

1 Running Head: CONTAGIOUS YAWNING AND STRETCHING IN BUDGERIGARS
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5 **UNCORRECTED PROOF**
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9 **Evidence for contagious behaviors in budgerigars (*Melopsittacus undulatus*): An**
10 **observational study of yawning and stretching**
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Abstract

Yawning is contagious in humans and some non-human primates. If there are social functions to contagious behaviors, such as yawning, they might occur in other highly social vertebrates. To investigate this possibility, we conducted an observational study of yawning and an associated behavior, stretching, in budgerigars (*Melopsittacus undulatus*), a social, flock-living parrot. Flock-housed budgerigars were videotaped for 1.5 hrs at three time-blocks during the day (early morning, afternoon and early evening), and the times of all yawns and stretches for each bird were recorded. Both yawning and stretching were temporally clumped within sessions, but were uniformly distributed across the trials of a particular time-block. This suggests that clumping was not a result of circadian patterning and that both behaviors could be contagious. There was additional evidence of contagion in stretching, which occurred in two forms – a posterior-dorsal extension of either one foot or both feet. Birds that could have observed a conspecific stretch, and that then stretched themselves within 20 sec, replicated the form of the earlier stretch significantly more often than expected by chance. This study provides the first detailed description of temporal patterns of yawning under social conditions in a flock-living species as well as the first support for contagious yawning and stretching in a non-primate species in a natural context. Experimental evidence will be necessary to confirm the extent of contagion in either behavior.

Key terms: contagion, yawning, stretching, signal, social coordination, imitation, response facilitation

40 Although yawning has been observed across vertebrate classes (Baenninger 1987;
41 Craemer 1924; Gallup et al. 2009; Luttenberger 1975), its function is still poorly understood
42 (Provine 2005). It is characterized by an involuntary opening of the mouth, with a deep
43 inspiration and shorter expiration, that is stereotyped within and across individuals, and is
44 morphologically similar across species (Provine 1986a). Yawning is contextually associated with
45 transitions between activity and inactivity, and for this reason it has been suggested that
46 yawning stimulates brain arousal (Baenninger 1997). Although physiological evidence in
47 support of this view is sparse (Guggisberg et al. 2010), contextual evidence is accumulating
48 (Greco et al. 1993). For instance, yawning is associated with fatigue in humans (Zilli et al. 2008)
49 and birds (Sauer and Sauer 1967), movement in humans (Baenninger et al. 1996) and primates
50 (Vick and Paukner 2010), stress in rodents (Moyaho and Valencia 2002) and birds (Miller et al.
51 2010), and boredom in humans (Provine et al. 1986b). Recent comparative research also
52 supports a role of yawning in brain thermoregulation (e.g., Gallup and Gallup Jr 2007; 2008;
53 Gallup and Hack 2011; Gallup and Eldakar 2011; Shoup-Knox et al. 2010), and it has been
54 suggested that the cooling component of yawning may facilitate arousal by reinstating optimal
55 brain temperature. Thus, building evidence from numerous laboratories suggests that yawning
56 is multifunctional (Vick and Paukner 2010; Gallup 2011), which may explain its ubiquity across
57 vertebrates (Baenninger 1987).

58 In contrast with spontaneous yawning, contagious yawning has been convincingly
59 documented only in humans and a few non-human primates. Contagion is defined as the
60 matching of reflexive or involuntary behaviors (Zentall 2003), of which yawning provides a
61 classic example. For instance, just observing or even reading about yawns stimulates yawning

62 in humans (Baenninger and Greco 1991), and attempts to shield a yawn do not stop its
63 contagion (Provine 2005). Under laboratory conditions, watching videotaped yawns produces
64 contagious yawning for roughly 50% of human participants (Gallup and Gallup Jr 2007; Platek et
65 al. 2003). Similar methods have been used to document contagious yawning in chimpanzees
66 (*Pan troglodytes*) (Anderson et al. 2004; Paukner and Anderson 2006), and recently this result
67 has been replicated using three-dimensional computer animations as a stimulus (Campbell et
68 al. 2009). Video-induced yawning has also been reported in stump-tail macaques (*Macaca*
69 *arctoides*) (Paukner and Anderson 2006), but since the same stimulus also induced significantly
70 more self-directed scratching responses, the degree to which the increased yawning represents
71 social contagion, rather than social tension or stress, remains unclear. A more recent study
72 tested for a contagious yawning in red-footed tortoises (*Geochelone carbonaria*) by either
73 displaying video clips of a yawning conspecific, or using a live model trained to yawn in the
74 presence of other tortoises (Wilkinson et al. 2011). In either case, however, there was no
75 evidence for contagious yawning in this species. Further research using a live demonstrator as
76 a stimulus has involved the testing of domesticated dogs (*Canis familiaris*). The first report of
77 this topic provided evidence to suggest that dogs yawn in response to human yawns (Joly-
78 Mascheroni et al. 2008). However, more recent research attempting to replicate this finding,
79 using both live demonstrators as well as video clips, has failed to demonstrate this cross-species
80 contagion effect (Harr et al. 2009; O'Hara & Reeve 2011). In addition, one report using video
81 clips of dog yawns also failed to provide evidence for conspecific contagious yawning (Harr et
82 al. 2009), casting doubt on whether dogs yawn contagiously at all. Using a different approach,
83 a recent observational study reported evidence of contagious yawning in gelada baboons

