for each individual across each networks. Here, we choose unweighted degree as our measure because we were interested in how many conspecifics across all networks an individual had contact with and could potentially learn from.

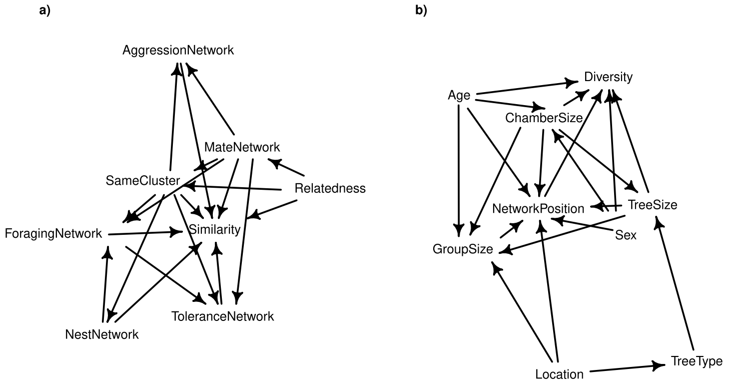

Figure 1. Directed acyclic graph of variables potentially influencing (a) contact call similarity, (b) contact call diversity and (c) contact call information content. All the variables derived from the social networks are included under the term 'NetworkPosition'. Arrows represent assumed causal effects.

2.4. Vocalizations

We used the vocalizations previously processed for Smeele, Senar, *et al.* [39]. This dataset consisted of 5599 vocalizations (3242 vocalizations total in 2020, with an average of 21 vocalizations per individual, numbers ranging between one and 190 vocalizations; 2357 vocalizations total in 2021, with an average of 19 vocalizations per individual, numbers ranging between 1 and 168 vocalizations) classified into 11 call types from 229 individually marked monk parakeets (164 individuals in 2020, 121 individuals in 2021, with 50 individuals overlapping between years).

2.5. Contact call similarity

To test the third prediction that more closely associated individuals have more similar contact calls we first modelled the acoustic distance between contact calls from different individuals. We used a Bayesian model with the following structure:

$$\begin{aligned}\text{acoustic distance} &\sim \text{normal}(\mu,\ \sigma)\\ \mu &= \alpha_{\text{dyad}} + \alpha_{\text{rec}}\\ \alpha_{\text{dyad}} &\sim \text{normal}(\bar{\alpha}, \sigma_{\text{dyad}})\\ \bar{\alpha} &\sim \text{normal}(0,\ 0.5)\\ \alpha_{\text{rec}} &\sim \text{normal}(0, \sigma_{\text{rec}})\\ \sigma, \sigma_{\text{dyad}}, \sigma_{\text{rec}} &\sim \text{exponential}(2).\end{aligned}$$

The parameter α_{rec} was used to control for repeated comparison of recordings. The parameter α_{dyad} represents the average acoustic distance between the dyads of individuals and was used in further models. We exported the mean and standard deviation to propagate uncertainty.

To model which variables could influence the similarity of contact calls between individuals, we visualized all hypothesized causal relationships (based on previous literature) in a directed acyclic graph (DAG; figure 1a). Based on this, we created multilevel Bayesian models for the foraging, mate, nesting, aggressive and tolerance networks, as well as for a matrix of pairwise genetic relatedness (see the electronic supplementary material for details).

2.6. Contact call diversity

Contact calls form a near continuous set of variants within individuals [39]. Some individuals have a more dominant variant, but these variants are not well defined. To test the first part of the first prediction, that more central individuals have more diverse contact calls, we first quantified contact call diversity by measuring the acoustic distance between contact calls from the same individual with dynamic time warping (see Smeele, Senar, *et al.* [39] for details). We then used a Bayesian model with the following structure to obtain the average acoustic distance within individuals, independent of sample size and recording:

$$
\begin{aligned}
\text{acoustic distance} &\sim \text{normal}(\mu,\ \sigma)\\
\mu &= \alpha_{\text{ind}} + \alpha_{\text{same rec}} + \alpha_{\text{rec pair}} + \alpha_{\text{call i}} + \alpha_{\text{call j}}\\
\alpha_{\text{ind}} &\sim \text{normal}(\bar{\alpha}, \sigma_{\text{ind}})\\
\bar{\alpha} &\sim \text{normal}(0,\ 0.25)\\
\alpha_{\text{rec pair}} &\sim \text{normal}(0, \sigma_{\text{rec pair}})\\
\alpha_{\text{call}} &\sim \text{normal}(0, \sigma_{\text{call}})\\
\sigma &\sim \text{exponential}(5)\\
\sigma_{\text{ind}}, \sigma_{\text{rec pair}}, \sigma_{\text{call}} &\sim \text{exponential}(3).
\end{aligned}
$$

