

Manuscript version: Author's Accepted Manuscript

The version presented in WRAP is the author's accepted manuscript and may differ from the published version or Version of Record.

Persistent WRAP URL:

http://wrap.warwick.ac.uk/115187

How to cite:

Please refer to published version for the most recent bibliographic citation information. If a published version is known of, the repository item page linked to above, will contain details on accessing it.

Copyright and reuse:

The Warwick Research Archive Portal (WRAP) makes this work by researchers of the University of Warwick available open access under the following conditions.

Copyright © and all moral rights to the version of the paper presented here belong to the individual author(s) and/or other copyright owners. To the extent reasonable and practicable the material made available in WRAP has been checked for eligibility before being made available.

Copies of full items can be used for personal research or study, educational, or not-for-profit purposes without prior permission or charge. Provided that the authors, title and full bibliographic details are credited, a hyperlink and/or URL is given for the original metadata page and the content is not changed in any way.

Publisher's statement:

Please refer to the repository item page, publisher's statement section, for further information.

For more information, please contact the WRAP Team at: wrap@warwick.ac.uk.

1	Investigating the potential for call combinations in a life-long vocal learner.
2	
3	Sarah L. Walsh ^a , Simon W. Townsend ^{b,c} , Kate Morgan ^a & Amanda R. Ridley ^a
4	
5	^a School of Biological Sciences, The University of Western Australia, Crawley, WA 6009, Australia;
6	^b Department of Comparative Linguistics, University of Zurich, Zurich, 8032, Switzerland; ^c Department of
7	Psychology, University of Warwick, Coventry CV47AL, United Kingdom.
8	
9	ABSTRACT
10	
11	The ability for humans to create seemingly infinite meaning from a finite set of sounds has
12	likely been a critical component in our success as a species, allowing the unbounded
13	communication of information. Syntax, the combining of meaningful sounds into phrases, is
14	one of the primary features of language that enables this extensive expressivity. The
15	evolutionary history of syntax, however, remains largely debated, and it is only very recently
16	that comparative data for syntax in animals has been revealed. Here, we provide further
17	evidence for a structural basis of potential syntactic-like call combinations in the vocal
18	communication system of a group-living songbird. Acoustic analyses indicate that Western
19	Australian magpies (Cracticus tibicen dorsalis) structurally combine generic alarm calls with
20	acoustically distinct alert calls to produce an alarm-alert sequence. These results are distinct
21	from previous examples of call combinations as, to our knowledge, evidence for this capacity
22	is yet to be demonstrated in a non-human species that is capable of vocal learning throughout
23	life. These findings offer prospects for experimental investigation into the presence and
24	function of magpie call combinations, extending our understanding of animal vocal
25	complexity.

- 27 Keywords: call combinations, syntax, animal vocal communication, language evolution,
- 28 Western Australian magpie, Cracticus tibicen dorsalis.
- 29

30 1. Introduction

31

32 The immensely generative nature of language has long been thought to be a key factor distinguishing humans from other animals (Collier et al., 2014; Hurford, 2011). The property 33 34 of language that enables extensive combinatorial power is known as double articulation and 35 refers to the combining of sounds into words (phonology), and the grammatical combining of meaningful words into phrases (syntax, Hurford, 2011). While there is no doubt humans are 36 37 capable of vast combinatorial power (Hurford, 2012), recent comparative research has begun 38 to draw parallels between language's combinatoriality and potential equivalents within non-39 human animal vocal communication systems (Arnold & Zuberbühler, 2006; Engesser et al., 40 2016; Ouattara et al., 2009; Suzuki et al., 2016; Townsend et al., 2018). 41 42 Many non-human animals, such as some cetacean and avian species for example, have been 43 found capable of stringing sounds together into larger sequences, that, at least superficially, 44 are reminiscent of the phonological layer of human language (Engesser et al., 2015; Hauser et 45 al., 2002; Suzuki et al., 2006; Tyack, 1983). Moreover, a growing body of work has revealed 46 interesting potential homologous and analogous examples of call combinations in animals 47 which can be feasibly compared with simple syntactic structures in language (Arnold & 48 Zuberbühler, 2006; Ouattara et al., 2009; Townsend et al., 2018).

50 The combination of context- specific calls into a meaningful sequence has been suggested in 51 two different studies in related monkey taxa (Arnold & Zuberbühler, 2006; Ouattara et al., 52 2009). Putty-nosed monkeys (Cercopithicus nictitans) combine two predator-specific alert 53 calls into a larger meaningful sequence (Arnold & Zuberbühler, 2006). However, despite the 54 discrete calls each being elicited upon discovery of the presence of a specific predator, the sequence evokes group movement regardless of predatory context. It is, therefore, uncertain 55 56 whether this call sequence is indicative of compositional or instead combinatorial syntax, 57 where the meaning of the resultant sequence (i.e. 'Let's go') is not a product of the 58 combination of the alarm calls' meanings (Collier et al., 2014; Hurford, 2012).