84 (*Theropithecus gelada*) (Palagi et al. 2009). The authors recorded all instance of yawning from a
85 colony of captive baboons, revealing that the frequency of this behavior increased among
86 individuals when in the presence of both visual and acoustic yawning signals from conspecifics.
87 Similar to other research on primates (Vick and Paukner 2010), several distinct types of yawns
88 were identified. Socially close baboons, especially females, were more likely to yawn
89 contagiously, and these females matched the observed yawn-type when they yawned
90 immediately after.

91 If contagious behaviors serve important functions, *e.g.*, group coordination, in social
92 mammals, it seems reasonable that yawning may be contagious in social, non-mammalian
93 species as well. Furthermore, different behaviors could also be contagious and serve the same
94 function, depending on the activity or social changes signaled. Here we present an
95 observational study, in which we documented patterns of yawning and an associated behavior,
96 stretching, in a flock of budgerigars (*Melopsittacus undulatus*) housed in an indoor aviary.
97 Budgerigars are highly social, small parrots indigenous to Australia. They move in highly
98 coordinated flocks throughout the year, even breeding as pairs within a larger flock (Wyndham
99 1980), and signals of intention to move could certainly play a role in coordinating group activity.
100 Stretching is a stereotyped behavior that is associated with yawning in humans and rodents
101 (Baenninger 1997), but there is little evidence that stretching is contagious in humans or other
102 animals (for evidence of synchronized group displays, see Stevens 1991). Nonetheless,
103 stretching and yawning may predict changes in activity and/or an individual's level of stress,
104 and therefore, the spread of either, or perhaps both behaviors, may coordinate group activity.
105 Similar to yawning, stretching is believed to be a reflexive, automatic action in these birds, so

106 unlike the copying of voluntary, learnt behaviors, known as imitation or response facilitation
107 (e.g., Hoppitt et al. 2007), in this study the temporal coupling of either behavior refers to
108 contagion.

109 Our previous research has recently explored the contagious nature of these behaviors in
110 budgerigars through video stimuli, finding mixed support for a social influence in yawning
111 (unpublished data). In particular, the latency to yawn was significantly reduced following clips
112 of conspecific yawns compared with control clips, but the frequency of yawning and stretching
113 did not increase following clips of the respective behavior (unpublished data). There were,
114 however, limitations in the quality of the stimulus (recorded from freely behaving birds) and
115 the degree to which the experimental birds were attending to the video screen. Therefore, in
116 this study we tried to lay a stronger foundation for future experimental work by taking a
117 naturalistic approach similar to the study performed on gelada baboons (Palagi et al. 2009). To
118 explore how individual birds responded to the actions of nearby group members, we video
119 recorded an undisturbed, established flock of captive budgerigars, and measured the time and
120 occurrence of each yawn and stretch. For yawning and stretching separately, we analyzed the
121 distribution of successive behaviors. We also looked for any diel patterns, and associations
122 between stretching and yawning at three different times of the day (early morning, afternoon
123 and early evening). It was hypothesized that, if contagious, each behavior would be non-
124 randomly clumped into closely spaced bouts within recording sessions, as birds were stimulated
125 by their neighbors' behavior, and separated by longer periods without these behaviors. Even if
126 clumped within a particular testing session, we further predicted that these behaviors would be
127 evenly spaced across multiple sessions, when comparing sessions that were recorded at the

128 same time of day. This would suggest that it is not a specific time of day that causes the
129 clumping pattern. Lastly, a strong circadian or other temporal pattern, previously established
130 for humans and rats (Baenninger 1997; Anias et al. 1984; Zilli et al. 2007), would potentially
131 illuminate the context and function of these behaviors, whether contagious or not. In
132 summary, although these behaviors may have a general circadian pattern over distinct periods
133 of the day (*i.e.*, they may occur more frequently in the morning or evening), we predict that
134 within a particular session, behaviors will be clumped due to social factors.