The α_{ind} represents the average acoustic distance between calls from the same individual and was used as the diversity measure for further analysis. Individuals that produce a larger diversity of contact calls will have a greater α_{ind}, since the acoustic distance between dissimilar calls is greater. The parameters $\alpha_{\text{same rec}}$, $\alpha_{\text{rec pair}}$ and α_{call} were included to control for the fact that calls from the same recording might be more similar, calls coming from certain pairs of recording might be more similar and certain calls might be more or less typical. To propagate uncertainty about the average acoustic distance within individuals we exported both the mean and standard deviation of the posterior distribution of $\alpha_{\text{same rec}}$ for each individual.

To model which variables could potentially influence the diversity of contact calls in individuals, we first visualized all hypothesized causal relationships in a DAG (see figure 1b). We then created Bayesian models comparing contact call diversity to age, unweighted degree, eigenvector centrality, betweenness centrality (previous three from the foraging network), degree versatility (from the multiplex network), sex, nest chamber group size and tree group size (see the electronic supplementary material for details).

2.7. Contact call information content

To test the second part of the first prediction that more central individuals have a dominant contact call with greater information content, we first measured the information content of contact calls for all individuals and subsetted our dataset to loud contact calls given in isolation, as defined by Smith-Vidaurre *et al.* [37]. Following Smith-Vidaurre, Perez-Marrufo, and Wright [38] we then measured the information content by counting the number of amplitude modulation peaks by using the smoothed fundamental frequency traces from Smeele, Senar, *et al.* [39] and using the function *calc.fm* from the R package *callsync* [60] with the setting *min_height = 30*.

To model which variables influenced the information content of contact calls in individuals, we first visualized all hypothesized causal relationships in a DAG (see figure 1c). We then created multilevel Bayesian models comparing information content to the predictor variables of age, network position and tree group size (see the electronic supplementary material for details).

2.8. Repertoire diversity

To test the second prediction that more central individuals have a more diverse repertoire, we identified 11 call types across all individuals. We then quantified repertoire diversity at the individual level by calculating the entropy of each individuals repertoire:

$$
-\sum_{i=1}^{n} p_i * \log(p_i),
$$

where p_i is the proportion of the repertoire constituted by the i'th out of n call types in that individuals repertoire. We only included individuals with at least 30 vocalizations, to get rid of outliers created owing to low sample size. This value was chosen because it ensured that either multiple recordings were included for each individual, or in a few cases, only one recording was included but this contained a warble sequence with many call types.

We modelled social and individual effects on repertoire entropy for each individual with models similar to the ones used for the contact call diversity, since we hypothesized that the explanatory variables and their causal relationships would be the same. The only prior that differed between the models was $\bar{\alpha}$, which was set to normal(1, 1).

To further test which variables influenced the composition of the repertoire, we used a modified version of the Dirichlet-multinomial model proposed by Harrison *et al*. [61]. It models the counts of all call types for each individual with a multinomial distribution, where the probabilities for each call type occurring are drawn from a Dirichlet distribution, which sums to 1. The α parameters are the average proportions for each call type and can include fixed effects for, e.g. sex. The β parameters predict the increase and decline for each call type as a function of the continuous variables. We followed the same rationale as presented for the diversity analysis with respect to which variables to include for each model. For a general model definition with age as a continuous variable, see below:

$$\begin{aligned}
&\vec{x}_i \sim \text{multinomial}(\vec{p}_i)\\
&\vec{p}_i \sim \text{dirichlet}(\vec{\pi}_i\theta)\\
&\vec{\pi}_i = \frac{\vec{s}_i}{\sum s_i}\\
&\vec{s}_i = \exp[\log(\vec{\alpha}) + \vec{\beta} * A_i]\\
&\theta \sim \text{exponential}(0.2)\\
&\vec{\alpha} \sim \text{dirichlet}(5, 0.5, 0.5, 0.5, 0.5, 0.5, 0.5, 0.5, 0.5)\\
&\vec{\beta} \sim \text{normal}(0, 0.5),
\end{aligned}$$

where θ is a parameter controlling how variable individuals are with respect to the predicted probabilities $\vec{\pi}$. Priors were set using prior predictive simulation. We chose the prior for the $\vec{\alpha}$ based on the knowledge that the first call type (contact call) is much more abundant than all other call types. The prior still allowed for a large range of possible values for all call types. We used the same dataset as for the entropy analysis, but excluded the *frill* and *other tonal* call types, because they were too rare to be modelled reliably (see the electronic supplementary material for details).