59

Perhaps more convincing evidence of rudimentary compositional syntax in primates is shown in a study on male Campbell's monkeys (*Cercopithecus campbelli campbelli*), where the use of an acoustically invariant suffix modifies the meaning of predator-specific alarm calls in a predictable way (from more specific to more general, Ouattara et al., 2009). Specifically, this has been argued to be akin to abstract meaning operators in language, such as "like", that generalises the meaning of words ("monkey" to "monkey-like") and is therefore suggestive of basic compositional syntax (Collier et al., 2014; see also Townsend et al., 2018).

67

Recently, additional evidence of simple syntax has been seen in more distantly related species. The combining of warning and recruitment calls in the Japanese great tit (*Parus minor*) elicits a compound response consisting of a combination of the behaviours prompted by each individual call (Suzuki et al., 2016). Critically, when artificially reversing the sequence, the authors find a change in behavioural response, which is argued to indicate the sequence is perceived as a single meaningful unit (Suzuki et al., 2016). Similarly, alert and 74 recruitment calls in the cooperatively breeding southern pied babbler (Turdoides bicolor) are 75 combined into a sequence eliciting mobbing behaviour from conspecifics in the presence of a territorial threat (Engesser et al., 2016). Experiments demonstrated that the individual calls 76 77 have an independent meaning that are distinct from, but contribute to, the meaning of the mobbing sequence and thus are strongly indicative of rudimentary syntax (Engesser et al., 78 79 2016; see Suzuki et al., 2018, Townsend et al., 2018 and Zuidema & de Boer, 2018). These 80 studies have laid the foundation for further research into basic syntactic abilities in non-81 human animals.

82

In this study, we build on emerging evidence of avian syntactic abilities by investigating the 83 84 occurrence of call combinations in the Western Australian magpie. Magpies in south-western 85 Australia are highly territorial, and cooperatively defend a year-round territory (Ashton et al., 86 2018; Farabaugh & Brown, 1988; Hughes et al., 1996). All group members participate in territorial defence behaviours throughout the year, including vocalizations, inter-group 87 88 fighting, and aggressive posturing (Farabaugh & Brown, 1988; Kaplan, 2004; Kaplan, 2006; 89 Kaplan et al., 2009). Both sexes have a similarly well-developed song and extensive vocal 90 repertoire (Kaplan, 2005; Suthers et al., 2011; Walsh, 2017). Males do not use song or any other specific vocalization for courtship and thus share the same basic repertoire with females 91 92 (Kaplan, 2005).

93

The vocal repertoire of adult Western Australian magpies (hereafter magpies) can be
separated into short alarm calls, distress or alert calls, begging, feeding grunts, and carols or
warbling calls (Baker, 2009; Kaplan, 2004; Silvestri, 2017; Walsh, 2017).Previous research
has revealed the potential for context specificity in a variety of magpie vocalizations, such as

98 carols and some alarm calls (Baker, 2009; Kaplan, 2008). For example, carolling calls may 99 signal territoriality and willingness to participate in defence of the group territory (Baker, 100 2009). Furthermore, there is evidence that some alarm calls may be predator specific in 101 nature (Kaplan, 2005; Kaplan, 2006; Kaplan, 2008; Kaplan et al., 2009; Kaplan & Rogers, 102 2013). In light of the context-specific nature of magpie calls (Kaplan, 2008), and due to the 103 clear capabilities for flexibility in call structure (Kaplan, 2000), we reasoned rudimentary 104 syntactic structuring might also exist in the vocal system of magpies. While basic 105 combinatoriality in magpie vocal communication has been alluded to in past research 106 (Kaplan, 2005) to date, systematic investigations have not been conducted. 107

108 Moreover, to our knowledge, syntactic capabilities have not yet been indicated in a life-long 109 vocal learner other than humans. Magpies have been shown to be capable of flexibly 110 interspersing mimicry into their own song, indicating a high plasticity of vocal learning and 111 high retention of learned material throughout life (Brown & Farabaugh, 1991; Kaplan, 2000; 112 Kaplan, 2005). The fact that mappies can be considered as open-ended vocal learners is 113 particularly interesting because theory suggests that the transition from a non-compositional 114 system to a compositional one, relates to a constraint in the number of available calls 115 (Nowack, 2000). As this would seemingly not be a constraint for a life-long vocal learner, if 116 syntactic capability is revealed in magpies it could provide additional insight into the 117 potential evolutionary forces promoting the progression of syntax. 118

One instrumental first step prior to unambiguously identifying a syntactic-like combination in
 non-human animal communication systems involves isolating naturally-occurring,

stereotyped, call combinations and then demonstrating that the calls comprising the

122 combination and the same calls produced alone are acoustically equivalent (*sensu* Hedwig et
123 al., 2014), such that the combination can be feasibly be considered as composed of
124 independently-occurring calls (see Hedwig et al., 2015, Engesser et al., 2016 & Suzuki et al.,
125 2016).