135 **Methods**

136 *Subjects.* A flock of budgerigars bred and housed at Binghamton University were used in
137 this study. At the start of the study, the flock contained 21 birds (9 males, 12 females), all non-
138 breeding, between 11 and 15 years of age and living in flocks throughout their lives. The study
139 was performed between April 2008 and October 2009. During this time, there were three
140 deaths due to natural causes apparently related to aging (one male and two females). Birds
141 were housed in an indoor aviary (1.8 × 1.8 × 1.8 m), and mixed seeds, water and fresh
142 vegetables were provided ad libitum. The room was kept on an automated light:dark cycle
143 (time on: 0700, time off: 1900) and the temperature was maintained at 23°C. Provisions for
144 animal care and use were approved by Binghamton University's Institutional Animal Care and
145 Use Committee (Protocol #629-08).

146 *Procedure.* This observational study used recordings of the undisturbed flock to
147 characterize natural patterns of stretching and yawning in this species. Taping sessions took
148 place within the flock's indoor aviary, on a total of 15 days throughout the study period. Each
149 taping session lasted 90 minutes and started at one of three times (early morning: 0730;

150 afternoon: 1200; early evening: 1630). During the late fall and winter, recording times shifted
151 to one hour earlier to accommodate the end of United States' day-light savings time. A
152 researcher entered the aviary five minutes before the start of each session to prepare the
153 recording equipment. During preparation, perches were repositioned, so that perched birds
154 would be in view of the camera. A camcorder, which continuously recorded picture and audio,
155 was placed inside the aviary, positioned at the corner diagonally across from two large perches,
156 allowing a view of the entire flock except during feeding and flying. Due to recent research
157 showing that certain environmental manipulations influence yawning in budgerigars (Gallup et
158 al. 2009; Miller et al. 2010), we controlled for factors such as time, temperature and relative
159 humidity. Furthermore, the audio track from the camcorder was used to confirm that there
160 were no external disturbances (*e.g.*, someone entering the room) influencing the pattern of
161 behaviors.

162 *Review.* A total of 23 sessions were recorded over 15 testing days (6 early morning, 8
163 afternoon and 9 early evening). Tapes were digitally transferred and viewed on an iMac
164 running iMovie (Apple Inc., Cupertino, CA). The first 15 minutes of each tape were ignored,
165 since disturbances caused by the researcher's entrance affect yawning (unpublished data). Two
166 reviewers trained to recognize avian yawns and stretches reviewed each tape together and
167 came to a consensus on the time and occurrence of all behaviors. Yawning was conspicuous as
168 a wide opening of the beak and slight closing of the eyes, followed by a brief pause with
169 stretching of the neck (Figure 1a). Stretches were scored when the bird lifted one or both
170 wings, along with a posteriodorsal extension of one or both legs (Figure 1b). When only a single
171 leg was extended (left or right), the stretch was recorded and characterized as monolateral, but

172 when both legs were extended sequentially, the stretch was bilateral. The time to the nearest
173 second at which a bird either yawned or stretched was also recorded, along with the number of
174 birds visible on the screen when a behavior was performed. To avoid treating recurring
175 behaviors from the same bird as evidence for a clustering effect within the group (*i.e.*, a single
176 bird yawning or stretching multiple times in a row), for all clustering analyses we removed any
177 repeated behaviors from the same bird within a one-minute span. For instance, if Bird A
178 stretched and subsequently stretched again within the next sixty seconds then the second
179 stretch was excluded from the runs tests and inter-behavior interval analyses (see below).

180 *Analysis.* For observational evidence of contagion, patterns of yawning and stretching
181 were analyzed in the following way (described for yawns). First, the time between adjacent
182 yawns was calculated (inter-yawn interval) and frequencies of occurrence were binned into 20-
183 second intervals. When a yawn followed the previous yawn by greater than 300 seconds, this
184 yawn was placed in the > 300 seconds inter-yawn interval. If contagious, one would expect a
185 high frequency of closely spaced yawns, separated by longer intervals until the occurrence of a
186 new, first yawn (priming yawns) (Baenninger 1987). Thus, very short intervals and quite long
187 intervals should both be more frequent than other intervals.