2.9. Statistical analysis

All analyses were run in R [62]. All models were run using the package *cmdstanr* [63] which runs the No-U-Turn sampler (a variant of Hamiltonian Monte Carlo) based on the Stan language [64]. We monitored Rhat values and report if divergence occurs in the results section. For each variable, we modelled the total and the direct effect by including covariates according to the back-door criterion (for details of each model see the electronic electronic supplementary material). To make sure we did not tailor our analysis to fit spurious results, we first analysed the data from 2021 and only after we had made the final figures replicated these with data from 2020.

3. Results

3.1. Social networks

After 23 days of data collection in October–November 2020, we had 86 individuals in the foraging network, 66 individuals in the mate network, 144 individuals in the affiliative network and 91 individuals in the aggression network (see the electronic supplementary material, figure S6) and 175 individuals for the multiplex network. We found 44 nesting trees with 65 nests and 196 individuals (see the electronic supplementary material, figure S7). After 31 days of data collection in November 2021, we had 129 individuals in the foraging network, 75 individuals in the mate network, 137 individuals in the tolerance network and 132 individuals in the aggression network (see figure 2) and 164 individuals for the multiplex network. We found 34 nesting trees with 45 nests and 111 individuals (see the electronic supplementary material, figure S8). Group size in nest chambers ranged 1 to 4 across years. Group size in nest trees ranged 1 to 20 across years.