126

127 Observational work has indicated that magpies do indeed produce such a sequence in the 128 form of an "alarm-alert sequence" appearing to be comprised of two independently occurring 129 calls, a generic alarm call and an alert vocalisation (Figure 1), and used in a variety of threat-130 related contexts. Furthermore, field observations suggest the call may convey information to 131 receivers with individuals responding predominantly with vigilance-type behaviours such as scanning, vigilance, mobbing a predator, and movement directly following the call (Walsh, 132 133 2017). Regarding the individual call types, observations indicated alarm calls produced 134 predominantly during the approach of humans, dogs and general disturbance (Silvestri, 2017; 135 Walsh, 2017). The alert call, however, coincides with the presence of a potential predatory 136 threat, often eliciting response behaviours such as vigilance, scanning or carolling 137 vocalisations from other group members (Silvestri, 2017; Walsh, 2017). 138 The fact that two independently occurring calls (alarm and alert calls) are concatenated into a 139 140 single structure (alarm-alert sequence) is suggestive that the call might represent a syntactic-141 like structure (Hurford, 2011), providing a solid basis for the investigation into this 142 combinatorial ability (Townsend et al., 2018). Here, we provide the first step in 143 demonstrating that magpies may be capable of producing call combinations by quantifying 144 the extent to which the calls comprising the combination are (a) acoustically distinct units 145 and (b) acoustically equivalent to those produced alone.

146		
147	2.	Methods
148		
149	2.1.	Study site and animals
150		
151	Fourte	en groups of free-living magpies were chosen for this study. The groups were situated
152	in the	urban Perth suburbs of Guildford (31°89'S, 115°96'E) and Crawley (31°98'S,
153	115°81	1'E), within Western Australia. Many individuals within these groups have been ringed
154	for ide	entification and are habituated to human presence, therefore allowing observation and
155	vocal 1	recording at a close distance (Ashton et al., 2018; Edwards et al., 2015; Mirville et al.,
156	2016).	
157		
158	2.2.	Natural observations and acoustic recording
159		
160	We rea	corded naturally occurring vocalizations and the context in which they were given,
161	while	following groups in the field to compile a database of independent calls and potential
162	call co	mbinations. Vocalizations were recorded at a 44.1 kHz sampling rate using a Roland
163	R-05 d	ligital wave/mp3 recorder coupled to a Rode NTG2 directional condenser microphone
164	encase	ed in a Rode Blimp Suspension Windshield. Data collection was conducted during
165	observ	vations sessions (4-6 hours/session) on 27 days between June and August 2017. Data
166	was pr	imarily collected in the morning to coincide with the higher activity levels of magpies
167	(Edwa	rds et al., 2015). Recording focused on adult magpies, with no restriction based on sex.
168		
169	We ob	tained over 500 recordings of distinct magpie vocalizations, which were extracted from

170 ~150 hours spent following groups in the field. The recordings we obtained were added to a 171 sound database that already contained over 2000 recordings (~12 hours of raw material) collected by the University of Western Australia's (UWA) magpie research group from 2014 172 173 to 2017. Within the database, the independent vocalizations were categorised into the following call types based primarily on auditory and observational features; begging, feeding 174 175 grunt, alarm, alert, carol, chorus (more than two individuals carolling at the same time), and 176 mimicry. Within each call type, calls were then further categorised into similar acoustic units 177 based on visual (spectrographic) features. The following contextual details were logged 178 where possible for each recording; caller identity and behaviour immediately prior 179 to/following vocalization, group members present, stimulus or disturbance, and group 180 response (vocal and behavioural).

181

182 Periods of silence have been used as a method of classifying boundaries between acoustic 183 units in numerous previous studies, including research on birdsong in zebra finches 184 (Taeniopygia guttata, Franz & Goller, 2002), killer whale (Orcinus orca) calls (Shapiro, 2011), and gorilla (Gorilla beringei beringei & G. gorilla gorilla) close calls (Hedwig et al., 185 186 2014). Previous research on magpie song production indicated duration of mini-breaths between song syllables to be roughly < 0.3 seconds (Suthers et al., 2011). As this study 187 188 focussed on alarm and alert calls rather than song production, we have slightly increased the 189 period of silence between calls to reflect the observed trend in periods of silence in call series 190 (independent calls produced consecutively) versus call combinations (two or more calls 191 produced in concatenation). As such, in this study, we defined calls as either discrete calls 192 (singular independent units separated by a period of silence equal to or greater than 0.5 193 seconds) or potential call combinations (independent units separated by a period of silence

less that 0.5 seconds). This is based on visual inspection of spectrograms of individual calls,discrete call series, and potential call combinations.

