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1 **TITLE**

2 Nest-associated vocal behaviours of the south-eastern red-tailed black-cockatoo,

3 Calyptorhynchus banksii graptogyne, and the Kangaroo Island glossy black-cockatoo, C.

4 lathami halmaturinus

5 ABSTRACT

6 Animal vocalisations can signify diverse behavioural contexts, knowledge of which 7 can be applied in bioacoustic monitoring programs. Australia's endemic black-cockatoos 8 (Calyptorhynchus sp., family Cacatuidae) are highly vocal species that are threatened in many locations. In this study, we describe the nest-associated vocal behaviours of two 9 10 endangered subspecies of black-cockatoo, the south-eastern red-tailed black-cockatoo, C. banksii graptogyne, and the Kangaroo Island glossy black-cockatoo, C. lathami 11 12 halmaturinus. Breeding success is limiting their recoveries and nest monitoring is challenging, but vocal recordings might provide valuable long-term information hard to 13 14 obtain otherwise. We recorded daily vocal activity at wild nests of both cockatoos using 15 autonomous sound recorders. Combined with behavioural observations and video footage, we identified vocalisations characteristic of six behavioural contexts at nests: birds in flight, 16 while perched, during begging (adult females), during courtship displays (adult males), when 17 18 entering or sitting near to the nest hollow entrance (adult females), and from nestlings. Linear discriminant analysis on 12 acoustic measurements correctly classified 58.4% of calls of the 19 red-tailed black-cockatoo (n = 907 calls from eight nests) and 62.9% of calls of the glossy 20 black-cockatoo (n = 1,632 calls from 11 nests). In both subspecies, the female nest call and 21 22 nestling calls are the most conspicuous vocal indicators of active nesting, and therefore 23 should be considered for their bioacoustic potential. Other adult vocalisations indicate a range

of behavioural contexts that could be informative for monitoring nesting behaviour, and its
association to habitat features, in these endangered subspecies.

26 **KEYWORDS**

27 Bioacoustics, Calyptorhynchus spp., Nesting, Discriminant analysis, Vocal behaviour

28 INTRODUCTION

Animal vocalisations can signify diverse behavioural states. For vocal species, sound 29 30 data collected in bioacoustic studies can therefore indicate particular behavioural contexts, which can benefit conservation if they provide new insights into a population's state, 31 trajectory or response to management (Teixeira et al. 2019). For example, critical life history 32 events like mating and recruitment may be detected via context-specific vocalisations (e.g. 33 African elephant copulation; Poole 2011) or changes in group-level vocalisations (e.g. a shift 34 35 in acoustic energy of Iberian Wolf packs when juveniles are present; Palacios et al. 2016). Therefore, knowledge on the behavioural contexts associated with particular vocalisations 36 37 can improve the resolution and application of bioacoustic data beyond population metrics 38 such as species presence-absence, population density or abundance. As technology advances, the efficiency and cost-effectiveness of acquiring data from species' vocalisations is likely to 39 improve, warranting improved incorporation of vocal behaviour into bioacoustic monitoring 40 programs. To achieve this, the vocal behaviours that could provide conservation-relevant data 41 must be described for the species of interest. 42

Parrots are among the most social, intelligent and vocally complex avian species
(Bradbury and Balsby 2016; Cussen 2017). They are one of few taxa able to learn new
vocalisations throughout life (open-ended vocal learning), an ability hypothesised to be an
adaptation to their highly social foraging behaviours (Bradbury and Balsby 2016). Australia's

endemic black-cockatoos, comprising five species of genus Calyptorhynchus (family 47 Cacatuidae), are highly social parrots, often found in large, noisy flocks (Higgins 1999). 48 Nesting is semi-communal, with nests often aggregated in the landscape (Johnstone et al. 49 2013; DT pers. obs.). Clutches comprise one or two eggs, and overall reproductive output is 50 low. Eggs hatch after about four weeks' incubation and fledging occurs ten to twelve weeks 51 later (Higgins 1999; Johnstone and Kirkby 2008). Fledgling cockatoos have a long parental 52 53 dependency period (Higgins 1999), possibly up to 24 months in some populations (forest redtailed black-cockatoo, C. banksii naso; Johnstone et al. 2013). As in other parrots, young 54 55 cockatoos likely learn their early vocalisations from their parents, with whom they have contact at the nest, and develop their adult repertoire from social interactions in larger flocks 56 during the fledgling period. 57

Given their sociality, it is likely that black-cockatoos' different vocalisations reflect 58 different behavioural contexts. This is shown in the other cockatoos, including the closely-59 60 related Carnaby's black-cockatoo, C. latirostris (Saunders 1983), and the palm cockatoo, 61 Probosciger aterrimus (Zdenek et al. 2015). As such, black-cockatoos are good candidates for bioacoustic monitoring of behaviour, with potential benefits for conservation. Indeed, 62 63 every black-cockatoo species is listed as threatened under state or national legislation in at least part of its range, and bioacoustics could aid monitoring. Currently, monitoring and 64 management vary among species and populations, but often rely on citizen science activities 65 coordinated by non-profit organisations (e.g. Birdlife Australia's Great Cocky Count). These 66 activities usually involve counting birds in flocks, such as at roosts or drinking sites. Such 67 68 data can be useful for understanding trends in flock size, demographic structure and occupancy in the landscape. However, methods for collecting data from other contexts, 69 70 particularly during the breeding season, are limited. If behaviour-specific vocalisations can be reliably identified, then obtaining data from other contexts, such as nesting, should beachievable using bioacoustic methods.

73 In this study, we investigated the nest-associated vocalisations of two endangered subspecies of black-cockatoo, the Kangaroo Island glossy black-cockatoo, C. lathami 74 75 halmaturinus, and the south-eastern red-tailed black-cockatoo, C. banksii graptogyne. We 76 focussed specifically on vocal behaviours associated with nesting because efforts to monitor breeding in these subspecies have been restricted, despite their recoveries being limited by 77 breeding success (Russell et al. 2018; Berris et al. 2018). The Kangaroo Island glossy black-78 79 cockatoo's population size is the smallest of any black-cockatoo (373 individuals counted in the 2016 census; Berris et al. 2018). Until 2016, when the recovery program's funding was 80 reduced dramatically, up to 50 nests were monitored each breeding season. However, human 81 resource requirements were substantial, and the funding reductions have seen monitoring 82 efforts greatly reduced. For the south-eastern red-tailed black-cockatoo, whose declining 83 84 population numbers about 1400 individuals, monitoring of breeding has always been limited 85 (Russell et al. 2018). Nests are difficult to monitor because they are remote, rare in the landscape and are often on private land, making it challenging to observe nests through to 86 87 fledging or failure. Breeding success is inferred from the demographic structure of flocks, and increases in the proportion of male birds over recent years suggests a decrease in 88 breeding output (Russell et al. 2018). For this reason, a high priority for conservation is to 89 develop efficient methods for nest monitoring. 90

91 This study aimed to describe the nest-associated vocalisations of the south-eastern
92 red-tailed black-cockatoo and the Kangaroo Island glossy black-cockatoo. For these
93 subspecies, the only adult vocalisation reported from nests is the nest call of the Kangaroo
94 Island glossy black-cockatoo, given by adult females when entering or prospecting a nest

hollow (Pepper 1996). Vocalisations of nestlings are not formally described in either red-95 tailed or glossy black-cockatoos, although Cameron (2009) in studying the eastern subspecies 96 of glossy black-cockatoo, C. lathami lathami, defined late-stage nests as those where 97 nestlings gave "harsh growling" calls upon the return of the nesting female. Here, for both 98 subspecies, we aimed to qualitatively describe the behavioural contexts associated with each 99 call type given at nests and to provide quantitative acoustic measurements for each. We 100 101 hypothesised that adult and nestling birds give unique vocalisations in various behavioural contexts, and that these are distinct in acoustic structure. This knowledge may reveal 102 103 important information about critical life history events and, more specifically, the potential for bioacoustics to provide a novel method with which to monitor nesting behaviour. 104

105 METHODS

106 Study sites

107 Data for the south-eastern red-tailed black-cockatoo were collected from areas near Casterton and Edenhope in south-west Victoria, Australia. The cockatoos commonly nest in 108 dead and isolated river red gums, *Eucalyptus camaldulensis*, that occur in livestock paddocks. 109 Given their relative ease of observation and accessibility, paddock trees were the focus of 110 data collection for this study. Nests were located through active searching in spring and 111 summer. Typically, cockatoos in flight were detected by their calls and then followed to 112 identify if they approached a nest hollow. This method allowed active nests to be confirmed 113 without the need for tree-climbing, which is normally unsafe as the trees are dead. Some trees 114 were inspected with a pole-mounted camera at later stages of nesting to confirm their 115 continued activity. 116

117 On Kangaroo Island, data for the glossy black-cockatoo were collected from several
118 nesting areas that are routinely monitored by the state government. To increase the

cockatoos' breeding opportunities, many artificial nest hollows have been installed on the 119 island, and these have been successfully used by the cockatoos for many years (Berris et al. 120 121 2018). Nesting occurs in several habitat types, including conservation estates, roadsides, regenerated woodlands, and residential and agricultural areas (MB, pers. obs.), all of which 122 are represented in this study. No preference was given to either natural or artificial hollows 123 for this study. Nest activity was confirmed via afternoon observations, as in the red-tailed 124 125 black-cockatoo, via nest inspection with a pole-mounted wireless camera, or via a female's presence at the nest hollow entrance. Laying is thought to peak in March and April (MB, 126 127 pers. obs.). For most nests, monitoring began during these months.

128 Acoustic data collection

129 For each active nest, an autonomous sound recorder (Frontier Labs Bioacoustic Audio Recorder, <u>https://frontierlabs.com.au/</u>) was installed on the nest tree or a nearby tree. If not on 130 the nest tree, recorders were within 5 metres of the nest tree to ensure that it was closer to the 131 nest of interest than to other nests; therefore, the loudest vocalisations could be confidently 132 assigned to the nest of interest. Recorders were approximately 8 - 30 metres from the nest 133 134 hollow, depending on whether they were fixed to the nest tree or a neighbouring tree. We chose to install recorders at this height, rather than at the hollow, because this is what would 135 be more feasible in a bioacoustic monitoring program. 136

Installed sound recorders were programmed to record for three hours per day, beginning at 2.5 hours before sunset (sunset-based schedule). This time period was chosen because this is when the cockatoos are most active at the nest (RH, MB, DT, pers. obs.). In addition, once a week, recording began half an hour before sunrise and ended half an hour after sunset (full-day schedule). This was done to capture any unexpected activity at the nest during the day. If a nestling was observed at a nest (i.e. a late-stage nest), we attempted to

update schedules to record at the full-day schedule every day, to maximise the likelihood of 143 recording the fledging event. This was not achieved for every nest. Recorders remained in 144 place until after the observed or expected date of fledging, unless nest failure was confirmed 145 sooner. All recordings were made using an omnidirectional microphone, with a fixed gain of 146 20 dB, at a sample rate of 44.1 kHz. Microphones had an 80 Hz high-pass filter to reduce the 147 effects of low frequency noise (e.g. wind). Recorders were fitted with four rechargeable 148 149 lithium ion batteries and one 128 GB SanDisk memory card, which were replenished at approximately 6-week intervals. All recordings were made in uncompressed wave (.wav) 150 151 format.