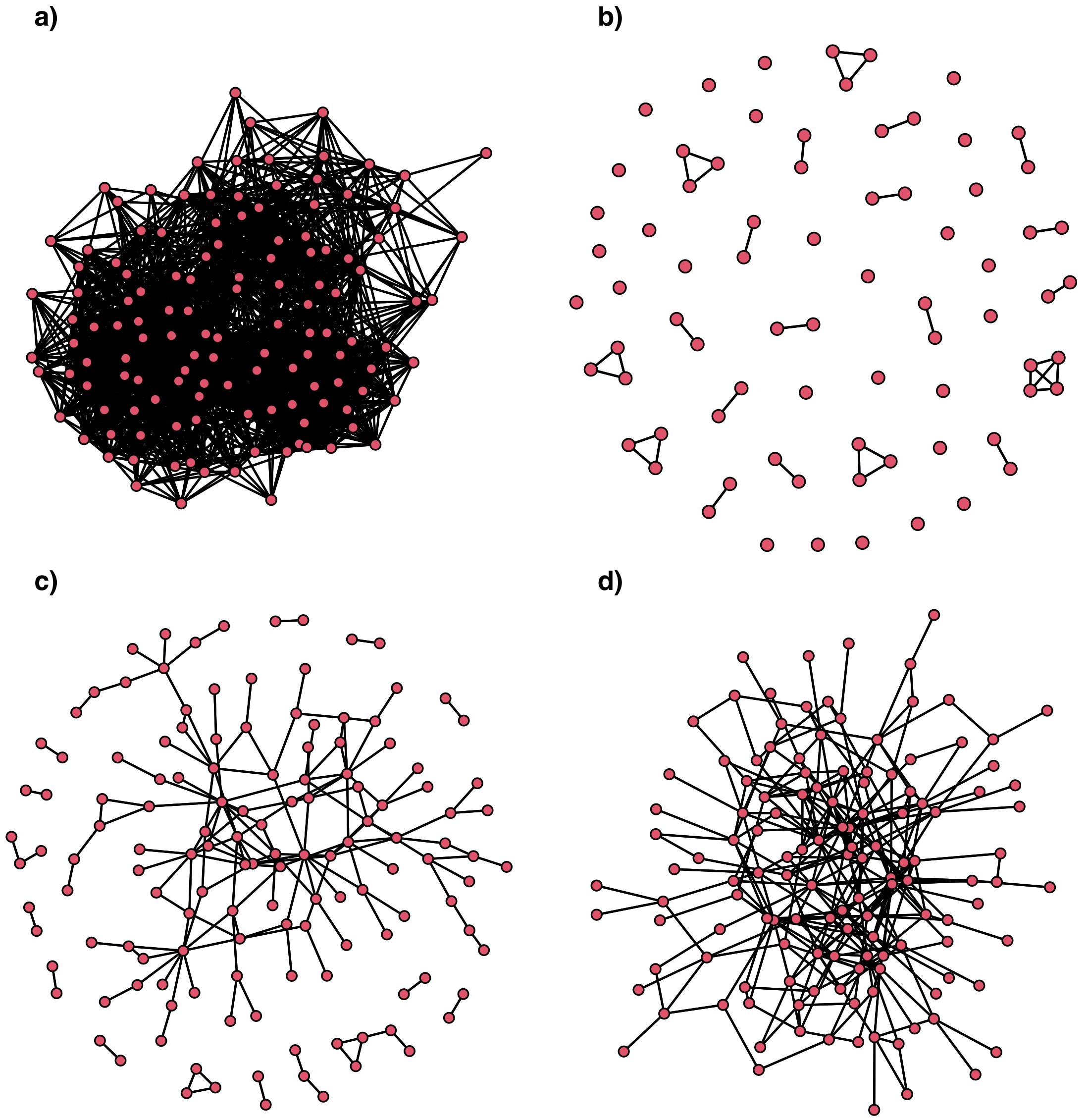

Figure 2. Graphs for (a) foraging network, (b) mate network, (c) affiliative network and (d) aggression network in 2021. Red nodes represent individuals, with the undirected binary edges between individuals in black. For the networks for 2020, see the electronic supplementary material.

3.2. Contact call similarity

Average similarity was estimated for 6551 dyads in 2020 and 5253 dyads in 2021. In general, the dyadic offset explained a modest amount of variation (σ_{dyad} = 0.42, 89% PI = 0.41–0.43 for 2020 and σ_{dyad} = 0.49, 89% PI = 0.48–0.50 for 2021).

In 2020, there was a weak total effect of the nest network on contact call similarity; individuals that nested further apart had less similar calls (see figure 3a,b). In 2021, this effect was absent, but there was a strong effect of the tolerance network (see figure 3a,c), whereby individuals that were frequently observed close together (greater edge weight) had less similar calls. None of the other variables had any effect (see the electronic supplementary material, figures S9 and S10). Contrary to our initial hypothesis, there was no effect of relatedness on call similarity.

3.3. Contact call diversity

Contact call diversity was estimated with 1706 calls from 115 individuals for 2020 and with 1488 calls from 103 individuals for 2021. In general, there was little variation between individuals in their contact call diversity (σ_{ind} = 0.04, 89% PI = 0.03–0.05 for 2020 and σ_{ind} = 0.05, 89% PI = 0.04–0.06 for 2021), with

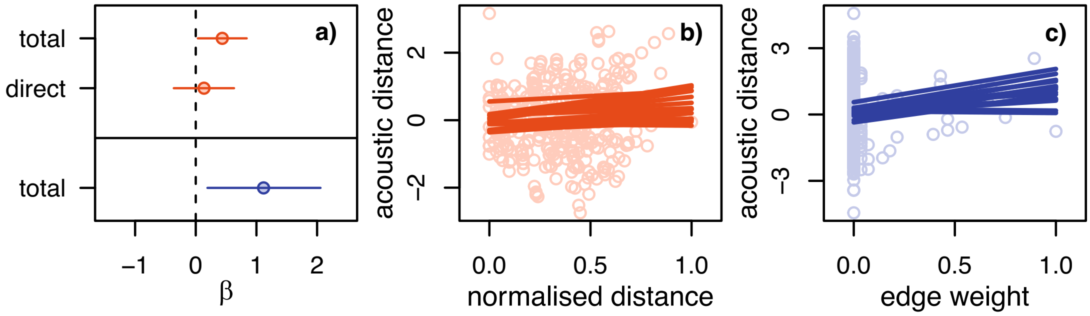

Figure 3. Model results for the effect of spatial (orange) and tolerance (blue) networks on contact call acoustic distance. (a) Total and direct effect estimates for the spatial network in 2020 (top—orange) and total effect estimate for the tolerance network in 2021 (bottom—blue). Dots represent model average and lines represents the 89% posterior interval. (b) Scatter plot of the raw data and 16 lines from the posterior distribution for the model of the direct effect of spatial network in 2020. (c) Scatter plot of the raw data and 16 lines from the posterior distribution for the model of the effect of tolerance network in 2021.