196

197 A subset database was created focussing on the calls that, from preliminary field observation 198 and acoustic investigation, were (a) given frequently and (b) flexibly combined into a larger 199 sequence (see Figure 2 for examples). The subset database included the number of recordings 200 obtained for each call type from each individual from each group, and their respective 201 observational contexts. From the subset database, one type of alarm-alert sequence (Figure 1) 202 was chosen for acoustic analysis. This sequence was chosen based on the number of different 203 groups recorded producing this vocalization (N=11) and the high frequency of occurrence of 204 this sequence (and its comprising calls) detected during observational research.

205

206 2.3. Acoustic analysis

207

208 Calls were assessed for quality (where high quality = high signal to background noise ratio), 209 and the percentage of the call demonstrating clear, tonal structures using Audacity 2.1.2 210 (Audacity Team, 2016). Due to a limitation in the number of good-quality recordings of each 211 discrete call type in all test groups, only 26 recordings of the alarm, 9 recordings of the alert 212 and 19 recordings of the alert-alarm sequence, were used for analysis (our study site is 213 located within an urban matrix and so many recordings were compromised by background 214 noise). Spectrographic cross-correlation (SPCC) analyses were run to compare the recordings 215 within each call-type to determine if the calls were correlated. Analyses were then undertaken 216 to determine if the two calls are distinct in structure, and to compare the recordings of 217 discrete calls with the respective sequence component to determine similarity in structure.

SPCC compares the structural features in time-frequency spectrograms of two calls or
sounds, taking a peak correlation value as a measure of similarity and generating a matrix of
similarity values for each pair of calls in the analysis (Cortopassi & Bradbury, 2012).

221

222 To verify that alarm and alert calls are independent units that are structurally distinct from 223 each other, both the discrete calls and their respective sequence components were cross-224 correlated with the other call type using SPCC. A procedure based on the Mantel test was 225 then used to test the null hypothesis that the calls grouped into the alarm or alert categories 226 were no more similar to other calls within their own group than to calls within the other call-227 type group. As such, the SPCC matrix was compared with a second 'hypothesis' matrix 228 which contained a binary code, whereby '1' represented same-group comparisons and '0' 229 represented different-group comparisons in equivalent positions ('group' is defined as the 230 recording being either an alarm or alert call, Schnell et al., 1985). A p-value less than the 231 alpha (set at 0.05) indicates the two calls are structurally distinct.

232

SPCC and Mantel testing were then used to test the null hypothesis that the discrete calls
were no more similar to each other than to their respective component in the call sequence,
using the same protocol as described above (Schnell et al., 1985). A p-value > 0.05 indicates
the structure of the discrete call is similar to the structure of its respective sequence
component, therefore confirming the two discrete calls are structurally combined into a
sequence.

239

All SPCC analyses were conducted using Batch Correlation Analysis in Raven (Bioacoustics
Research Program, Cornell University, Ithaca, 2017) using normalized Hamming window

242	spectrographic correlation analysis on peak values, with a band pass filter from 500Hz to 22,
243	000Hz.
244	
245	
246	3. Results
247	
248	Spectrographic cross-correlation analyses revealed distinct call structure, with calls correlated
249	within each call-type. The mean correlation coefficient was consistent across cross-
250	comparisons of alarm calls (SPCC: $\overline{x} = 0.30$, n = 325), alert calls (SPCC: $\overline{x} = 0.34$, n = 36),
251	and alarm-alert sequences (SPCC: $\overline{x} = 0.34$, n = 171).
252	
253	Mantel tests comparing correlation coefficients for alarm and alert call-type comparisons
254	were highly significant (10,000 permutations, $r = 0.284$, $p < 0.0001$), indicating the two calls
255	(alert and alarm) are structurally distinct from one another (Table 1).
256	
257	Pairwise comparison analysis indicated the two discrete calls were correlated with their
258	respective sequence counter-parts. Mantel tests comparing correlation coefficients from
259	pairwise comparisons of each of the discrete calls with their respective cut-sequence
260	components were non-significant for both alarm (10,000 permutations, $r = 0.022$, $p = 0.488$)
261	and alert calls (10,000 permutations, $r = 0.019$, $p = 0.706$) (Figure 3, Table 1). Therefore,
262	recordings of the discrete calls were no more similar to one another than to their respective
263	component cut from the sequence.
264	