152 Behavioural classification

To describe the behavioural contexts of vocalisations recorded, observations of 153 cockatoos were carried out at and near nest trees. This included nests that were monitored 154 with autonomous sound recorders, as well as other nests that were opportunistically observed. 155 Cockatoos were filmed using a Canon 5D mark III DSLR camera and Canon 100-400 II IS 156 USM telephoto lens with a Rode VideoMic Pro microphone attached. Observation distance 157 158 was usually a minimum of 10 metres from the cockatoos' location but varied between 159 sessions. Observations were usually made in the late afternoon and early evening when the cockatoos are most active at the nest. Recording usually commenced when the cockatoos 160 161 were in plain sight and actively vocalising. Individuals were not marked but could be identified by their association with a nest. Observation length varied and depended primarily 162 on the length of time that the birds were within visual and auditory distance. Observations 163 164 were usually terminated by the cockatoos flying out of sight or by the female entering the nest hollow. Observations were also terminated in poor weather (rain or high wind). We did 165 not standardise observation time, frequency or recording length among nests, since most 166

observations were opportunistic and dependent on recording conditions and nest status.
Where possible, preference was given to nests where a nestling was observable at the hollow
entrance. Behavioural observations were conducted in both early and late stages of nest
development, although nestlings were only observed at late stages (DT, pers. obs.).

Call types and their associated behavioural contexts (Table 1) were putatively 171 described from field observations and video footage. Sound files were extracted from videos 172 using Adobe Media Encoder CC 2017. Spectrograms (Hann window; window size = 1024 173 samples; hop size = 512 samples; 50% overlap) and waveforms (oscillograms) were 174 inspected using RavenPro 1.5 (Cornell Lab of Ornithology, Ithaca, New York) and viewed in 175 tandem with videos to determine the behaviours associated with each call type. Behaviours 176 for both subspecies were classified into broad categories in line with the ethogram provided 177 by Pepper (1996) for the Kangaroo Island glossy black-cockatoo. Since the camera records 178 sound in compressed MPEG-4 AVC/H.264 format, spectrograms created from video data 179 180 were used only for visual purposes when classifying putative call types and behavioural 181 contexts. Quantitative measurements of each call type (Table S1) were only taken from recordings made with the autonomous sound recorders. 182

183 Quantitative structure of vocalisations

To efficiently select calls for quantitative analysis, we used recordings made in the final two weeks before fledging (or failure), as this time period represents the complete repertoire of conspicuous vocalisations at nests. This includes nestlings, which can be difficult to detect in earlier weeks (DT, pers. obs.). Most selections were made from nests where nestlings were recorded. Additional nests were included to increase sample sizes of adult calls, if required (see below). Selections were not made on days or during time periods where recording conditions were poor (e.g. high wind or rain).

For the south-eastern red-tailed black-cockatoo, selections were made from recordings 191 obtained at eight nests. For the Kangaroo Island glossy black-cockatoo, selections were made 192 193 from 11 nests. Calls were manually selected and annotated from spectrograms (Hann window; window size = 1024 samples; hop size = 512 samples; 50% overlap) and waveforms 194 using RavenPro 1.5. For each selection, upper and lower bounds (i.e. low frequency and high 195 frequency of the selection box) were set via inspection of the spectrogram, while start time 196 197 and end time were set via inspection of the waveform. For each call type, we aimed to select a minimum of 20 calls per nest, to sufficiently represent within-individual variation in call 198 199 structure (Fischer et al. 2013). For flight calls, we initially aimed to annotate at least 40 calls per nest, because both male and female adult birds give this call, however this was difficult to 200 achieve for the glossy black-cockatoo because male and female flight calls are often 201 202 overlapping and therefore unsuitable for acoustic analysis.

203 Calls that were selected were chosen *ad hoc* from those that showed relatively high 204 signal to noise ratio on the spectrogram and were not overlapping with other calls or 205 background noise. Each call selected was categorised by call type (behavioural category), age (adult or nestling) and, except for flight calls, sex (adult birds only). Quantitative 206 207 measurements recorded for each selected call were: (1) low frequency (Hz), (2) peak frequency (kHz), (3) centre frequency (kHz), (4) aggregate entropy (bits), (5) average entropy 208 (bits), (6) minimum entropy (bits), (7) maximum entropy (bits), (8) delta time (seconds), (9) 209 interquartile range duration (seconds), (10) peak amplitude (U), (11) peak frequency contour 210 average slope (Hz/ms), and (12) peak frequency contour maximum slope (Hz/ms) (Table S1). 211 212 We excluded high frequency measurements (e.g. high frequency, delta frequency, interquartile range bandwidth) because high frequency components were often attenuated by 213 distance. This differed among nests because the distance of the sound recorder to the nest 214

hollow varied, as did the distance between the sound recorder and the vocalising birds whennot in the nest hollow (i.e. the birds' position in the nest tree or nearby trees varied).

217 Statistical analysis

To examine for differences in putative call types (response variable), we conducted 218 linear discriminant analyses on the acoustic measurements (predictors; Table S1) using the 219 MASS package in R (Venables and Ripley 2002; R Core Team 2019). Acoustic 220 measurements were inspected for normality and transformed where necessary. For each 221 222 subspecies, the data (n = 907 selections of calls for the red-tailed black-cockatoo; n = 1,632selections of calls for the glossy black-cockatoo) were randomly divided into two separate 223 datasets, one as training data (70% of the original dataset), from which the discriminant 224 225 models were built, and the other as test data (30% of the original dataset). To account for different units of acoustic predictors, test data were centred and scaled using the caret 226 227 package (Kuhn 2008). Test data were used to classify call types. To further confirm model performance, each discriminant model was tested using leave-one-out cross validation on the 228 complete dataset. Results were very similar between the two approaches (Table S3). Finally, 229 230 each discriminant model was tested using a Multivariate Analysis of Variance (MANOVA). 231 Plots were made using ggplot2 in R (Wickham 2016).

232 **RESULTS**

For the south-eastern red-tailed black-cockatoo, 23 nests from eight locations were located over two breeding seasons. All nests were located on livestock farms, except for one nest that was in an artificial hollow in a plantation of Australian blue gum, *E. globulus*. In total, four nests were in artificial nest hollows. The remainder were most often in large, dead river red gums, *E. camaldulensis*. One nest was found in a live river red gum. Nesting occurred from September through March. Nestlings were recorded at nine nests. For the

Kangaroo Island glossy black-cockatoo, data were recorded from 28 nests in eight locations
over two breeding seasons. 18 nests were in artificial nest hollows. Natural nest hollows were
all in live sugar gums, *E. cladocalyx*. Nesting occurred from March through November.
Nestlings were recorded at 15 nests. Observed behaviours at nests were similar for the
Kangaroo Island glossy black-cockatoo and the south-eastern red-tailed black-cockatoo.

244 South-eastern red-tailed black-cockatoo

For the red-tailed black-cockatoo, we putatively described 11 call types (including 245 246 subtypes) from six behavioural categories (Table 1 and Figure 1). *Flight calls* were typically loud and harmonic in structure, given by adult birds (male and female) when flying to and 247 from the nest tree (Figure 1A). We considered the take-off call (adult male and female) to be 248 249 a subtype of the flight call, differing by having more arched frequency components 250 (downward inflection) (Figure 1B). *Begging calls* given by adult females were highly variable in structure and amplitude. These calls clearly exhibited non-linear phenomena, 251 252 including deterministic chaos, frequency jumps and sub-harmonics, often within a single bout of begging (Figs. 1C and 1D). Begging calls typically elicited head-bobbing and allofeeding 253 from the adult male. Early in the nesting period, females could often be heard begging from 254 inside the nest hollow in response to the approaching males' flight calls. Display calls were 255 256 sometimes given by males in response to females' begging. Display calls were highly 257 stereotypical and repetitive (Figure 1F) and involved head-bobbing and fanning of the tail 258 feathers. At two nests, display calls were given soon after alarm calling. Perch calls and nestling calls each comprised three subtypes, differentiated by their apparent loudness and 259 260 harmonic, chaotic or pulsatile structure. Perch calls (three subtypes) were given by adult males when the adult female was near or inside the nest hollow, presumably to maintain 261 262 contact with the female (Figure 1J-L). Perch calls were usually the final calls given in the day, except for take-off and flight calls as the male went to roost. Females sometimes called 263

when perched soon after flight, but we considered these calls to be flight calls because they 264 were not obviously different in sound or spectrographic structure. Adult females' nest call (or 265 nest entry call) was highly pulsatile, sometimes resembling nestlings' calls (Figure 1E). 266 These calls were not detected every day. The most commonly recorded *nestling calls* were 267 loud and broadband (Figure 1G). These calls usually began as the parents were flying to the 268 nest. These calls were easily heard up to 30 metres from the nest and were distinct on 269 270 spectrograms. Two subtypes of nestling calls (nestling subtype 2 and subtype 3; Figs. 1H and 1J) were quieter and given some time after the parents' arrival at the nest. These softer 271 272 varieties were more difficult to detect on spectrograms. Vocal behaviours and interactions between individuals at the nest were evident in spectrograms (Figure 3). 273

Acoustic measurements were obtained from a total of 939 selections of annotated 274 vocalisations, representing 11 call types (including subtypes) from eight nests, for the south-275 eastern red-tailed black-cockatoo. Descriptive statistics of each call type's acoustic 276 measurements are provided in Table S4. The sample size (i.e. number of annotated 277 vocalisations) of each call type varied between n = 5, for nestling subtype 3, and n = 251 for 278 the flight call. Three call subtypes (perch subtype 3, nestling subtype 3, and take-off) had 279 fewer than 20 annotations and were therefore excluded from subsequent analyses. The final 280 dataset used for analyses, therefore, comprised 907 selections of vocalisations. Linear 281 282 discriminant analysis correctly classified 58.4% of calls (MANOVA: Wilk's $\lambda = 0.16$, F =22.518, p < 0.001) (Figure 5). LD1 and LD2 explained 68.0% of the overall variance in the 283 model. Accuracy was highest for the display call (73.7%), followed by the flight call 284 (72.0%), and lowest for nestling subtype 2 (28.6%) (Table S2). Nestling subtype 2 was most 285 often misclassified as nestling subtype 1 or begging (Table S2). Perch subtype 1, with an 286 accuracy of 34.8%, was commonly misclassified as a flight call (Table S2). 287