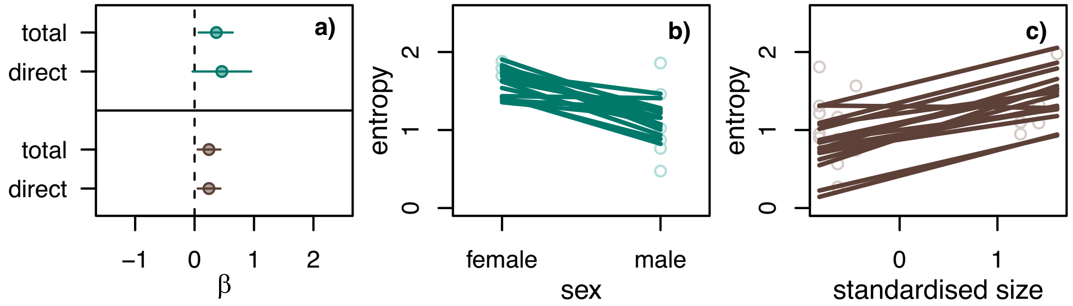

Figure 4. Model results for variables hypothesized to influence repertoire entropy with greatest effects. (a) Total and direct effect estimates of sex in 2020 (top—green) and tree size in 2021 (bottom—brown). Dots represent model average and lines represents the 89% posterior interval. (b) Scatter plot of the raw data and 16 lines from the posterior distribution of the model for the direct effect of sex in 2020. (c) Scatter plot of the raw data and 16 lines from the posterior distribution of the model for the direct effect of tree size in 2021.

all individuals exhibiting a high degree of diversity. We then modelled the total and direct effect of age, sex, degree, eigenvector centrality, betweenness centrality (latter three derived from foraging network), degree versatility (multiplex network), nest chamber group size and nest tree group size on contact call diversity. We had data on age and sex for 337 individuals across both years, degree, eigenvector centrality and betweenness centrality for 90 individuals in 2020 and 128 individuals in 2021, nest chamber group size for 109 individuals in 2020 and 81 individuals in 2021 and nest group size for 161 individuals in 2020 and 99 individuals in 2021. Age and nest chamber size had a positive direct effect in 2021, but no effect in 2020 (see the electronic supplementary material, figures S11 and S12).

3.4. Contact call information content

We measured information content (number of amplitude modulation peaks) for 664 loud contact calls from 75 individuals in 2020 and 1005 loud contact calls from 89 individuals in 2021. None of the explanatory variables had any effect on the information content of the loud contact calls (see the electronic supplementary material), and the variation between individuals was generally also very low (mean σ_{ind} across models ranging between 0.02 and 0.16).

3.5. Repertoire diversity

In order to examine repertoire diversity, we subsetted the dataset to only include individuals with at least 30 calls, leading to a dataset that included repertoires for 38 individuals in 2020 and 34 individuals in 2021. There was an effect of sex in 2020 with females having greater entropy (see figure 4). This effect was also supported in 2021, but the 89% posterior interval overlapped 0 (see the electronic supplementary material, figure S16). The distribution analysis supported this finding that females had greater repertoire