188 To identify significantly non-random distributions of intervals, a separate runs test was
189 performed for each session and each behavior (23 total per behavior). Each taping session was
190 broken into 150 thirty-second bins and the number of observed yawns/stretchers in each bin
191 was calculated. A run was composed of consecutive bins identified as either having at least one
192 yawn (1), or having no yawns (0). For instance, '11110000' contains two runs, the first
193 represents two minutes, during which time there were multiple yawning, possible more than

194 one in each of the four bins (1111). The second run represents two minutes without any yawns
195 (0000). Thus, there was no distinction between bins with one versus multiple yawns. The same
196 was done for stretches. The runs test compares the observed number of runs to the expected
197 number of runs. The generated Z-score is normally distributed, with negative values indicating
198 a greater degree of clumping. We then used a combined probability test, as described by Sokal
199 and Rohlf (1995, pp. 778-782), to determine the probability of non-random clumping across the
200 23 test sessions for each behavior separately. The combined probability test was used to
201 evaluate a common null hypothesis that was independently tested by each runs test. For each
202 behavior, it indicated if there was an overall significant bias in one direction across these
203 sessions. To test whether the clustering we observed was specific to a single time-interval, in
204 this case 30-second bins, this analysis was also re-performed with binning the data into 225
205 twenty-second bins (see *Supplemental Material*). In addition, to investigate whether larger
206 groups of birds exhibited behaviors that are more tightly spaced in time, we ran Pearson
207 correlations between the Z-scores and the average visible group-size per session for each
208 behavior. If larger groups of birds produced more temporal clustering, we would expect
209 significant negative correlations to emerge.

210 Contagious stretching was also evaluated by calculating the number of matched stretch-
211 type pairings between adjacent stretches. Only stretches spaced by 20 seconds were
212 considered in this analysis. If there was more than one consecutive stretch within 20 seconds
213 of a potential initiating stretch, only the first pair was considered in the analysis. Matched
214 pairings occurred when monolateral stretches followed monolateral stretches (MS → MS) or
215 bilateral stretches followed bilateral stretches (BS → BS), while the other two combinations

216 (MS → BS and BS → MS) were unmatched pairings. The frequencies of matching or non-
217 matching pairs were compared in a 2 × 2 contingency table (χ^2 test of independence).

218 In order to determine the circadian pattern of each behavior, yawn and stretch
219 frequencies were compared across the three time periods. To control for variation in bird
220 visibility across all analyses, the frequency of each behavior during a recording session was
221 divided by the average number of birds visible on the screen.

222 Lastly, the association between yawns and stretches was evaluated by counting the
223 number of times an individual yawned while stretching within ± 30 seconds (“associated
224 yawns”). The number of stretches that were performed within ± 30 seconds of a yawn was also
225 calculated (“associated stretches”). The proportions of yawns and stretches temporally
226 associated with the other behavior by the same individual were compared across the three
227 time periods.

228 Results

229 *Distribution of yawning and stretching within recording sessions.* The pattern of inter-
230 behavior intervals for both yawning and stretching was strongly biased toward very short (< 20
231 sec) and very long (> 300 sec) intervals (Figure 2). Although both yawning and stretching
232 behaviors were clustered within trials, neither behavior routinely occurred at specific times
233 from the start of a session across multiple recordings at the same time of day. Figure 3 shows
234 an even distribution of spacing in behaviors across trials. This suggests that the clumping of
235 these behaviors (< 20 sec) within any particular taping session was due to social influences, and
236 not to underlying physiological effects as a result of similar circadian patterns.

237 A summary of the statistics for each runs test, when analyzed with 30-second intervals,
238 is shown in Figure 4 (negative Z-scores indicate clumping). Yawns were significantly more
239 clumped than expected in four of the 23 trials (17.4%, p values < 0.022). Similarly, stretches
240 were significantly non-random and clumped in 16 of the 23 trials (69.6%, p values < 0.048). The
241 average (\pm SEM) Z-score for yawning was $-0.59 (\pm 0.31)$, and for stretching it was $-2.86 (\pm 0.37)$,
242 where negative scores indicate greater clumping rather than dispersion. None of the positive Z-
243 scores (indicating greater than expected dispersion) for either behavior were statistically
244 significant. Across the 23 sessions for each behavior, Z-scores were below zero significantly
245 more often than chance for both yawning (combined probabilities test: $\chi^2_{46} = 87.01$, $p < 0.001$)
246 and stretching (combined probabilities test: $\chi^2_{46} = 316.71$, $p < 0.001$). Pearson correlations
247 show that a higher number of visible birds within a session did not produce more tightly
248 clustered bouts of either behavior (negative correlations would be expected if this were the
249 case) (yawning: $r_{23} = 0.400$, $p = 0.059$; stretching: $r_{23} = 0.197$, $p = 0.368$).