288 Kangaroo Island glossy black-cockatoo

We putatively described 14 call types (including subtypes) from six behavioural 289 categories for the Kangaroo Island glossy black-cockatoo (Table 1 and Figure 2). Flight calls 290 291 were typically loud and overlapping, given by the adults when flying to and from the nest (Figure 2A). *Begging calls* were given by females and usually elicited allofeeding from the 292 male. Begging calls usually contained harmonics (Figure 2B) but were highly variable in 293 structure and showed clear non-linear phenomena (Figure 2C). Display calls were given by 294 295 males in the presence of the female. Display calls were highly stereotypical and repetitive (Figure 2D) and involved head-bobbing and fanning of the tail feathers. Adult females gave 296 297 nest calls when perched at, or near, the nest hollow entrance, but not on every occasion. Nest calls were highly pulsatile in structure, giving the call a 'growling' characteristic (Figure 2E). 298 Perch calls were given by adult males and females when perched on or near the nest tree. 299 300 They comprised six graded call types (Figure 2I-O). Perch subtypes 2 and 3, given by males, were the most common perch calls observed in the field and in sound recordings (Figure 2J-301 L). They are usually the final calls recorded on any given day. Female perch calls (subtypes 302 4, 5 and 6) were less commonly observed (Figure 2M-O). Nestling calls were typically loud, 303 given in response to the parents' arrival at the nest (subtype 1; Figure 2F). Nestling calls were 304 highly resemblant of the female nest call. Nestling subtype 2 was softer, given when the 305 306 nestling appeared less stimulated following the arrival of its parents (Figure 2G). Nestling subtype 3 was the softest subtype, given only when the female was close to the nestling 307 308 (Figure 2H). Vocal behaviours and interactions between individuals at the nest were evident in spectrograms (Figure 4). 309

Acoustic measurements were obtained from a total of 1,641 selections of annotated vocalisations, representing 14 call types (including subtypes) from 11 nests, for the Kangaroo Island glossy black-cockatoo. Descriptive statistics of each call type's acoustic measurements are provided in Table S4. The sample size of call types varied from n = 9, for the take-off

call, to n = 303 for nestling subtype 1. Due to low sample size, the take-off call was excluded 314 from further analysis. Therefore, the final dataset used for analyses comprised 1,632 315 selections. Linear discriminant analysis correctly classified 62.9% of calls (MANOVA: 316 Wilk's $\lambda = 0.04$, F = 47.362, p < 0.001) (Figure 5). LD1 and LD2 explained 81.2% of the 317 overall variance in the model. Nestling subtype 1 had the greatest classification accuracy 318 (87.8%) followed by begging (84.7%) (Table S2). Nestling subtype 2 had an accuracy of 319 320 73.2% and misclassifications were mostly nestling subtype 1 (Table S2). There was misclassification among flight calls and perch calls (Table S2). Perch subtypes 1 and 3 had no 321 322 correct classifications (Table S2). Perch subtype 1 was mostly classified as flight and perch subtype 5 was mostly classified as the female nest call (Table S2). 323

324 **DISCUSSION**

Bioacoustic sound recordings can provide a rich source of behavioural data for 325 species whose vocal diversity is known (see review by Teixeira et al. 2019). Particularly for 326 social species, which usually exhibit more complex repertoires (Freeberg et al. 2012; 327 328 Leighton 2017), vocalisations can indicate specific behaviours, demographics (e.g. age and sex of the caller) and interactions among individuals. Bioacoustic studies often focus on what 329 vocalisations a species makes; this helps determine presence-absence, a common objective of 330 bioacoustic studies. However, the ability to understand from vocalisations who the signaller is 331 and why they are vocalising (behavioural context) can greatly improve the resolution of data 332 acquired from bioacoustic programs (Teixeira et al. 2019). Through context-specific 333 vocalisations, bioacoustics could help to monitor species' behaviours and the relationship to 334 335 habitat features, and thereby inform conservation decision-making. A necessary first step, then, is to understand a species' vocal repertoire to the extent required for monitoring or 336 conservation. 337

In this study, we provide the first descriptions of the diversity of nest-associated vocal 338 behaviours of two endangered subspecies of black-cockatoo, the Kangaroo Island glossy 339 black-cockatoo, C. lathami halmaturinus, and the south-eastern red-tailed black-cockatoo, C. 340 banksii graptogyne. Through behavioural observations, we found that these subspecies gave 341 distinct vocalisations in each of six behavioural contexts at nests. Specifically, vocalisations 342 were identified from birds in flight, while perched, during begging (females), during 343 344 courtship displays (males), when entering or sitting near to the nest hollow entrance (females), and from nestlings when in the presence of their parents. This knowledge can be 345 346 used to develop novel nest monitoring methods using bioacoustic technology. This is important because bioacoustics using remote sound recorders allows for data to be collected 347 at spatial and temporal scales much greater than that feasible by human observers. This offers 348 an advantage for these subspecies as traditional monitoring is limited by human survey effort 349 and available funding. Even where active nests are known, monitoring their subsequent 350 development and outcome (fledging or failure) is difficult or, in many cases, is not achieved. 351 Moreover, bioacoustics could be used to monitor not only known active nests, but also 352 potential nests, such as tree hollows of unknown status, hollows used in previous years, and 353 newly deployed artificial nest hollows. 354

The female nest call and the nestling calls are the most conspicuous vocal indicators 355 of active nesting in these subspecies. These calls are loud, distinct and are, to the best of our 356 knowledge, the only calls that are unique to active nests (DT, RH, MB, pers. obs.). These 357 calls, therefore, are most relevant to bioacoustic monitoring programs. The female nest call 358 359 appears to function in close-range communication with the nestling and with the adult male when he is perched on the nest tree. In both subspecies, but especially the Kangaroo Island 360 glossy black-cockatoo, the nest call resembled the nestling call, which reduced linear 361 362 discrimination (Table S2). This may be a product of nestlings learning their calls from the

adult female, who is the only parent to enter the nest hollow in these species. Late-stage 363 nestling calls are characteristically loud upon the parents' arrival to the nest tree (subtype 1) 364 365 in both subspecies. These loud calls were clear and easily identified in spectrograms of sound recordings. Calls become softer and less-stimulated after the parents' arrival (subtype 2), but 366 the acoustic structure is otherwise similar. Although discrimination accuracy varied (glossy 367 black-cockatoo: 87.8% and 73.2% for subtypes 1 and 2, respectively; red-tailed black-368 369 cockatoo: 54.6% and 28.6% for subtypes 1 and 2, respectively; Table S2), nestling calls of both subspecies were distinct to the human ear and unlike other call types, except for some 370 371 cases of the female's nest call (DT, pers. obs.).

Female begging calls were highly variable within- and between-individuals of both 372 subspecies. Calls showed a range of nonlinear phenomena including deterministic chaos, 373 subharmonics and frequency jumps. The acoustic structure of calls observed on spectrograms 374 often varied substantially within a single begging bout (Figs. 1c and 2c). Though largely 375 376 untested in birds, one hypothesis regarding nonlinear sound states that the more variable and random (nonlinear) a call is, the less likely a receiver is able to ignore it (Blumstein and 377 Récapet 2009). That is, nonlinearity in animal communication has possibly evolved to attract 378 and maintain attention to increase fitness. For example, in African elephants, Loxodonta 379 africana, infant roars increase in chaos with the urgency of the situation (Stoeger et al. 2011). 380 In red deer, Cervus elaphus, the harsher the males' roars, the more attention they receive 381 from potential mates (Reby and Charlton 2012). It is possible, therefore, that the highly 382 nonlinear structure of female begging calls functions to limit habituation by the male and 383 384 consequently increase his provisioning of the female. Since females are solely responsible for provisioning the nestling, it is plausible that female begging has been subject to strong 385 selection pressures to increase provisioning rates. Likewise, the soft, begging-like nestling 386 387 call (subtype 3) also appeared to be nonlinear and has possibly evolved to stimulate

allofeeding by the female. Moreover, since both subspecies are highly specialised in diet,
begging call structure may relate to the availability or quality of food in the habitat near nests
and, subsequently, nestling body condition or the likelihood of breeding success.
Alternatively, the soft, high-pitched characteristics of the female and nestling begging calls
may function to limit detection by nest predators during allofeeding (c.f. loud calls given in
other contexts).

The male display call is highly stereotypical and repetitive in both subspecies and 394 involves head-bobbing and tail-fanning. The call contains two elements; the first element is 395 396 longer in duration and may show harmonics, while the second element is a short, broadband 'chuck'. Characterised by its rhythm, with each two-element call being repeated over time, 397 the call may function as a signal of male fitness. Recent literature on rhythm in birds, though 398 in its infancy, suggests the possibility of sexual selection for highly rhythmic calls or other 399 sounds. For instance, palm cockatoos, *Probosciger aterrimus*, are renowned for their 400 401 drumming behaviour, wherein males use a tool (a stick) to drum on a tree branch or a nest 402 hollow. Drumming is most often directed towards females. Individualised drumming styles, including variations in rhythm, suggest that information about the male may be conveyed to 403 404 females (Heinsohn et al. 2017). In budgerigars, *Melopsittacus undulatus*, experiments show that females prefer rhythmic sounds, which may relate to a preference for rhythm (as yet 405 406 untested) in the head-bobbing sexual display given by males of the species (Hoeschele and Bowling 2016). In the current study, observed display calls were always given by adult males 407 and directed towards their bonded females. Often, females seemingly ignored the display, or 408 409 lunged to the male, or moved to a different position in the tree (DT. pers. obs.). Copulation sometimes followed the display call and was, in all observations, preceded by it (DT. pers. 410 411 obs.; copulation not observed in the red-tailed black-cockatoo). Thus, the call appears to be a 412 sexual display by males to elicit copulation, or to reinforce the pair bond, to which females

respond variably. Selection for rhythm may be acting on the call, in which case individualisedrhythmic features may provide a bioacoustic index of male fitness.