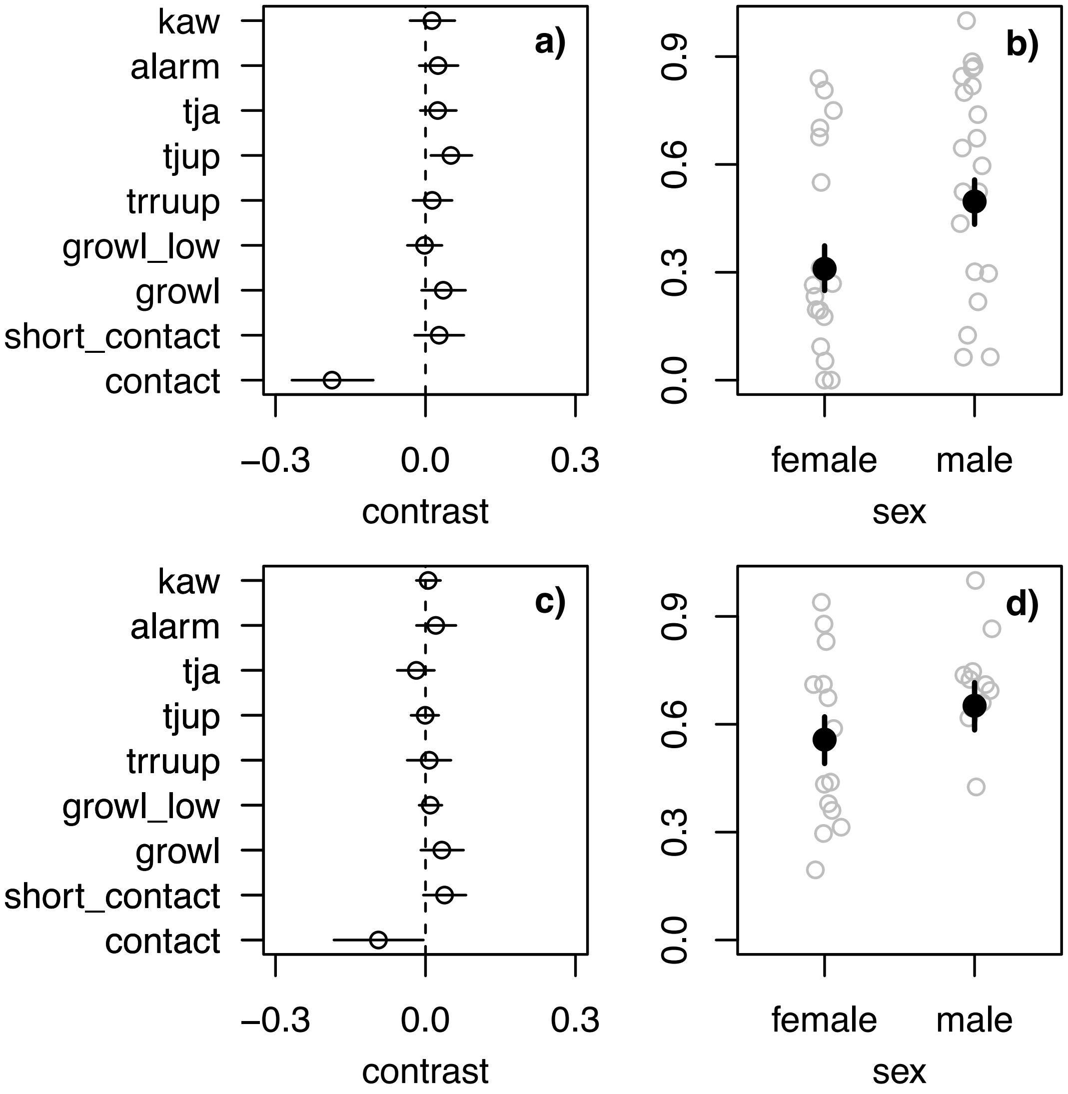

Figure 5. Model results for effect of sex on repertoire distribution. (a) Contrast estimates between sexes ($\alpha_F - \alpha_M$) for each call type in 2020. (b) Scatter plot of the proportion of contact calls for females and males in 2020. Grey circles are raw data (proportion of that call type for each individual). Black dot is the mean estimate for the α parameter and the black line the 89% posterior interval. (c) Contrast estimates between sexes ($\alpha_F - \alpha_M$) for each call type in 2021. (d) Scatter plot of the proportion of contact calls for females and males in 2021. Grey circles are raw data (proportion of that call type for each individual). Black dot is the mean estimate for the α parameter and the black line the 89% posterior interval.

diversity. Females produced a lower proportion of contact calls in both 2020 and 2021 (see figure 5) and overall produced other call types more often, which explains the greater entropy in the diversity analysis. Apart from sex, we found that the nest group size had a positive effect in 2021 (see figure 4), but overlapped 0 in 2020 (see the electronic supplementary material, figure S15). For the results of the other variables, see the electronic supplementary material, figure S17.