250 Similar results were also observed when behaviors were counted in 20-second bins (see
251 *Supplemental Material*), although yawning became less clustered. For instance, yawns were
252 significantly clumped in only one session (average Z-score \pm SEM = -0.62 ± 0.20 , combined
253 probabilities test: $\chi^2_{46} = 56.44$, $p = 0.139$), but negative Z-scores were still observed in 17 of the
254 23 sessions. For stretching, this behavior was significantly clumped in 15 sessions (average Z-
255 score \pm SEM = -2.67 ± 0.30 , combined probabilities test: $\chi^2_{46} = 294.60$, $p < 0.001$) and negative
256 Z-scores were observed in all 23 sessions. Again, Pearson correlations show that this temporal
257 clustering was not simply a product of larger group-sizes (yawning: $r_{23} = 0.191$, $p = 0.383$;
258 stretching: $r_{23} = 0.019$, $p = 0.931$).

259 *Stretch-type matching.* A total of 339 stretch-stretch pairings met the criterion of unique
260 pairs occurring within 20 seconds. In 63% of these, the second stretch matched the form of the
261 first stretch (either MS → MS or BS → BS) significantly more than expected by chance (χ^2 test
262 of independence: $\chi^2_{1} = 12.36, p < 0.001$, Figure 5).

263 *Circadian patterns.* During the 28.75 hours of video analyzed, 566 yawns and 1752
264 stretches were observed. The average rate of yawning (yawns per bird for the whole session)
265 within the three time periods was not normally distributed (Shapiro-Wilk Tests: p values <
266 0.05), so differences among periods were analyzed using a non-parametric alternative. The
267 number of yawns varied significantly between the three time periods (Kruskal-Wallis Test: $H_2 =$
268 13.44, $p = 0.001$; Figure 6). Significantly more yawns occurred in the evening when compared
269 to the early morning session (Post-hoc Dunn's Test: $Q = 6.52, p < 0.05$). No other pair-wise
270 comparisons were significant. On the other hand, stretching, which was normally distributed,
271 did not vary across the three time periods (1-way ANOVA: $F_2 = 1.909, p = 0.17$).

272 *Yawn-stretch association.* A total of 247 yawns occurred within ± 20 seconds of
273 stretches by the same individual. Averaged across all recording sessions, the proportion of
274 yawns associated with stretching was 42% ($\pm 3\%$). There was a nearly significant difference in
275 proportion of yawns associated with stretches across the three time periods (1-way ANOVA: F_2
276 = 3.460, $p = 0.051$). Although pair-wise comparisons were not applicable, there was a gradual
277 increase in the proportion of yawns associated with stretches across the three time periods,
278 from 34% in the early morning to 49% in the evening.

279 A total of 230 stretches were temporally associated with yawns produced by the same
280 individuals. Averaged across all recording sessions, the average proportion of stretches

281 associated with yawning was 13% (\pm 2%). The proportion of associated stretches varied
282 significantly across the three time periods (Kruskal-Wallis ANOVA: $H_2 = 10.319$, $p = 0.006$). The
283 proportion of yawn-associated stretches in the evening was significantly greater than the
284 proportion during the early morning (Post-hoc Dunn's test: $Q = 3.171$, $p < 0.05$). All other pair-
285 wise comparisons were not significant.

286 Discussion

287 Occurrences of both yawning and stretching were temporally clumped in an
288 unmanipulated, captive flock of budgerigars, as would be expected if these behaviors are
289 contagious. Despite the low frequency of yawning (1.28 – 2.96 yawns per bird per hour,
290 depending on time of day), a bird was more likely to yawn within 40 seconds or less of another
291 bird's yawn (Figure 2a, intervals 1 and 2). There were also a substantial number of yawns
292 separated by at least 300 seconds from the previous yawn, but few spaced at intermediate
293 intervals. Taken together, the inter-yawn spacing distribution (Figure 2a) suggests that yawns
294 were socially influenced (*i.e.*, contagious). In other words, long periods of no yawns were
295 broken by a budgerigar's yawn that was then followed by a cascade of yawns among the others.
296 A similar, although less strongly bimodal temporal distribution of stretching was observed. In
297 part, fewer stretches were separated by very long intervals because there were a substantially
298 greater number of stretches than yawns per session (566 yawns versus 1752 stretches) and
299 stretching continued for longer bouts among flock members. Stronger evidence to support the
300 social influence of this behavior comes from stretch-type matching, illustrating that birds were
301 more likely to replicate the specific stretch-type of a previous bird than would be expected by
302 chance. This result is similar to the observational research on gelada baboons (Palagi et al.

303 2009), showing yawn-type matching. Although no functional distinctions between mono- and
304 bi-lateral stretches were identified, this temporal pairing of identical behaviors suggests that
305 stretches of conspecifics were sufficiently closely observed and that the form influenced the
306 subsequently stretching bird. It has been suggested that different yawn-types may produce
307 distinct physiological outcomes among chimpanzees (Vick and Paukner, 2010), and thus the
308 matching of different behavioral-types may help coordinate group activity.