415 Notwithstanding, the display call appears to have at least two secondary functions. Pepper (1996) noted that, in the Kangaroo Island glossy black-cockatoo, the display call 416 417 (referred to as the *kwee-chuck* call) was sometimes given by unpaired juvenile males when 418 perched prominently, suggesting a secondary function in dominance. Pepper (1996) also noted that the call was given after disturbance by human observers. This concords with two 419 opportunistic findings in sound recordings from nests of the south-eastern red-tailed black-420 421 cockatoo. In both cases, display calls were given following a period of alarm calling or loud banging sounds in the hollow. Cockatoos were not detected in recordings thereafter, which 422 suggests that display calls may accompany nest failure in some cases (e.g. a predation event). 423 The function of the display call in such a context is not yet clear. 424

We classified perch calls as any vocalisation that did not resemble another call type 425 and was given by adult birds when perched on the nest tree. These represented a range of 426 427 graded contact calls, which were sometimes difficult to differentiate on spectrograms, and 428 classification accuracy was mixed (Table S2). These results support the hypothesis that animal calls are often graded, variations of each other, rather than distinct categories; thus 429 categorisation is somewhat subjective (Fischer et al. 2016). In parrots, loud contact calls tend 430 431 to elicit a vocal response from conspecifics and, therefore, are generally thought to function 432 in establishing connections between individuals (Bradbury 2003). This appeared to be the case in this study, where males and females, and sometimes nestlings, would often engage in 433 434 vocal exchanges while perched on the nest tree (Figs. 3 and 4). In both subspecies, the males' soft perch call (referred to as subtype 2) was relatively common and detected most days. This 435 call provided a clear acoustic signal of the birds' presence at the nest tree. These soft contact 436

calls were given by males after landing on the nest tree, after the female had entered the 437 hollow, as well as in response to female begging. Therefore, its function appeared mostly 438 one-way, directed from male to female, usually without response. Parrots' soft contact calls 439 often do not elicit responses and are thought to function in coordinating flock movements 440 through vegetation. Indeed, in the glossy black-cockatoo, this soft perch call appears 441 synonymous with the feeding call shown in Pepper (1996) wherein it was noted "mated pairs 442 443 gave soft, short calls at intervals while foraging". Like the display call, perch calls appear to function in several behavioural contexts. 444

Vocal behaviours in this study were described from bioacoustic methods that align 445 with those likely to be feasible in a larger monitoring program for these subspecies. 446 Specifically, sound data were collected from nest trees, usually in the late afternoon as this is 447 when birds are most active at nests (DT, pers. obs.), from approximately 8 - 30 metres 448 distance from the nest hollow. Tree-climbing was avoided as it is unsafe for nests in dead 449 450 trees, which are important for the south-eastern red-tailed black-cockatoos, and has high 451 human resource costs. Vocalisations were clearer from recorders that were closer to the nest hollows (e.g. where hollows were lower to the ground), although loud calls, including 452 nestling calls, were easily identified in recordings from all distances included in this study. 453 Since loud nestling calls are one of the most useful indicators of active nesting, we believe 454 that the approach used here is appropriate for these subspecies. A limitation is that this 455 requires a sound recorder at every nest tree monitored. However, since the cockatoos often 456 nest in loose aggregations, it is possible that a smaller number of recorders could monitor 457 458 several nests simultaneously. Nest location could be measured from the time difference in the arrival of calls at each recorder (Stevenson et al. 2015). Designing an appropriate recorder 459 460 array requires an understanding of the distances at which key vocalisations can be detected by the sound recorders in each habitat type (e.g., forest vs paddock). This was not explicitly 461

462 examined in this study but warrants attention as it could reduce the number of sound
463 recorders required. Another important consideration is post-processing sound data using
464 automated or semi-automated recognition methods (Blumstein et al. 2011; Priyadarshani et
465 al. 2018; Crump and Houlahan 2017). Although not examined here, we believe that nestling
466 calls are a good candidate for automated detection, since they are loud, distinct and are a
467 good indicator of active nesting.

This study aimed to describe the nest-associated vocal behaviours of the Kangaroo 468 Island glossy black-cockatoo and the south-eastern red-tailed black-cockatoo, to provide the 469 470 knowledge necessary for the development of a bioacoustic nest monitoring program. Nest monitoring is important for understanding how breeding activity varies across the landscape, 471 which can help inform management decisions. For instance, two important conservation 472 actions for these subspecies are managing fire impacts to feeding habitat (especially close to 473 nests) and supplementing natural nest hollows with artificial nest hollows. However, spatial 474 475 prioritisation of these actions could be better informed by a greater understanding of the 476 habitat features that influence the choice of nest location and the likelihood of fledging success. Acquiring sufficient data to test relevant hypotheses is resource intensive if using 477 traditional human-observer methods. Moreover, using traditional methods, it is not feasible to 478 collect behavioural data such as nest visitation rates by the adult birds or the date of fledging 479 or nest failure. The vocal behaviours described in this study suggest that a wide range of 480 behavioural data could be extracted from sound data. Bioacoustics can, therefore, aid 481 monitoring by reducing human survey effort while also providing a range of behavioural 482 483 data. With continued advances in recording technology and automated sound processing, it is foreseeable that bioacoustics could provide daily data from potential and active nests, with 484 human field effort limited to the deployment and retrieval of sound recorders. 485

486 CONCLUSION

Both subspecies examined in this study are nationally endangered and breeding 487 488 success is a limiting factor in their recoveries (Berris et al. 2018; Russell et al. 2018). However, monitoring of breeding is difficult in both subspecies, largely because of 489 490 accessibility and resource restrictions. This potentially limits conservation decision-making as it pertains to nesting. Bioacoustics may help address this issue. For both subspecies, the 491 most important objective of nest monitoring is to confirm the birds' daily presence or absence 492 at nests. To this end, we conclude that most useful calls for bioacoustic nest monitoring are 493 494 female nest call and loud nestling calls. These call types are the most conspicuous signs of active nesting, since they are loud, distinct and unique to active nests. They are usually easily 495 496 identifiable to the human ear and on spectrograms. Additionally, because they are relatively stereotypical and loud, these calls could be the focus of automated or semi-automated 497 detection of nesting activity. Failure to detect these calls on any given day could indicate nest 498 499 failure or successful fledging.

500 Further, with knowledge on vocal behaviour, bioacoustics can be used to monitor not 501 only nesting activity, but also specific behaviours of the cockatoos at nests. It is also possible that calls are individually distinct, as shown in the palm cockatoo (Zdenek et al. 2018) and 502 Carnaby's black-cockatoo (Saunders 1983), in which case bioacoustics may help monitor 503 504 nest site fidelity. Indeed, bioacoustics offers a range of monitoring options for blackcockatoos and this study provides a preliminary description of conservation-relevant 505 vocalisations for two highly threatened subspecies. As bioacoustic technology and analytical 506 507 methods continue to advance and become more accessible, large-scale bioacoustic nest monitoring programs could be implemented for the conservation benefit of the Kangaroo 508 Island glossy black-cockatoo and the south-eastern red-tailed black-cockatoo. 509

510 SPECIES NOMENCLATURE

511 Calyptorhynchus lathami subsp. halmaturinus

512 *Calyptorhynchus banksii* subsp. *graptogyne*

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612 Table 1: Description of nest-associated call types and associated behavioural contexts of the south-eastern red-tailed black-cockatoo (RTBC), Calyptorhynchus banksii

graptogyne, and the Kangaroo Island glossy black-cockatoo (GBC), *C. lathami halmaturinus*.

Call type	Caller	Behavioural	Description	Notes
(behaviour)	identity	context		
Flight	Adult male and female	Adults give flight calls when flying to and from the nest tree.	 Typically loud with harmonics. May contain pulsatile elements. Common at nests. Reliably recorded every day. Take-off call subtype: Given upon take-off flight. Shorter in duration. May show a downward inflection. RTBC: Clear harmonics, with or without pulsatile elements. Males and female calls are usually not overlapping. Take-off call is usually the final call of the day, given by the male as he leaves the nest tree to roost. Take-off call is common at RTBC nests because the male tends not to roost in the nest tree (isolated paddock tree). GBC: Often contain pulsatile elements. Male and female flight calls are often overlapping. Take-off call is less common at GBC nests because the male tends to roost in the nest tree or a nearby tree. 	Did not differentiate between the sexes.
Begging	Adult female	Female begs in the presence of her mate to elicit allofeeding.	Often given when the pair is perched on the nest tree or a nearby tree. During incubation and brooding, a female may beg from within the nest hollow in response to her mate's flight call. The main purpose of begging appears to be to elicit allofeeding from the male, however females also appear to beg to maintain contact with their mate. Calls are given repetitively. Begging bouts can be long in duration. Calls are highly variable in structure within and among individuals. Calls vary from loud to soft. Common at nests. RTBC: Commonly contain harmonics and deterministic chaos. Some calls appear largely chaotic with little harmonic structure. Subharmonics are sometimes present. GBC: Usually show harmonics, with or without deterministic chaos and frequency jumps. Subharmonics are sometimes present.	Highly variable in structure.
Display (courtship)	Adult male	Male displays to his mate in courtship, to maintain pair bonds	Display calls are given by adult males when perched close to their mate. Calls appear to function in courtship and in maintaining the pair bond. Given prior to copulation. Display involves non-vocal elements, namely head- bobbing and tail-panning wherein the male's red tail feathers are displayed to the female. Call are given	Termed the <i>kwee-chuck</i> call for the

		and to instigate copulation.	 repetitively. Display bouts can be long in duration. Call contains two elements. Second element is usually louder. Usually soft. RTBC: First element is harmonic with a dominant frequency band at around 1.8 kHz. Other harmonic elements are clear. Harmonic at 3.6 kHz can also be high in energy. First element usually contains some noise. Second element is short and broadband without clear harmonics. Second element is usually louder but elements can be similar in energy. GBC: First element is soft with most energy around 3.4 kHz. Other harmonic element sare usually low in energy and less clear. Second element is short and broadband with harmonics. Second element typically much louder than the first element. 	glossy black- cockatoo by Pepper (1996). Not heard every day.
Nest (nest entry)	Adult female	Given by females when near the nest or entering the nest hollow.	Very pulsatile. Varies from loud to soft. Appears to function in communication with her mate and the nestling. Female will vocalise once sitting at the nest hollow entrance. Sometimes given when perched near the hollow. Can be drawn out and relatively long in duration RTBC: Guttural, 'purring' sound. Pulsatile GBC: Guttural, 'growling' sound. Can be very similar to nestling call, but pulses are more distinct (less noisy).	Not given every time nest is visited or entered.
Nestling	Nestling	Given by large nestlings in the nest hollow or when sitting at the nest hollow entrance.	Call given in the presence of parents. Calling begins upon parents' return to the nest. Can resemble females' nest call. Subtypes 1 and 2 are common once the nestling is close the fledging; reliably heard every day. Subtype 1: Very loud, broadband, chaotic. May contain harmonics towards the end of the call. Nestling stimulated upon parents' first return to the nest. Can be associated with wing-flapping in older nestlings. Subtype 2: Softer call but otherwise similar in structure to subtype 1. Nestling is less stimulated. Subtype 3 (begging): Soft, highly variable. Can resemble female begging calls. Appears to function as a close contact call with the adult female. Elicits allofeeding by female. Sounds high-pitched and 'squeeky'. RTBC: Very noisy and chaotic. Sounds 'throaty' or 'wheezy'. Not pulsatile. Harmonics sometimes present. GBC: Noisy, chaotic call, often with some harmonic structure. Highly pulsatile. Can be very similar to females' nest call, but more chaotic and less harmonic.	Type 3 is soft; can be difficult to detect on a recorder. Identified from a small sample of nests with video footage, but expected at every nest.