4. Discussion

267	Using acoustic analyses, we investigated a potential call combination in the Western
268	Australian magpie. Our results indicate that the alarm and alert calls are both acoustically
269	distinct from one another but similar in structure to their respective sequence counterparts.
270	Furthermore, spectrographic correlation analyses revealed similarity across recordings from
271	multiple individuals, of the alarm, alert and sequence calls. These results provide evidence
272	that the alarm and alert calls are distinct, highly repeatable calls that occur across all study
273	groups and, at least at the structural level, are combined into an alarm-alert sequence.
274	
275	The extent to which the detected combination of alarm and alert calls in the Western
276	Australian magpie represents a syntactic-like structure, however, requires follow up
277	experimental verification. Such experiments are key to unpacking the function of the
278	independent calls and the combination via assessing receiver response in the absence of the
279	stimuli that naturally elicit the vocalisations (see Suzuki et al., 2016 & Engesser et al., 2016).
280	
281	Furthermore, although initial evidence is provided here for one potential call combination,
282	preliminary observational data indicate magpies may be capable of flexibly creating
283	combinations larger than a two-call construction, which has, to our knowledge, yet to be
284	demonstrated in a non-human animal communication system (see Figure 2 e-h for potential
285	examples, Russell & Townsend, 2017). Hence, follow up work is critical to assess the extent
286	to which (a) magpies use call combinations, (b) whether these combinations are functionally
287	relevant and meaningful to receivers, and (c) whether these combinations are indeed
288	indicative of compositional syntax, or rather combinatoriality.
289	

290 Our finding of a candidate call combination in magpies (if validated under future 291 experimental investigation), in addition to previous research indicating similar rudimentary compositionality in primates (Ouattara et al., 2009) and other bird species (Engesser et al., 292 293 2016; Suzuki et al., 2016), further suggests that the capability for syntactic-like structuring in 294 vocal communication is not confined to humans, and may instead be phylogenetically 295 widespread (Collier et al., 2014). Such research can aid in bridging the gap between human 296 and animal communication, and potentially shed light on the evolutionary development of 297 complex vocal communication systems (Russell & Townsend, 2017).

298

299 It has been hypothesized that a transition to syntax may have evolved as a result of natural 300 selection favouring the combining of meaningful calls when the number of relevant events 301 needing to be communicated exceeds the number of calls available (Nowack et al., 2000). 302 Thereafter, simple two-word or sign combinations may have occurred as a means of 303 increasing lexicon size (Russell & Townsend, 2017). Interestingly, previous and ongoing 304 work suggests mappies' already have an extensive vocal repertoire facilitated in part by their 305 capacity to vocally imitate (Brown & Farabaugh, 1997; Kaplan, 2005; Suthers et al., 2011). 306 Why magpies would need to combine calls to communicate new events if they could instead 307 incorporate a new call/sound into their repertoire is therefore unclear. A bias towards 308 combinatoriality could, in principle, be driven by working memory constraints on the part of 309 the receiver: deriving meaning compositionally places less load on working memory than 310 learning and storing a new call type (Nowack et al., 2000). Further work investigating the 311 processing of calls will help shed light on the pressures driving combinatoriality in magpies, 312 which in turn has the potential to shed light on the evolution of human syntax given that 313 humans are also open-ended vocal production learners.