309 An alternative interpretation of the temporal patterns we observed is that flocking birds
310 tend to simultaneously reach the same physiological state (*i.e.*, well-rested, hungry, alerted by
311 outside event, *etc.*) (Sauer and Sauer 1967), and this tendency produced more, or less, yawning
312 or stretching among group members. Differences in frequencies across the day would be a
313 reflection of these shared changes, since there are clear diel patterns of yawning in humans and
314 rodents (Anias et al. 1984; Baenninger et al. 1996). If yawning patterns are related to daily
315 rhythms of body temperature, metabolism, and resultant arousal, it is possible that flock
316 members both share a physiological rhythm and respond with some low degree of contagion to
317 another's behavior, thus strengthening the diel pattern and producing higher degrees of
318 clumping. Although plausible, this interpretation seems insufficient. Analyses show that
319 yawning was significantly clustered within sessions, as would be expected by contagion, but
320 when looking across sessions recorded at the same time of day, we notice that both yawns and
321 stretches occurred evenly throughout the videos, and were not repeatedly clustered at a
322 particular time of day (see Figure 3). This suggests that a related circadian physiological rhythm
323 experienced by the birds does not explain our results.

324 The combined temporal patterning and significant “matching” of adjacent stretches
325 suggest that this behavior is contagious and thus a potential social signal in this species.
326 Although the function of stretching is largely unstudied, it is another stereotyped, unlearned
327 behavior that is ubiquitous among tetrapods. Both yawning and stretching are homeostatic
328 behaviors believed to serve a purpose in the maintenance of bodily functions through
329 enhanced circulation (Sauer and Sauer 1967). Stretching in humans is confined to specific, yet
330 intense state-change, occurring most frequently after waking, but not prior to sleep (Provine et
331 al. 1987). Research on both humans and animals show that yawning also typically occurs during
332 broader state-changes (Provine et al. 1987), and is followed by modified activity or increased
333 locomotion (Baenninger et al. 1996; Giganti et al. 2002; Vick and Paukner 2010). Taken
334 together with the current results, we suggest that these behaviors may coordinate collective
335 flock behavior, in addition to serving as important preparatory responses to flight. As evidence
336 for this, flight and other movement among perches is often preceded by stretching or yawning
337 in budgerigars (unpublished data). Responding to another’s intention-movements has clear
338 adaptive value for any group-moving species. Based on these observations, the study of
339 yawning, stretching and transitions in activity may provide a novel approach to studying
340 collective behavior. When perched, budgerigars sit in close proximity to one another and
341 remain oriented towards adjacent group members, providing a setting where behaviors can
342 spread across a line of birds, coordinating flock movement. Recently we have shown that
343 auditory disturbances enhance both stretching and yawning contagion among budgerigars in
344 small groups (Miller et al., in press), suggesting that the close coupling of these behaviors may
345 be involved in collective response to environmental stimuli. Future research could investigate

346 the role of yawning and stretching contagion in group vigilance, and more specifically how
347 spatial position within a group reflects another bird's information processing, and how birds
348 use local behaviors of nearby conspecifics to infer collective-state (Couzin 2009).

349 *Conclusions.* Signals may frequently originate from physiologically relevant behaviors
350 adapted for social purposes. Spontaneous yawning is associated with stress, arousal and
351 thermoregulation in a variety of species, including budgerigars. While the physiological
352 function of stretching is less clear, vertebrates frequently stretch before beginning to move.
353 Stretching also co-occurs with yawning in a variety of species and may therefore be associated
354 with arousal. The observational results presented here suggest that yawning and stretching are
355 at least mildly contagious in budgerigars under semi-natural flock-living conditions. In line with
356 each behavior's presumed physiological function, contagious yawning and stretching may
357 ultimately coordinate mental state and a group's collective movements, but future research
358 needs to test these predictions. While experimental studies are needed to confirm and clarify
359 the degree and precision of contagion, we propose that experiments be designed using live
360 birds as the target stimulus. Nonetheless, the current results provide a strong basis for
361 understanding the functional context of, and inferring an adaptive role for, contagion in
362 coordinated flock-living species.