Perch	Adult male	Given when perched	Perch calls comprise several, variable contact calls given by adult birds when perched on or near the nest tree.	Graded contact
	(RTBC).	on or near the nest	Appear to maintain contact between male, female and nestling in hollow. In the GBC, both sexes commonly call	calls. Soft
	Adult male	tree.	when perched. In the RTBC, only male calls are reliably heard in recordings. Perch calls range from loud to soft.	perch calls are
	and female		Male perch call (subtype 2) is most common. Recorded often. After female has entered the nest hollow for the	easily masked
	(GBC).		night, male will call intermittently, often for a long duration. Perch calls are often the final vocalisations of the	by other
			day. Subtypes 2 and 3 (soft perch calls) often given in response to female begging.	sounds and
			RTBC: Given by male. Always begins with pulsatile or chaotic elements. Has a 'crackling' quality to the sound.	therefore
			• Male loud perch call (perch subtype 1): Loud. Sounds 'trumpet-like'. Clear harmonic structure in	appear to be
			second part of call. Often with subharmonics. First part of call is chaotic and pulsatile. First part of call	uncommon in
			may be lacking, showing only harmonics; typically given soon after landing on the nest tree.	sound
			• Male soft perch call (perch subtype 2): Beginning of call is highly pulsatile, with a 'crackling' sound	recordings.
			quality, ending in harmonics. Can be loud or soft. Typically given when male is perched on the nest tree,	
			including after the female has entered the hollow.	
			• Male soft perch call (perch subtype 3): Soft, guttural. Lacks harmonics but otherwise is similar to	
			subtype 2. Entire call is chaotic or pulsatile.	
			GBC: Highly variable, graded calls. Subtypes 1, 2 and 3 are given by adult males. Subtypes 4, 5 and 6 are given	
			by adult females. Perch calls by both adult birds are commonly given at nests, often in interactions.	
			• Male loud perch call (perch subtype 1): Contains harmonics. May contain some pulses and chaos. Less	
			common than soft perch calls. Usually loud but can be relatively soft. May precede take-off.	
			• Male soft perch call (perch subtype 2): Most common adult male soft perch call. Usually very soft,	
			'fuzzy' sound. Often appears as a single, wide frequency band between 2.5-4.5 kHz, ending with a	
			downward inflection. Louder variations have additional high and low frequency bands but maintain the	
			'fuzzy' quality to the sound. Common at nests. Often given in response to female perch calls or begging.	
			Given when the female is in the nest hollow.	
			• Male soft perch call (perch subtype 3): Very similar to subtype 2. Begins as subtype 2 but abruptly	
			changes to end with a louder harmonic element. Some individuals appear to use subtype 3 more often than	
			subtype 2.	

0	C	Female loud perch call (perch subtype 4): Clear harmonics. Sometimes shows frequency modulation.
		Often given when the female is perched high on the nest tree or on a nearby tree.
0	C	Female loud, alarm perch call (perch subtype 5): Loud, pulsatile call. Can resemble nest entry call.
		Given when female is alarmed near the nest, usually when defending the nest tree from other birds (e.g.
		other glossy black-cockatoos or galahs).
0	C	Female soft perch call (perch subtype 6): Soft. Resembles male perch call subtype 2 but contains more
		than one frequency band. Often appears as two dominant frequency bands around 3-3.5 kHz and 6-6.5
		kHz. Uncommon and easily masked by other sounds.
614		







623 subtype 2; (i) Nestling call, subtype 3; (j) Male perch call, subtype 1; (k) Male perch call, subtype 2

- 624 (1) Male perch call, subtype 3. Spectrograms created using Raven Pro 1.5 (Cornell Lab of
- 625 Ornithology; Hann window; window size = 1024 samples; hop size = 512 samples; 50% overlap).





Fig. 2: Vocalisations of the Kangaroo Island glossy black-cockatoo, *Calyptorhynchus lathami*

halmaturinus, at nests. (a) Flight call; (b) Female begging call, clear harmonics; (c) Begging bout,

630 showing nonlinearity; (d) Male display call (courtship call); (e) Female nest call (nest entry call); (f)

631 Nestling call, subtype 1; (g) Nestling call, subtype 2; (h) Nestling call, subtype 3; (i) Male perch call,

subtype 1; (j) Male perch call, subtype 2, loud version; (k) Male perch call, subtype 2, soft version; (l)

Male perch call, subtype 3; (m) Female perch call, subtype 4; (n) Female perch call subtype 5; (o)

- 634 Female perch call, subtype 6. Spectrograms created using Raven Pro 1.5 (Cornell Lab of Ornithology;
- Hann window; window size = 1024 samples; hop size = 512 samples; 50% overlap).





Fig. 3: Spectrograms of vocalisations and behavioural interactions of adult and nestling south-eastern
red-tailed black-cockatoo, *Calyptorhynchus banksii graptogyne*, at nests. Symbols denote sex of adult
birds. (a) Nestling call (subtype 1), male perch call (subtypes 1 and 2) and the begging of a beginning
bout by the female; (b) Nestling call (subtype 2), male soft perch call (subtype 3) and female begging;

- 641 (c) Nestling call (subtype 3) showing clear nonlinearity. Female responds with soft nest call and male
- 642 with soft version of perch subtype 3; (d) Loud female begging bout showing clear subharmonics.
- 643 Take-off flight by male and female. Other species' vocalisations are not indicated. Spectrograms
- 644 created from video footage using Raven Pro 1.5 (Cornell Lab of Ornithology; Hann window; window
- size = 1024 samples; hop size = 512 samples; 50% overlap). X axis denotes time into the video file.





- male soft perch (subtype 2); (e) Female begging bout and male response (perch 2). Other species'
- vocalisations are not indicated. Spectrograms created from video footage using Raven Pro 1.5
- 659 (Cornell Lab of Ornithology; Hann window; window size = 1024 samples; hop size = 512 samples;
- 660 50% overlap). X axis denotes time into the video file.



Fig. 5: Linear discriminant analysis of nest-associated vocalisations of (a) the Kangaroo Island glossy black-cockatoo, *Calyptorhynchus lathami halmaturinus* (MANOVA: Wilk's $\lambda = 0.04$, F = 47.362, p < 0.001) and (b) the south-eastern red-tailed black-cockatoo, *C. banksii graptogyne* (MANOVA: Wilk's $\lambda = 0.16$, F = 22.518, p < 0.001). Solid lines represent 95% confidence intervals. Dashed lines represent Euclidean distances.

Table S1: Quantitative acoustic measurements calculated for each call selected in recordings made with the autonomous sound recorders. Definitions adapted from the user manual for Raven Pro software.

Acoustic measurement	Definition
Low frequency (Hz)	The lowest frequency bound of the selection.
Peak frequency (Hz)	The frequency at which greatest energy occurs within the selection.
Centre frequency (Hz)	The frequency at which the selection is divided into two parts of equal energy.
Aggregate entropy (bits)	A measure of overall disorder (chaos) in a sound. A higher value corresponds to greater disorder. A pure tone has zero entropy.
	Aggregate entropy measures the energy distribution across a selection.
Average entropy (bits)	The average entropy of each time slice within a selection. Describes the typical disorder within a spectrum of the selection.
Minimum entropy (bits)	The minimum entropy for a spectrogram slice that occurs within the selection.
Maximum entropy (bits)	The maximum entropy for a spectrogram slice that occurs within the selection.
Delta time (s)	Duration of the selection. The difference between start time and end time of the selection.
Interquartile range duration (s)	The difference between the first and third quartile times. The first quartile divides the selection into two time intervals containing
	25% and 75% of the energy in the selection. The third quartile divides the selection into two time intervals containing 75% and
	25% of the energy in the selection.
Peak amplitude (U)	The greatest absolute amplitude value in the selection (i.e., greatest of maximum amplitude and minimum amplitude). Raven Pro
	amplitude measurements are dimensionless (U). They are calculated relative to an arbitrary reference point, to enable comparisons
	between selections made with the same recording equipment and settings.
Peak frequency contour (PFC)	Tracks the 'pitch' of the sound in the selection by measuring its slope (i.e., the change in frequency over time). This measurement
average slope (Hz/ms)	provides the average slope of the peak frequency across spectrogram slices in the selection.
Peak frequency contour (PFC)	Tracks the 'pitch' of the sound in the selection by measuring its slope (i.e., the change in frequency over time). This measurement
maximum slope (Hz/ms)	provides the maximum slope of the peak frequency in the selection.

Table S2: Linear discriminant analysis confusion matrix and classification accuracy for each call type of (a) the south-eastern red-tailed black-cockatoo (RTBC; n = 907 selections) and (b) the Kangaroo Island glossy black-cockatoo (GBC; n = 1,632 selections). Model trained and tested on 70% and 30% of the dataset, respectively. Take-off subtype of the flight call, nestling subtype 3 and perch subtype 3 (RTBC only) were not included in the analysis due to low sample size.

		Begging	Display	Flight	Nest entry	Nestling1	Nestling2	Perch1	Perch2	Perch3		
	Begging	19	3	8	0	1	4	2	2	0		
	Display	1	14	2	0	0	0	0	1	0		
	Flight	8	1	54	1	6	3	11	7	0		
	FlightT	0	0	0	0	0	0	0	0	0		
	Nest entry	2	0	0	11	4	3	0	3	0		
C	Nestling1	7	0	4	1	18	4	0	3	0		
RTB	Nestling2	1	1	0	2	4	6	0	2	0		
	Nestling3	0	0	0	0	0	0	0	0	0		
	Perch1	0	0	6	0	0	1	8	1	0		
	Perch2	2	0	1	5	0	0	2	19	0		
	Perch3	0	0	0	0	0	0	0	0	0		
	Accuracy	47.5%	73.7%	72.0%	55.0%	54.6%	28.6%	34.8%	50.0%	0		
		Begging	Display	Flight	Nest entry	Nestling1	Nestling2	Perch1	Perch2	Perch3	Perch4	Perch5
۲)	Begging	61	10	2	1	0	0	1	3	2	1	2
GB(Display	3	9	1	0	0	0	0	2	0	0	0
	Flight	0	0	51	1	5	1	9	17	11	2	3

Perch6

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Nest entry	1	0	2	15	0	1	1	0	1	0	4	0
Nestling1	0	0	6	5	79	9	0	1	0	0	0	0
Nestling2	0	0	3	4	4	30	0	0	1	2	1	0
Perch1	0	0	0	0	1	0	0	0	1	0	0	0
Perch2	1	1	0	0	0	0	0	31	0	1	0	4
Perch3	0	0	3	0	1	0	5	2	17	3	0	3
Perch4	0	0	4	0	0	0	0	2	0	3	0	0
Perch5	0	0	1	0	0	0	0	1	0	0	0	0
Perch6	6	0	1	0	0	0	0	7	0	1	0	8
Accuracy	84.7%	45.0%	68.9%	57.7%	87.8%	73.2%	0.00%	47.0%	51.5%	23.1%	0.00%	36.4%

Table S3: Linear discriminant analysis confusion matrix and classification accuracy for each call type of (a) the south-eastern redtailed black-cockatoo and (b) the Kangaroo Island glossy black-cockatoo. Model tested using leave-one-out cross validation using the complete dataset. Take-off subtype of the flight call (FlightT) and nestling subtype 3 were not included in the analysis due to low sample size.