315	Investigating the presence of combinatoriality in animals is a critical first step to
316	understanding the origins and phylogenetic spread of this key linguistic ability. Our results
317	demonstrating combinatorial structures in Western Australian magpies contributes to recent
318	work showing that avian species are capable of producing and processing call combinations
319	(Engesser et al., 2016; Suzuki et al., 2016), in turn indicating that the phylogenetic spread of
320	this capacity is greater than previously thought. Critically, our research provides important
321	initial evidence of the presence of call combinations in a vocal learning species (excluding
322	Homo sapiens), which has interesting implications for theories explaining the evolution of
323	combinatoriality more generally. These results set the foundation for further experimental
324	investigations into syntactic-like structures in this species – a vital step in furthering our
325	understanding of this largely enigmatic field (Suzuki et al., 2018; Townsend et al., 2018).
326	
327	Acknowledgements
327 328	Acknowledgements This project was funded by the School of Biological Sciences and a University Collaboration
328	This project was funded by the School of Biological Sciences and a University Collaboration
328 329	This project was funded by the School of Biological Sciences and a University Collaboration Award from the University of Western Australia and an Australian Research Council
328 329 330	This project was funded by the School of Biological Sciences and a University Collaboration Award from the University of Western Australia and an Australian Research Council Discovery Grant (DP140101921) to ARR. SWT was funded by the Swiss National Science
328329330331	This project was funded by the School of Biological Sciences and a University Collaboration Award from the University of Western Australia and an Australian Research Council Discovery Grant (DP140101921) to ARR. SWT was funded by the Swiss National Science
 328 329 330 331 332 	This project was funded by the School of Biological Sciences and a University Collaboration Award from the University of Western Australia and an Australian Research Council Discovery Grant (DP140101921) to ARR. SWT was funded by the Swiss National Science Foundation (Grant number: PP00P3_163850).
 328 329 330 331 332 333 	This project was funded by the School of Biological Sciences and a University Collaboration Award from the University of Western Australia and an Australian Research Council Discovery Grant (DP140101921) to ARR. SWT was funded by the Swiss National Science Foundation (Grant number: PP00P3_163850).
 328 329 330 331 332 333 334 	This project was funded by the School of Biological Sciences and a University Collaboration Award from the University of Western Australia and an Australian Research Council Discovery Grant (DP140101921) to ARR. SWT was funded by the Swiss National Science Foundation (Grant number: PP00P3_163850). References
 328 329 330 331 332 333 334 335 	This project was funded by the School of Biological Sciences and a University Collaboration Award from the University of Western Australia and an Australian Research Council Discovery Grant (DP140101921) to ARR. SWT was funded by the Swiss National Science Foundation (Grant number: PP00P3_163850). References Arnold, K., & Zuberbühler, K. (2006). Semantic combinations in primate calls. <i>Nature, 441</i> ,
 328 329 330 331 332 333 334 335 336 	This project was funded by the School of Biological Sciences and a University Collaboration Award from the University of Western Australia and an Australian Research Council Discovery Grant (DP140101921) to ARR. SWT was funded by the Swiss National Science Foundation (Grant number: PP00P3_163850). References Arnold, K., & Zuberbühler, K. (2006). Semantic combinations in primate calls. <i>Nature, 441</i> ,

338	Ashton, B., Ridley, A., Edwards, E., & Thornton, A. (2018). Cognitive performance is linked
339	to group size and affects fitness in Australian magpies. Nature, 554(7692), 364-367. doi:
340	10.1038/nature25503
341	
342	Audacity Team. (2016). Audacity (R): Free Audio Editor and Recorder (Version 2.1.2)
343	[Computer Program]. Retrieved from http://audacity.sourceforge.net/
344	
345	Baker, M. C. (2009). Information Content in Chorus Song of the Group-Living Australian
346	Magpie (Cracticus tibicen dorsalis) in Western Australia. Ethology, 115, 227-238. doi:
347	10.1111/j.1439-0310.2008.01606.x
348	
349	Bioacoustics Research Program. (2017). Raven Pro: Interactive Sound Analysis Software
350	(Version 1.5) [Computer Software]. Ithaca, NY: The Cornell Lab of Ornithology. Retrieved
351	from www.birds.cornell.edu/raven
352	
353	Brown, E., & Farabaugh, S. (1991). Song sharing in a group-living songbird, the Australian
354	magpie, Gymnorhina tibicen, III: Sex Specificity and individual specificity of vocal part in
355	communal chorus and duet songs. Behaviour, 118, 244-274.
356	
357	Brown, E., & Farabaugh, S. (1997). What birds with complex relationships can tell us about
358	vocal learning: vocal sharing in avian groups. Social influences on vocal development, 98127.
359	
360	Collier, K., Bickle, B., van Schaik, C. P., Manser, M. B., & Townsend, S. W. (2014).
361	Language evolution: syntax before phonology? Proceedings of the Royal Society B,

362 281(1788), 20140263. doi: 10.1098/rspb.2014.0263

- 363
- 364 Cortopassi, K. A., & Bradbury, J. W. (2012). The Comparison of Harmonically Rich Sounds
- 365 using Spectrographic Cross-Correlation and Principal Coordinates Analysis. *Bioacoustics:*
- 366 *The International Journal of Animal Sound and its Recording*, *11*(2), 89-127. doi:
- 367 10.1080/09524622.2000.9753454
- 368
- 369 Edwards, E., Mitchell, N., & Ridley, A. (2015). The impact of high temperatures on foraging
- behaviour and body condition in the Western Australian Magpie Cracticus tibicen dorsalis.
- 371 Ostrich, 86(1-2), 137-144. doi: 10.2989/00306525.2015.1034219
- 372
- 373 Engesser, S., Crane, J. M., Savage, J. L., Russell, A. F., & Townsend, S. W. (2015).
- 374 Experimental Evidence for Phonemic Contrasts in a Nonhuman Vocal System. *PLoS Biol*,
- 375 *13*(6), e1002171. doi: 10.1371/journal.pbio.1002171
- 376
- 377 Engesser, S., Ridley, A., & Townsend, S. W. (2016). Meaningful call combinations and
- 378 compositional syntax in the southern pied babbler. *Proceedings of the National Academy of*
- 379 Sciences, 113(21), 5976-5981. doi: 10.1073/pnas.1600970113
- 380
- 381 Farabaugh, S., & Brown, E. (1988). Song sharing in a group living songbird, the Australian
- 382 magpie, *Gymnorhina tibicen*. Part I. Vocal sharing within and among social groups.
- 383 Behaviour, 104, 1-29.
- 384
- 385 Franz, M., & Goller, F. (2002). Respiratory units of motor production and song imitation in