4. Discussion

Our study aimed to use social network approaches to test the influence of social factors on individual-level variation in vocal complexity in wild monk parakeets. In line with the social complexity hypothesis, we predicted that individuals with higher centrality in their foraging and/or nesting networks would have greater diversity and higher information content in their contact calls and have a larger repertoire across call types. We further predicted that, if contact calls are socially influenced throughout life, then individuals should exhibit more similar vocalizations to their close associates, while if contact calls are largely learnt and crystallized in the nest, than individuals should exhibit more similar vocalizations to kin. We tested these predictions over two autumn periods, and effects varied between years, perhaps because the first field season had a lower sample size, and included fewer young individuals (mean age 2020 = 1447 days, mean age 2021 = 975) and fewer individuals living in larger nest chambers (mean tree size 2020 = 2.9 individuals, mean tree size 2021 = 3.2 individuals). However, overall, we found that most individuals had diverse contact calls, with little variation in contact call diversity or information content across individuals. Individuals had no discrete contact call variants with a dominant contact call variant, in line with the findings of Smeele, Senar, *et al*. [39], but very different from, e.g. bugerigars [42] or orange-fronted conures [65]. Contrary to the predictions, none of our social network variables predicted contact call diversity or information content, including our measure derived from the multiplex network that incorporated four types of social interactions (foraging, affiliative, foraging and nesting). Yet, contact call diversity did increase with age in 2020 and with nest chamber group size in 2021. This result suggests that contact call variants continue to be acquired throughout life and that individuals use different variants to interact with different individuals that share the same nest chamber. Individuals nesting in larger groups also had a greater repertoire diversity in 2021, although this was better predicted by the size of the nest tree rather than the nest chamber. This result is in line with the predictions of both the social complexity hypothesis and the primary ratchet model. Finally, and contrary to expectation, we did not find any evidence that individuals sharing a nest chamber or nest tree had more similar contact calls, although at a larger scale there was a weak effect of nesting proximity on call similarity in 2020. In addition, there was no effect of relatedness on call similarity either. Instead, there was a strong effect in 2021 for close affiliates to have greater dissimilarity in calls.

Altogether, our results suggest that nesting organization has a much larger effect on vocal complexity in monk parakeets than foraging associations, with nesting group size at the chamber and tree level correlated with contact call diversity and repertoire diversity. Monk parakeets both roost and brood in stick nests, and work year-round to build and maintain these structures. These nests contain variable numbers of pairs and cooperative breeding groups in different nest chambers (often related: Dawson Pell *et al*. [49]). Nests are valuable structures that individuals defend, for example from intruders stealing sticks, yet birds also tolerate others to build nests nearby [32]. Such nesting organization could potentially require extensive negotiation. In support of this, we observed that monk parakeets appear to use very little communication during foraging, but are very vocal around their nest (S. Q. Smeele 2021, personal observation). We did not measure call rate in our study, but future work could add this variable to investigate this difference more explicitly. Future studies could also examine which call types are used more frequently around the nest and how call types are used in call-response interactions, to test whether greater variability in calls allows individuals to better navigate the social interactions associated with nesting. During such a project, focus should be on recording the full repertoire of fewer individuals. One drawback of our focus on collecting social data as well, and recording as large a set of individuals as possible, is the limited amount of acoustic data for a large subset of individuals. Our modelling approach allowed us to account for the unbalanced sampling in the dirichlet-multinomial model and the contact call diversity model, but not in the model of repertoire entropy. We do not believe this introduced a bias, but results should include much less uncertainty and be less variable across years when enough acoustic data are sampled to achieve a full repertoire description for most individuals. It should also be noted that some individuals in our study were recorded in both years, resulting in some pseudo-replication across years. However, since some individuals might have shifted position in the social network and gained (or lost) vocal diversity, we opted to included data from these individuals to allow for a large enough sample size. Especially since only the lower frequency of contact calls for females was present across years, this decision should not have any effect on the overall conclusions.

Future studies could also investigate how variation in contact call diversity is distributed across time. For instance, the work by Vehrencamp *et al*. [66] suggests that some diversity might be most pronounced when interacting and imitating other individuals. Also peach-fronted conures (*Eupsittula aurea*) have a stable individual call [3], but do modify this call during interactions [67]. Similar processes could explain some of the variation observed in monk parakeets. For example, if calls are modified during vocal interactions, or dependent on the audience, variability would be high across and even within recordings. Furthermore, if individuals have a general template with relatively inflexible individuality (as found in previous studies [37,39]), then we would not expect variation in the degree of contact call diversity or strong similarity between individuals, since all individuals use the same set of contact calls to interact.

This notion is also supported by our findings on the information content of contact calls, where within-individual variability in how many amplitude modulation peaks were present in their contact call was high, but variability across individuals was very low.

We did find, however, that individuals tended to sound more dissimilar to their close affiliates (usually mates) than expected from the population level. We also found the surprising result that females have on average a more diverse repertoire. We did not find any effect of relatedness. Our results are not in line with a stable individual signal or a shared signal within nests or foraging groups. It is much more likely that the contact call is a flexible tool that is frequently modified. Interestingly, while most studied parrots exhibit vocal convergence in groups [68] and between mates [69,70], the evidence from previous studies in monk parakeets has instead found some signal of individual identity in contact calls [37,39]. Our results support this, but additionally suggest that the contact call can be used more flexibly than previously assumed.