		Begging	Display	Flight	Nest entry	Nestling1	Nestling2	Perch1	Perch2	Perch3	-	
	Begging	66	10	19	0	12	12	4	8	0	-	
	Display	11	38	4	1	2	1	0	2	0	-	
	Flight	27	4	189	2	19	11	35	14	0	-	
	FlightT	0	0	0	0	0	0	0	0	0	-	
	Nest entry	5	1	0	44	12	8	0	4	0	-	
C	Nestling1	11	1	8	4	59	16	3	4	0	-	
RTB	Nestling2	6	11	2	4	4	20	0	5	0	-	
	Nestling3	0	0	0	0	0	0	0	0	0	-	
	Perch1	0	0	16	2	0	0	24	9	0	-	
	Perch2	9	0	13	12	2	5	11	81	0	-	
	Perch3	0	0	0	0	0	0	0	0	0	-	
	Accuracy	48.9%	58.5%	75.4%	63.8%	53.6%	27.4%	31.2%	63.8%		-	
(۲		Begging	Display	Flight	Nest entry	Nestling1	Nestling2	Perch1	Perch2	Perch3	Perch4	Perch5
GBC	Begging	206	34	3	7	1	4	2	8	7	2	2

Perch6

Display	19	31	2	0	0	1	0	2	0	0	0	1
Flight	0	0	184	3	9	2	38	47	45	9	10	1
Nest entry	2	0	7	54	4	8	1	2	4	1	11	1
Nestling1	0	0	15	14	264	34	2	4	0	1	8	0
Nestling2	1	0	5	8	22	86	0	2	2	2	3	3
Perch1	0	0	4	0	2	1	2	2	3	1	0	0
Perch2	1	2	0	0	0	1	0	120	2	3	0	20
Perch3	1	2	20	0	1	1	11	17	44	10	1	13
Perch4	0	0	6	0	0	0	0	4	3	10	0	0
Perch5	0	0	0	2	0	0	0	0	0	0	0	0
Perch6	13	0	2	1	0	0	0	13	2	5	0	18
Accuracy	84.8%	44.9%	74.2%	60.7%	87.1%	62.3%	3.6%	54.3%	39.3%	22.7%	0.00%	24.3%

	Call Type	Low Freq (Hz)	Peak Freq (Hz)	Centre Freq (Hz)	Aggregate Entropy (bits)	Average Entropy (bits)	Min Entropy (bits)	Max Entropy (bits)	Delta Time (s)	IQR Duration (s)	Peak Amplitude (U)	PFC Average Slope (Hz/ms)	PFC Maximum Slope (Hz/ms)
	n = 243	23.33	49.09	36.89	4.69 ± 0.06	4.37 ± 0.05	2.88 ± 0.06	5.94 ± 0.04	0.32 ± 0	0.1 ± 0	77.03	1.92 ± 0.28	7.11
	Display $n = 69$	876.64 ± 70.74	3445.94 ± 67.22	3345.45 ± 45.52	5.19 ± 0.05	4.54 ± 0.07	2.88 ± 0.08	6.05 ± 0.05	0.32 ± 0.01	0.12 ± 0.01	$\begin{array}{c} 1944.8 \pm \\ 205.26 \end{array}$	1.83 ± 0.44	$\begin{array}{c} 146.23 \pm \\ 10.57 \end{array}$
	Flight <i>n</i> = 248	577.58 ± 4.42	3900.64 ± 32.84	3843.85 ± 23.94	5.22 ± 0.04	4.68 ± 0.04	3.27 ± 0.04	5.92 ± 0.03	0.75 ± 0.01	0.24 ± 0	3489.48 ± 167.79	0.89 ± 0.13	222.3 ± 9.24
	Take-off $n = 9$	567.46 ± 16.09	3919.04 ± 97.1	3761.13 ± 76.64	4.72 ± 0.14	4.05 ± 0.12	2.74 ± 0.17	5.71 ± 0.16	0.61 ± 0.05	0.2 ± 0.03	4839.67 ± 756.4	0.28 ± 0.24	$\begin{array}{c} 205.26 \pm \\ 65.93 \end{array}$
ckatoo 	Nest entry <i>n</i> = 89	484.41 ± 8.69	3270.14 ± 70.83	3244.98± 33.71	5.76 ± 0.06	5.36 ± 0.05	4.51 ± 0.07	6.17 ± 0.05	0.59 ± 0.02	0.2 ± 0.01	4311.6 ± 447.71	0.93 ± 0.39	257.58 ± 12.1
black-co	Nestling 1 <i>n</i> = 303	507.27 ± 4.39	3359.46 ± 48.77	3499.18± 29.59	6.17 ± 0.03	5.54 ± 0.02	4.31 ± 0.04	6.37 ± 0.02	0.8 ± 0.01	0.21 ± 0	11903.99 ± 457.22	1.37 ± 0.11	231.56 ± 7.86
Glossy l	Nestling 2 <i>n</i> = 138	534.63 ± 17.85	2825.53 ± 65.94	3002.79± 32.3	5.95 ± 0.04	5.44 ± 0.04	4.24 ± 0.06	6.38 ± 0.04	0.59 ± 0.01	0.17 ± 0	4610.28 ± 287.57	0.89 ± 0.25	192.78 ± 9.99
	Perch 1 <i>n</i> = 56	610.76 ± 9.44	3819.84± 126.74	3889.82± 65.96	5.09 ± 0.07	4.57 ± 0.06	3.32 ± 0.08	5.87 ± 0.06	0.67 ± 0.02	0.2 ± 0.01	4140.2 ± 351.27	0.48 ± 0.36	201.5 ± 13.55
	Perch 2 <i>n</i> = 221	$\begin{array}{c} 1632.37 \pm \\ 67.22 \end{array}$	$\begin{array}{r} 3425.83 \pm \\ 31.86 \end{array}$	3438.69 ± 21.03	4.59 ± 0.04	4.2 ± 0.04	3.04 ± 0.04	5.55 ± 0.05	0.62 ± 0.01	0.19 ± 0	1984.57 ± 146.05	0.04 ± 0.12	110.39 ± 8.14
	Perch 3 <i>n</i> = 112	614.14 ± 8.22	3581.43 ± 74.52	3601.43 ± 37.62	5.19 ± 0.05	4.53 ± 0.05	3.23 ± 0.07	5.91 ± 0.05	0.64 ± 0.01	0.19 ± 0.01	2619.02 ± 129.13	0.42 ± 0.25	221.51 ± 11.35
	Perch 4 <i>n</i> = 44	678.79 ± 48.39	3472.72 ± 95.78	3394.42 ± 67.16	4.53 ± 0.12	4.08 ± 0.1	2.72 ± 0.12	5.83 ± 0.1	0.64 ± 0.02	0.2 ± 0.01	2870.75 ± 275.21	1.07 ± 0.36	218.77 ± 25.19

Table S4: Descriptive statistics (mean \pm SE) of acoustic parameters of call types of the Kangaroo Island glossy black-cockatoo, Calyptorhynchus lathami halmaturinus,

and the south-eastern red-tailed black-cockatoo, Calyptorhynchus banksii graptogyne, at nests. Nestling subtype 3 not shown due to low sample size.