386 the zebra finch. *Journal of Neurobiology*, *51*(2), 129-141. doi: 10.1002/neu.10043

387

Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The Faculty of Language: What Is It,
Who Has It, and How Did It Evolve? *Science*, *298*(5598), 1569-1579.

390

- 391 Hedwig, D., Hammerschmidt, K., Mundry, R., Robbins, M., & Boesch, C. (2014). Acoustic
- 392 structure and variation in mountain and western gorilla close calls: a syntactic approach.
- 393 Behaviour, 151, 1091-1120. doi: 10.1163/1568539X-00003175

394

- Hedwig, D., Mundry, R., Robbins, M., & Boesch, C. (2015). Contextual correlates of
- 396 syntactic variation in mountain and western gorilla close-distance vocalizations: Indications
- 397 for lexical or phonological syntax? Animal Cognition, 18, 423-435. doi: 10.1007/s10071-

398 0140812-6

- 399
- 400 Hughes, J., Hesp, J., Kallioinen, R., Kempster, M., Lange, C., Hedstrom, K., Mather, P.,

401 Robinson, A., & Wellbourn, M. (1996). Differences in Social Behaviour Between

402 Populations of the Australian Magpie *Gymnorhina tibicen*. *EMU*, *96*, 65-70.

403

- 404 Hurford, J. (2011). The evolution of human communication and language. In P. D'Ettorre &
- 405 H. D. P (Eds.), *Sociobiology communication: and interdisciplinary perspective*. Oxford, UK:
- 406 Oxford University Press.

- 408 Hurford, J. (2012). The Origins of Grammar: Language in the Light of Evolution II. Oxford,
- 409 UK: Oxford University Press.

411	Kaplan, G. (2000). Song structure and function of mimicry in the Australian magpie
412	(Gymnorhina tibicen) compared to the lyrebird (Menura ssp.). Int J Comp Psych, 12, 219241.
413	
414	Kaplan, G. (2004). Australian Magpie: Biology and Behaviour of an Unusual Songbird.
415	Collingwood, Victoria: CSIRO Pub.
416	
417	Kaplan, G. (2005). Vocal behaviour of Australian Magpies (Gymnorhina tibicen): A Study of
418	Vocal Development, Song Learning, Communication and Mimicry in the Australian Magpie.
419	PhD Thesis, University of Queensland.
420	
421	Kaplan, G. (2006). Alarm calls, communication and cognition in Australian magpies
422	(Gymnorhina tibicen). Act Zool Sinica, 52, 614-617.
423	
424	Kaplan, G. (2008). Alarm calls and referentiality in Australian magpies: Between midbrain
425	and forebrain, can a case be made for complex cognition? Brain Research Bulletin, 76,
426	253263. doi: 10.1016/j.brainresbull.2008.02.006
427	
428	Kaplan, G., Johnson, G., Koboroff, A., & Rogers, L. J. (2009). Alarm calls of the Australian
429	Magpie (Gymnorhina tibicen): Predators Elicit Complex Vocal Responses and Mobbing
430	Behaviour. The Open Ornithology Journal, 2, 7-16. doi: 10.2174/1874453200902010007
431	
432	Kaplan, G., & Rogers, L. J. (2013). Stability of referential signalling across time and
433	locations: testing alarm calls of Australian magpies (Gymnorhina tibicen) in urban and rural