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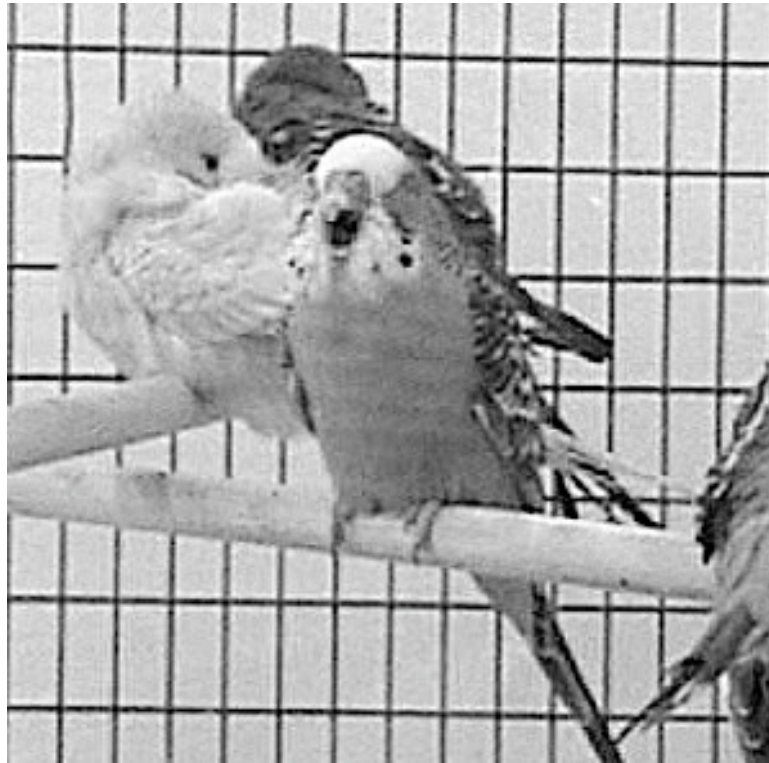
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469

470

Figures



(a)

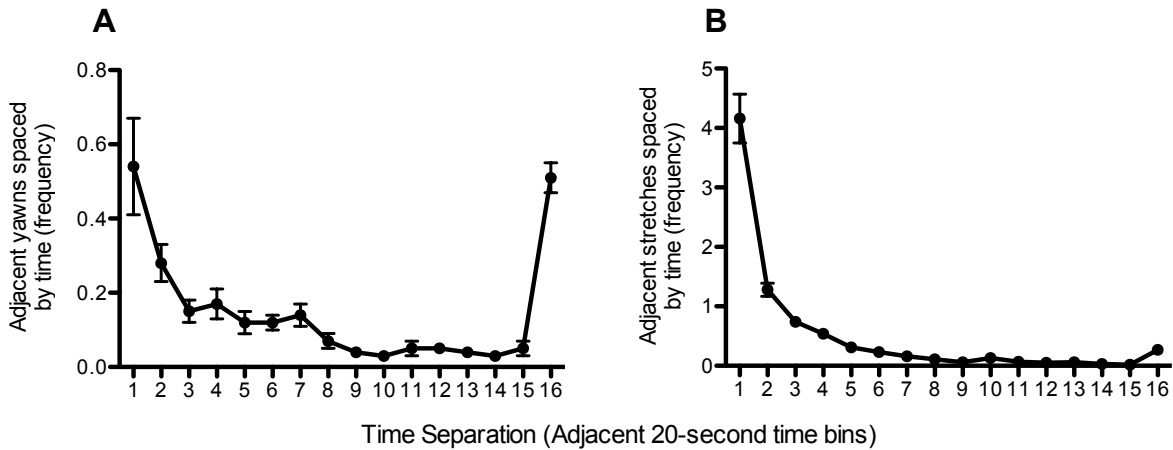
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(b)

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Figure 1. Representative examples of budgerigars yawning (a) and stretching (b) during video-recording.



478

479 **Figure 2.** To measure contagion, the time-interval between adjacent behaviors was measured in