To better understand the learning and usage learning of call types, studies of vocal ontogeny are indispensable. Rowley & Chapman [71] showed that galahs (*Eolophus roseicapilla*) cross-fostered by Major Mitchell's cockatoo (*Lophochroa leadbeateri*) produce calls typical to both species, suggesting that calls are socially learned, but also have an innate component, since Major Mitchell's cockatoo raised by Major Mitchell's cockatoo parents also appear in mixed flocks but do not produce galah calls. Several studies have shown that parrot chicks go through a babbling phase, where juvenile begging calls and other sounds produced when parents are away from the nest slowly develop into species typical calls [72–75]. No such study has been done for monk parakeets, but it would be very important to understand when calls are learned, and if they are learned before fledgling, how much they are modified after fledglings gain independence. While we did not study ontogeny directly, our results found no effect of relatedness, either suggesting that individuals modify their contact calls after fledging or that they do not use their parents' call as a template to begin with. If only a general contact call develops in the nest and birds first learn multiple variants of this call when out of the nest, it could explain the weak signal of spatial distance, since there would be a bias towards learning calls from birds nesting in close proximity. This effect would be weakened once the juveniles disperse. Limited dispersal and relatively high philopatry in monk parakeets in Parc de la Ciutadella would still make it likely for juveniles to nest closer to their parents [31], leaving a weak signal of proximity.

Our result, that individuals living in larger nest trees have more diverse repertoires, supports the predictions of the social complexity hypothesis—that individuals in larger groups need to communicate more diverse messages [5]. Likewise and more generally, this result supports the predictions made by the primary ratchet model that larger groups maintain a larger diversity of behaviours [14]. We also found that contact call diversity was high across individuals, suggesting that variation in contact call diversity exists within rather than between individuals. The predictions from the social complexity hypothesis are based on production, with individuals producing more variable calls in larger groups because they need to convey more messages [5]. The predictions from the primary ratchet model, on the other hand, are based on acquisition, with individuals acquiring more diverse calls in larger groups, because these larger groups can maintain a more diverse population-level repertoire [14]. It should also be pointed out that the predictions from the primary ratched model stem from a mathematical model and have broader implications for any socially learned behaviour. By tracking individuals over longer time spans, it might be possible to ascertain the directionality and separate the predictions from the primary ratched model and social complexity hypothesis. In particular, if individuals disperse to a new nesting location, their vocal diversity and repertoire size should shift if their new nesting tree is different in size. Alternatively, if vocal complexity is related to accumulative experience, dispersal should lead to no change or an increase in diversity and repertoire size.

Previous research has found extensive support for the coevolution of social and vocal complexity across species [9]. There is also an extensive history of work focusing on the drivers of population-level differences in vocalizations, for example identifying song cultures and cultural evolution in song [76,77]. However, studies on the drivers of individual-level differences in vocal complexity are rare. Here, we demonstrate a social influence on call content, diversity and repertoire diversity in a vocal-learning parrot, exhibiting how fine-scale variation in social structure can influence expressed vocal complexity. We further identify that this influence is related to the nesting organizations. Leighton [8] showed that cooperative breeding birds have a greater diversity of contact and alarm calls. Our results extend this to intra-species variation. Future research could extend this further to examine more species with variable breeding systems, as well as use more detailed sampling to identify the fine-scale social dynamics driving expressed vocal variation.

Ethics. The ringing and taking of blood samples was done with special permission EPI 7/2015 (01529/1498/ 2015) from Direcció General del Medi Natural i Biodiversitat, Generalitat de Catalunya, following Catalan regional ethical guidelines for the handling of birds. J.C.S. received authorization (001501-0402.2009) for the handling for research purposes from Servei de Protecció de la Fauna, Flora i Animal de Companyia, according to Decree 214/1997/30.07.

Data accessibility. Data and relevant code for this research work are stored in GitHub [78] and have been archived within the Zenodo repository [79]. Some data files are too large for GitHub and are therefore only available on Zenodo.

Supplementary material is available online [80].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. S.Q.S.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, software, validation, visualization, writing—original draft, writing—review and editing; J.C.S.: data curation, funding acquisition, investigation, methodology, project administration, resources, writing—review and editing; M.B.M.: conceptualization, funding acquisition, methodology, resources, supervision, writing—review and editing; L.M.A.: conceptualization, funding acquisition, methodology, resources, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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