- 434 Australia and in Fiji. *PeerJ*, e112. doi: 10.7717/peerj.112
- 435
- 436 Mirville, M., Kelley, J., & Ridley, A. (2016). Group size and associative learning in the
- 437 Australian magpie (*Cracticus tibicen dorsalis*). Behavioural ecology and sociobiology, 70(3),
- 438 417-427. doi: 10.1007/s00265-016-2062-x
- 439
- Nowack, M., Plotkin, J., & Jansen, V. (2000). The evolution of syntactic communication. *Nature*, 404, 495-498. doi: 10.1038/35006635
- 442
- 443 Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009). Campbell's Monkeys use Affixation
- to Alter Call Meaning. *PLoS ONE*, 4(11), e7808. doi: 10.1371/journal.pone.0007808
- 445
- Russell, A. F., & Townsend, S. W. (2017). Communication: Animal Steps on the Road to
 Syntax? *Current Biology*, *27*, R753-R755. doi: 10.1016/j.cub.2017.06.066.
- 448
- 449 Schnell, G. D., Watt, D. J., & Douglas, M. E. (1985). Statistical comparison of proximity
- 450 matrices: applications in animal behaviour. *Animal Behaviour, 33,* 239-253.
- 451
- 452 Shapiro, A. D., Tyack, P. L., Seneff, S. (2011). Comparing call-based versus subunit-based
- 453 methods for categorizing Norweigian killer whale, *Orcinus orca*, vocalizations. Animal
- 454 *Behaviour*, 81(2), 377-386.
- 455
- 456 Silvestri, A. (2017) The discrimination of alarm callers based on reliability in Western
- 457 Australian magpies (Cracticus tibicen dorsalis). Honours' Thesis, University of Western

- 458 Australia.
- 459
- 460 Suthers, R. A., Wild, J. M., & Kaplan, G. (2011). Mechanisms of song production in the
- 461 Australian magpie. J Comp Physiol A Neuroethol Sens Neural Behav Physiol, 197(1), 45-49.
- 462 doi: 10.1007/s00359-010-0585-6.
- 463
- Suzuki, R., Buck, J. R., & Tyack, P. L. (2006). Information entropy of humpback whale
 songs. *Journal of the Acoustical Society of Amercia*, *119*(3), 1849-1866. doi:
- 466 10.1121/1.2161827
- 467
- 468 Suzuki, T. N., Wheatcroft, D., & Griesser, M. (2016). Experimental evidence for
- 469 compositional syntax in bird calls. *Nature Communications*, 7, 10986. doi:
- 470 10.1038/ncomms10986
- 471
- 472 Suzuki, T. N., Wheatcroft, D., & Griesser, M. (2018). Call combinations in birds and the
- 473 evolution of compositional syntax. *PLoS Biol*, 16 (8): e2006532
- 474
- 475 Townsend, S. W., Engesser, S., Stoll, S., Zuberbühler, K., Bickel, B. (2018).
- 476 Compositionality in animals and humans. *PLoS Biol, 16.*
- 477
- 478 Tyack, P. L. (1983). Differential response of humpback whales, *Megaptera noveangliae*, to
- 479 playback of song or social sounds. *Behavioral Ecology and Sociobiology*, 13, 49-55.
- 480
- 481 Walsh, Sarah. (2017). Evidence for potential compositional syntax in an Australian songbird:

- 482 a step toward understanding the evolution of language. Honours' Thesis, University of
- 483 Western Australia.
- 484
- 485 Zuidema, W & de Boer, B. (2018). The evolution of combinatorial structure in language.
- 486 *Current Opinion in Behavioural Sciences*, 21: 138-144.
- 487
- 488 **TABLE**
- 489

490 **Table 1. Comparisons of different calls types using Mantel test.**

Comparison	Mean Correlation	r	Р
Alarm vs Sequence-Cut Alarm	0.315	0.022	0.488
Alert vs Sequence-Cut Alert	0.355	0.019	0.706
Alarm vs Alert	0.269	0.284	<0.0001*

491 Mantel tests were based on correlation coefficients obtained from SPCC on discrete calls versus respective

492 sequence components and alarm call versus alert call. 18 recordings of each sequence-cut call, 26 recordings of

493 alarm calls, and 9 recordings of alert calls were used in analysis. Asterisks indicates significant difference in call
494 comparison whereby p<0.05.

495

496**FIGURE LEGENDS**

497

498 Figure 1. Spectrograms of the independent (a) alarm and (b) alert calls, and the (c) sequence

they comprise which was used for acoustic analysis. Calls are separated into independent

500 units (indicated by black lines) based on their occurrence with a period of at least 0.5 second

501 of silence in between calls.

503	Figure 2. Spectrograms of magpie alarm (a & b), alert (c & d) calls and potential call
504	combinations (e-h). Calls are separated into independent units (indicated by black lines)
505	based on their occurrence with a period of at least 0.5 second of silence in between calls.
506	
507	Figure 3. Distribution of correlation coefficients obtained from SPCC on pairwise
508	comparison of each alarm and alert call-types. Calls were correlated within each call-type.
509	Boxes show the medians and interquartile ranges, and whiskers show the ranges (n = number

510 of comparisons).