Perch 5	$553.4\pm$	$3590.51 \pm$	$3580.66\pm$	5.58 ± 0.11	5.12 ± 0.1	3.99 ± 0.14	5.99 ± 0.06	0.68 ± 0.04	0.21 ± 0.01	$6164.86 \pm$	1 ± 0.28	$224.47 \pm$
<i>n</i> = 35	14.28	124.76	72.99							848.93		19.57
Perch 6	$1155.03 \pm$	$3236.38 \pm$	$3218.34 \pm$	43 ± 0.11	4.11 ± 0.08	2.75 ± 0.08	5.83 ± 0.07	0.45 ± 0.01	0.13 ± 0	$1395.18 \pm$	0.49 ± 0.31	$155.5 \pm$
<i>n</i> = 74	90.43	43.96	28.6	4.5 ± 0.11	4.11 ± 0.08	2.75 ± 0.08	5.85 ± 0.07	0.45 ± 0.01	0.13 ± 0	107.85	0.49 ± 0.31	16.29
Begging	$754.78 \pm$	$2678.41 \pm$	$2844.93 \pm$	5.41 ± 0.06	4.7 ± 0.05	3.11 ± 0.06	6.15 ± 0.05	0.39 ± 0.01	0.13 ± 0	$4661.61 \pm$	0.37 ± 0.32	$151.29 \pm$
<i>n</i> = 135	37.05	99.55	79.5	5.41 ± 0.00	4.7 ± 0.05	3.11 ± 0.00	0.15 ± 0.05	0.59 ± 0.01	0.13 ± 0	500.44	0.57 ± 0.52	6.52
Display	$673.53 \pm$	$1999.61 \pm$	$2234.82 \pm$	4.95 ± 0.1	4.38 ± 0.08	3.14 ± 0.08	5.8 ± 0.05	0.28 ± 0.01	0.07 ± 0	$3825.09 \pm$	1.16 ± 0.45	$138.68 \pm$
<i>n</i> = 65	40.67	107.08	81.69	4.95 ± 0.1	4.56 ± 0.06	5.14 ± 0.00	3.0 ± 0.03	0.20 ± 0.01	0.07 ± 0	388.85	-1.10 ± 0.45	8.98
Flight	$593.12 \pm$	$3041.41 \pm$	$3125.32 \pm$	5.16 ± 0.04	4.48 ± 0.02	2.2 ± 0.02	5.02 ± 0.04	0.4 ± 0.01	0.12 ± 0	$10280.29 \pm$	0.70 ± 0.2	$212.19 \pm$
<i>n</i> = 251	9.96	54.88	40.81	3.10 ± 0.04	4.48 ± 0.03	5.5 ± 0.05	3.93 ± 0.04	0.4 ± 0.01	0.13 ± 0	451.15	0.79 ± 0.2	8.94
Take-off	$572.85 \pm$	$2806.49 \pm$	$3075.66 \pm$	5.17 ± 0.21	4.45 ± 0.17	2.26 ± 0.12	5.00 ± 0.14	0.28 ± 0.02	0.1 ± 0.01	$12468.08 \pm$	1.00 ± 0.85	$269.55 \pm$
<i>n</i> = 12	28.31	272.93	253.7	3.17 ± 0.21	4.45 ± 0.17	3.30 ± 0.13	3.99 ± 0.14	0.38 ± 0.02	0.1 ± 0.01	2176	1.09 ± 0.03	51.54
Nest entry	$423.84 \pm$	$2240.7 \pm$	$2308.73 \pm$	5.08 ± 0.06	5 58 ± 0.06	4.56 ± 0.00	6.22 ± 0.05	0.4 ± 0.02	0.12 ± 0.01	$4580.93 \pm$	1.00 ± 0.26	$180.2 \pm$
<i>n</i> = 69	22.49	78.38	63.82	3.98 ± 0.00	5.58 ± 0.00	4.30 ± 0.09	0.53 ± 0.05	0.4 ± 0.02	0.13 ± 0.01	461.81	1.09 ± 0.30	11.03
Nestling 1	$457.65 \pm$	$2333.02 \pm$	$2491.2 \pm$	5 (5 + 0.05	4.04 + 0.05	2.72 + 0.07	5.01 + 0.05	0.41 + 0.01	0.14 + 0	$8481.12 \pm$	0.26 + 0.25	105 70 + 0 4
<i>n</i> = 110	17.51	51.33	37.16	5.05 ± 0.05	4.94 ± 0.05	3.73 ± 0.07	5.91 ± 0.05	0.41 ± 0.01	0.14 ± 0	739.31	-0.30 ± 0.23	125.78 ± 8.4
Nestling 2	$546.63 \pm$	$2493.13 \pm$	$2499.62 \pm$	5.50 ± 0.05	5.02 ± 0.05	2.85 ± 0.07	5.02 ± 0.04	0.26 ± 0.01	0.12 ± 0	$6422.25 \pm$	0.18 ± 0.22	$147.51 \pm$
<i>n</i> = 73	34.27	61.16	49.35	3.39 ± 0.03	5.02 ± 0.05	3.83 ± 0.07	5.95 ± 0.04	0.30 ± 0.01	0.12 ± 0	710.04	0.18 ± 0.33	14.42
Perch 1	$570.8 \ \pm$	$3177.41 \pm$	$3151.12 \pm$	5 ± 0.08	4.62 ± 0.07	2.20 ± 0.06	6.18 ± 0.06	0.47 ± 0.01	0.14 ± 0	$8021.9 \pm$	1.85 ± 0.22	$194.91~\pm$
<i>n</i> = 77	17.51	127.06	94.08	5 ± 0.08	4.02 ± 0.07	3.29 ± 0.00	0.18 ± 0.00	0.47 ± 0.01	0.14 ± 0	567.92	1.65 ± 0.52	11.13
Perch 2	$600.73~\pm$	$2328.98 \pm$	$2386.96 \pm$	5 25 + 0.07	5 + 0.00	2.26 ± 0.06	(22 + 0.05)	0.51 + 0.01	0.12 + 0.01	$5485.15 \pm$	12+020	$234.42 \pm$
<i>n</i> = 127	10.87	87.89	70.37	3.23 ± 0.07	5 ± 0.00	3.30 ± 0.06	0.32 ± 0.05	0.31 ± 0.01	0.13 ± 0.01	413.91	1.3 ± 0.26	13.59
Perch 3	$590.43~\pm$	$3399.37 \pm$	$3109.39\pm$	6.06 ± 0.10	5 66 1 0 15	469 + 0.10	6.40 ± 0.12	0.46 ± 0.02	0.14 ± 0.01	$6957.73 \pm$	0.01 + 1.00	$278.21 \pm$
n = 15	20.00	220.81	162.2	0.00 ± 0.19	3.00 ± 0.15	4.00 ± 0.19	0.49 ± 0.13	0.40 ± 0.02	0.14 ± 0.01	677 41	-0.01 ± 1.09	26.12
	Perch 5 $n = 35$ Perch 6 $n = 74$ Begging $n = 135$ Display $n = 65$ Flight $n = 251$ Take-off $n = 12$ Nest entry $n = 69$ Nestling 1 $n = 77$ Perch 1 $n = 777$ Perch 2 $n = 127$ Perch 3	Perch 5 $553.4 \pm$ $n = 35$ 14.28Perch 6 $1155.03 \pm$ $n = 74$ 90.43Begging $754.78 \pm$ $n = 135$ 37.05 Display $673.53 \pm$ $n = 65$ 40.67Flight $593.12 \pm$ $n = 251$ 9.96Take-off $572.85 \pm$ $n = 12$ 28.31Nest entry423.84 \pm $n = 69$ 22.49Nestling 1 $457.65 \pm$ $n = 73$ 34.27Perch 1 $570.8 \pm$ $n = 77$ 17.51Perch 2 $600.73 \pm$ $n = 127$ 10.87Perch 3 $590.43 \pm$	Perch 5 $553.4 \pm$ $3590.51 \pm$ $n = 35$ 14.28 124.76 Perch 6 $1155.03 \pm$ $3236.38 \pm$ $n = 74$ 90.43 43.96 Begging $754.78 \pm$ $2678.41 \pm$ $n = 135$ 37.05 99.55 Display $673.53 \pm$ $1999.61 \pm$ $n = 65$ 40.67 107.08 Flight $593.12 \pm$ $3041.41 \pm$ $n = 251$ 9.96 54.88 Take-off $572.85 \pm$ $2806.49 \pm$ $n = 12$ 28.31 272.93 Nest entry $423.84 \pm$ $2240.7 \pm$ $n = 69$ 22.49 78.38 Nestling 1 $457.65 \pm$ $2333.02 \pm$ $n = 73$ 34.27 61.16 Perch 1 $570.8 \pm$ $3177.41 \pm$ $n = 77$ 17.51 127.06 Perch 2 $600.73 \pm$ $2328.98 \pm$ $n = 127$ 10.87 87.89 Perch 3 $590.43 \pm$ $3399.37 \pm$	Perch 5 $553.4 \pm$ $3590.51 \pm$ $3580.66 \pm$ $n = 35$ 14.28 124.76 72.99 Perch 6 $1155.03 \pm$ $3236.38 \pm$ $3218.34 \pm$ $n = 74$ 90.43 43.96 28.6 Begging $754.78 \pm$ $2678.41 \pm$ $2844.93 \pm$ $n = 135$ 37.05 99.55 79.5 Display $673.53 \pm$ $1999.61 \pm$ $2234.82 \pm$ $n = 65$ 40.67 107.08 81.69 Flight $593.12 \pm$ $3041.41 \pm$ $3125.32 \pm$ $n = 251$ 9.96 54.88 40.81 Take-off $572.85 \pm$ $2806.49 \pm$ $3075.66 \pm$ $n = 12$ 28.31 272.93 253.7 Nest entry $423.84 \pm$ $2240.7 \pm$ $2308.73 \pm$ $n = 69$ 22.49 78.38 63.82 Nestling 1 $457.65 \pm$ $2333.02 \pm$ $2491.2 \pm$ $n = 73$ 34.27 61.16 49.35 Perch 1 $570.8 \pm$ $3177.41 \pm$ $3151.12 \pm$ $n = 77$ 17.51 127.06 94.08 Perch 2 $600.73 \pm$ $2328.98 \pm$ $2386.96 \pm$ $n = 127$ 10.87 87.89 70.37 Perch 3 $590.43 \pm$ $3399.37 \pm$ $3109.39 \pm$	Perch 5 $553.4 \pm$ $3590.51 \pm$ $3580.66 \pm$ 72.99 5.58 ± 0.11 n = 35 14.28 124.76 72.99 5.58 ± 0.11 Perch 6 $1155.03 \pm$ $3236.38 \pm$ $3218.34 \pm$ $a \pm 0.11$ 4.3 ± 0.11 n = 74 90.43 43.96 28.6 4.3 ± 0.11 Begging $754.78 \pm$ $2678.41 \pm$ $2844.93 \pm$ $a \pm 0.11$ 5.41 ± 0.06 n = 135 37.05 99.55 79.5 5.41 ± 0.06 Display $673.53 \pm$ $1999.61 \pm$ $2234.82 \pm$ 4.95 ± 0.1 4.95 ± 0.1 n = 65 40.67 107.08 81.69 4.95 ± 0.1 Flight $593.12 \pm$ $3041.41 \pm$ $3125.32 \pm$ $a = 251$ 9.96 54.88 40.81 Take-off $572.85 \pm$ $2806.49 \pm$ $3075.66 \pm$ $a = 12$ 28.31 272.93 253.7 Nest entry $423.84 \pm$ $2240.7 \pm$ $2308.73 \pm$ $a = 5.98 \pm 0.06$ 5.98 ± 0.06 n = 69 22.49 78.38 63.82 5.98 ± 0.06 Nestling 1 $457.65 \pm$ $2333.02 \pm$ $2491.2 \pm$ $a = 110$ 7.51 5.59 ± 0.05 n = 73 34.27 61.16 49.35 5.59 ± 0.05 Perch 1 $570.8 \pm$ $3177.41 \pm$ $3151.12 \pm$ $a = 77$ 7.51 127.06 94.08 Perch 2 $600.73 \pm$ $2328.98 \pm$ $2386.96 \pm$ $a = 127$ 5.25 ± 0.07 n = 127 10.87 87.89 70.37 5.25 ± 0.07 Perch 3 $590.43 \pm$ $3399.37 \pm$ $3109.39 \pm$ <	Perch 5 $553.4 \pm$ $3590.51 \pm$ $3580.66 \pm$ 5.58 ± 0.11 5.12 ± 0.1 n = 3514.28124.7672.99 5.58 ± 0.11 5.12 ± 0.1 Perch 6 $1155.03 \pm$ $3236.38 \pm$ $3218.34 \pm$ 4.3 ± 0.11 4.11 ± 0.08 n = 7490.4343.96 28.6 4.3 ± 0.11 4.11 ± 0.08 Begging $754.78 \pm$ $2678.41 \pm$ $2844.93 \pm$ 4.3 ± 0.11 4.11 ± 0.05 n = 135 37.05 99.55 79.5 5.41 ± 0.06 4.7 ± 0.05 Display $673.53 \pm$ 1999.61 \pm $2234.82 \pm$ 4.95 ± 0.1 4.38 ± 0.08 n = 65 40.67 107.08 81.69 4.95 ± 0.1 4.38 ± 0.08 n = 2519.96 54.88 40.81 5.16 ± 0.04 4.48 ± 0.03 n = 12 28.31 272.93 253.7 5.17 ± 0.21 4.45 ± 0.17 n = 12 28.31 272.93 253.7 5.98 ± 0.06 5.58 ± 0.06 n = 69 22.49 78.38 63.82 5.98 ± 0.06 5.58 ± 0.06 n = 110 17.51 51.33 37.16 5.65 ± 0.05 4.94 ± 0.05 n = 73 34.27 61.16 49.35 5.59 ± 0.05 5.02 ± 0.05 n = 77 17.51 127.06 94.08 5 ± 0.08 4.62 ± 0.07 n = 127 10.87 87.89 70.37 5.25 ± 0.07 5 ± 0.06 Perch 1 $570.8 \pm$ $3399.37 \pm$ $3109.39 \pm$ 6.06 ± 0.19 5.66 ± 0.15	Perch 5 $553.4 \pm$ 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0.14$$0.38 \pm 0.02$Nest entry$423.84 \pm$$2240.7 \pm$$2308.73 \pm$$5.98 \pm 0.06$$5.58 \pm 0.06$$4.56 \pm 0.09$$6.33 \pm 0.05$$0.4 \pm 0.02$Nest ling 1$457.65 \pm$$233.02 \pm$$2499.62 \pm$$5.65 \pm 0.05$$5.02 \pm 0.05$$3.73 \pm 0.07$$5.91 \pm 0.05$$0.41 \pm 0.01$$n = 73$$34.27$$61.16$$49.35$$5.59 \pm 0.05$$5.02 \pm 0.05$$3.85 \pm 0.06$$6.$</td> <td>Perch 5$553.4 \pm$$3590.51 \pm$$3580.66 \pm$$5.58 \pm 0.11$$5.12 \pm 0.1$$3.99 \pm 0.14$$5.99 \pm 0.06$$0.68 \pm 0.04$$0.21 \pm 0.01$Perch 6$1155.03 \pm$$3226.38 \pm$$3218.34 \pm$$4.3 \pm 0.11$$4.11 \pm 0.08$$2.75 \pm 0.08$$5.83 \pm 0.07$$0.45 \pm 0.01$$0.13 \pm 0$Begging$754.78 \pm$$2678.41 \pm$$2846.93 \pm$$4.3 \pm 0.11$$4.11 \pm 0.08$$2.75 \pm 0.08$$5.83 \pm 0.07$$0.45 \pm 0.01$$0.13 \pm 0$Display$673.53 \pm$$1999.61 \pm$$2234.82 \pm$$4.95 \pm 0.1$$4.38 \pm 0.08$$3.14 \pm 0.08$$5.8 \pm 0.05$$0.28 \pm 0.01$$0.07 \pm 0$Flight$593.12 \pm$$3041.41 \pm$$3125.32 \pm$$5.16 \pm 0.04$$4.48 \pm 0.03$$3.3 \pm 0.03$$5.93 \pm 0.04$$0.4 \pm 0.01$$0.13 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2234.82 ± 4.95 ± 0.1 4.38 ± 0.08 3.14 ± 0.08 5.8 ± 0.05 0.28 ± 0.01 0.13 ± 0 $468.161.61 \pm 500.4$ Display 673.53 ± 1999.61 ± 2234.82 ± 4.95 ± 0.1 4.38 ± 0.08 3.14 ± 0.08 5.8 ± 0.05 0.28 ± 0.01 0.13 ± 0 $458.16.61.61 \pm 500.4$ Take-off 572.85 ± 2806.49 ± 3075.66 ± 5.16 ± 0.04 448 ± 0.03 3.3 ± 0.03 5.99 ± 0.14 0.38 ± 0.02</td><td>Perch 5$553.4 \pm$$3590.51 \pm$$3580.66 \pm$ $r = 33$$5.58 \pm 0.11$$5.12 \pm 0.1$$3.99 \pm 0.14$$5.99 \pm 0.06$$0.68 \pm 0.04$$0.21 \pm 0.01$$6164.86 \pm$ $848.93$$1 \pm 0.28$Perch 6$1155.03 \pm$$3236.38 \pm$$3218.34 \pm$ $43.96 \pm$$4.3 \pm 0.11$$4.11 \pm 0.08$$2.75 \pm 0.08$$5.83 \pm 0.07$$0.45 \pm 0.01$$0.13 \pm 0$$6164.86 \pm$ $848.93$$1 \pm 0.28$Begging$754.78 \pm$$2678.41 \pm$$2844.93 \pm$ $286.4$$4.3 \pm 0.11$$4.11 \pm 0.08$$2.75 \pm 0.08$$5.83 \pm 0.07$$0.45 \pm 0.01$$0.13 \pm 0$$6161.1 \pm$ $500.44$$0.37 \pm 0.32$Display$673.53 \pm$$1999.61 \pm$$2234.82 \pm$ $4.95 \pm 0.1$$4.38 \pm 0.08$$3.14 \pm 0.08$$5.8 \pm 0.05$$0.28 \pm 0.01$$0.07 \pm 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0$$6161.1 \pm$ $500.44$$0.37 \pm 0.32$Display$673.53 \pm$$1999.61 \pm$$2234.82 \pm$ $4.95 \pm 0.1$$4.38 \pm 0.08$$3.14 \pm 0.08$$5.8 \pm 0.05$$0.28 \pm 0.01$$0.07 \pm 0$$3825.09 \pm$ $388.85$$-1.16 \pm 0.45$Flight$593.12 \pm$$3041.41 \pm$$3125.32 \pm$ $n = 251$$4.95 \pm 0.1$$4.38 \pm 0.08$$3.14 \pm 0.08$$5.8 \pm 0.05$$0.28 \pm 0.01$$0.07 \pm 0$$3825.09 \pm$ $451.15$$-1.16 \pm 0.45$Take-off$572.85 \pm$$2806.49 \pm$$3075.66 \pm$ $5.17 \pm 0.21$$4.45 \pm 0.17$$3.36 \pm 0.13$$5.99 \pm 0.14$$0.38 \pm 0.02$$0.1 \pm 0.01$$12468.08 \pm$ $2176$$1.09 \pm 0.38$n = 12$28.31$$272.93$$253.7$$5.17 \pm 0.21$$4.45 \pm 0.17$$3.36 \pm 0.13$$5.99 \pm 0.14$$0.38 \pm 0.02$$0.1 \pm 0.01$$12468.08 \pm$ $2176$$1.09 \pm 0.36$n = 12$28.31$$272.93$$253.7$$5.17 \pm 0.21$$4.45 \pm 0.17$$3.36 \pm 0.07$</td>	Perch 5 553.4 ± 3590.51 ± 3580.66 ± 5.58 ± 0.11 5.12 ± 0.11 3.99 ± 0.14 5.99 ± 0.06 0.68 ± 0.04 0.21 ± 0.01 6164.86 ± 848.93 Perch 6 1155.03 ± 3236.38 ± 3218.34 ± 3218.34 ± 306 $2.38.6$ 4.3 ± 0.11 4.11 ± 0.08 2.75 ± 0.08 5.83 ± 0.07 0.45 ± 0.01 0.13 ± 0 107.85 Begging 754.78 ± 2678.41 ± 2844.93 ± 5.41 ± 0.06 4.7 ± 0.05 3.11 ± 0.06 6.15 ± 0.05 0.39 ± 0.01 0.13 ± 0 4661.61 ± 500.4 Display 673.53 ± 1999.61 ± 2234.82 ± 4.95 ± 0.1 4.38 ± 0.08 3.14 ± 0.08 5.8 ± 0.05 0.28 ± 0.01 0.13 ± 0 $468.161.61 \pm 500.4$ Display 673.53 ± 1999.61 ± 2234.82 ± 4.95 ± 0.1 4.38 ± 0.08 3.14 ± 0.08 5.8 ± 0.05 0.28 ± 0.01 0.13 ± 0 $458.16.61.61 \pm 500.4$ Take-off 572.85 ± 2806.49 ± 3075.66 ± 5.16 ± 0.04 448 ± 0.03 3.3 ± 0.03 5.99 ± 0.14 0.38 ± 0.02	Perch 5 $553.4 \pm$ $3590.51 \pm$ $3580.66 \pm$ $r = 33$ 5.58 ± 0.11 5.12 ± 0.1 3.99 ± 0.14 5.99 ± 0.06 0.68 ± 0.04 0.21 ± 0.01 $6164.86 \pm$ 848.93 1 ± 0.28 Perch 6 $1155.03 \pm$ $3236.38 \pm$ $3218.34 \pm$ $43.96 \pm$ 4.3 ± 0.11 4.11 ± 0.08 2.75 ± 0.08 5.83 ± 0.07 0.45 ± 0.01 0.13 ± 0 $6164.86 \pm$ 848.93 1 ± 0.28 Begging $754.78 \pm$ $2678.41 \pm$ $2844.93 \pm$ 286.4 4.3 ± 0.11 4.11 ± 0.08 2.75 ± 0.08 5.83 ± 0.07 0.45 ± 0.01 0.13 ± 0 $6161.1 \pm$ 500.44 0.37 ± 0.32 Display $673.53 \pm$ $1999.61 \pm$ $2234.82 \pm$ 4.95 ± 0.1 4.38 ± 0.08 3.14 ± 0.08 5.8 ± 0.05 0.28 ± 0.01 0.07 ± 0 $3825.09 \pm$ 388.85 -1.16 ± 0.45 Flight $593.12 \pm$ $3041.41 \pm$ $3125.32 \pm$ $n = 251$ 4.95 ± 0.1 4.38 ± 0.08 3.14 ± 0.08 5.8 ± 0.05 0.28 ± 0.01 0.07 ± 0 $3825.09 \pm$ 451.15 -1.16 ± 0.45 Take-off $572.85 \pm$ $2806.49 \pm$ $3075.66 \pm$ 5.17 ± 0.21 4.45 ± 0.17 3.36 ± 0.13 5.99 ± 0.14 0.38 ± 0.02 0.1 ± 0.01 $12468.08 \pm$ 2176 1.09 ± 0.38 n = 12 28.31 272.93 253.7 5.17 ± 0.21 4.45 ± 0.17 3.36 ± 0.13 5.99 ± 0.14 0.38 ± 0.02 0.1 ± 0.01 $12468.08 \pm$ 2176 1.09 ± 0.36 n = 12 28.31 272.93 253.7 5.17 ± 0.21 4.45 ± 0.17 3.36 ± 0.07