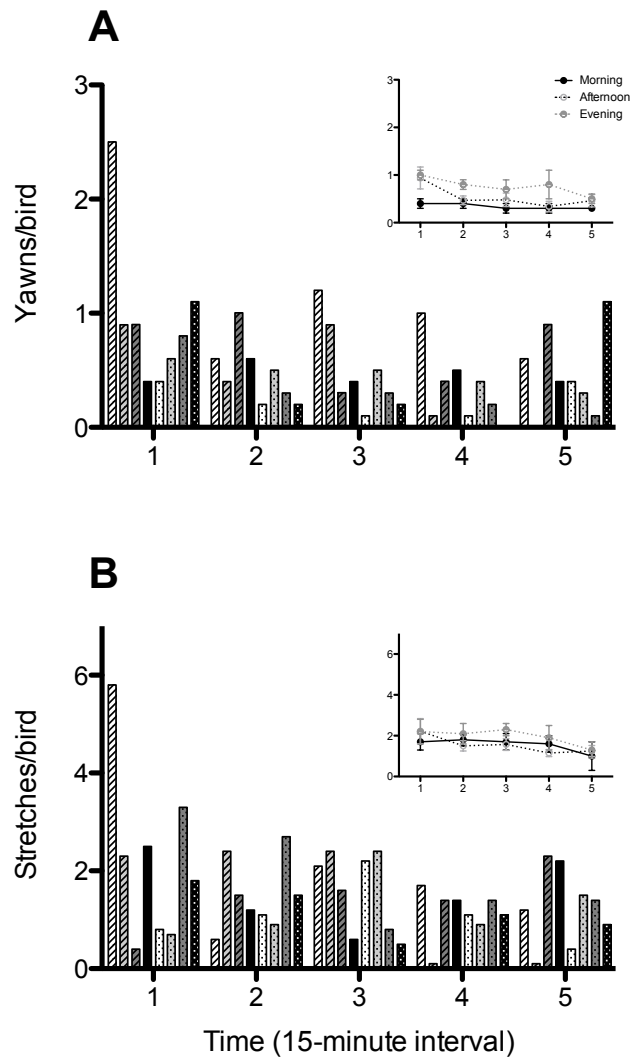
480 20-second bins, ranging from (1) < 20 seconds to (16) > 300 seconds (16). (a) Adjacent yawns

481 were likely to occur within 20 and 40 seconds of each other, or after a long period without

482 yawns (> 300 seconds). This distribution (*i.e.*, bouts of yawning separated by long periods

483 without yawning) would be expected with contagious yawning. (b) A similar, but less bimodal

484 distribution was observed for stretching.



485

486

Figure 3. Yawns and stretches were evenly distributed within sessions. For each afternoon

487

session, the number of yawns (a) and stretches (b) are shown for a given 15-minute bin (each

488

bar represents a single afternoon trial, $n = 8$ sessions total). Since neither yawns nor stretches

489

were observed at any particular time point – across sessions – within-trial clumping was

490

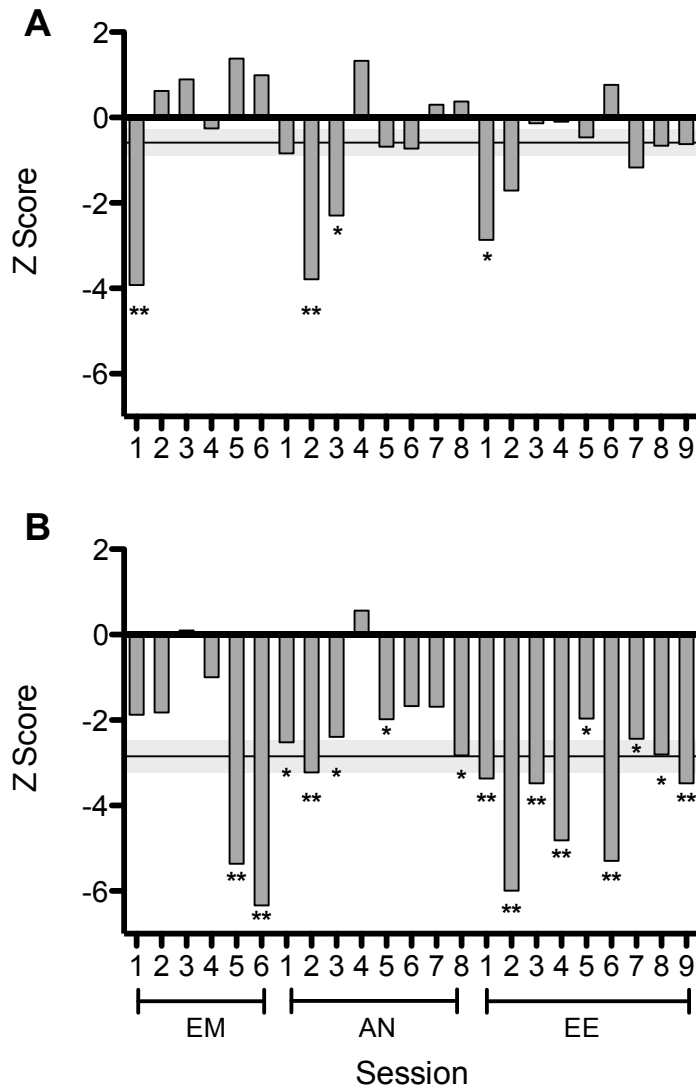
unlikely caused by time-dependent physiological state. Furthermore, insets show the average

491

distribution from the three testing periods (early morning, afternoon and early evening),

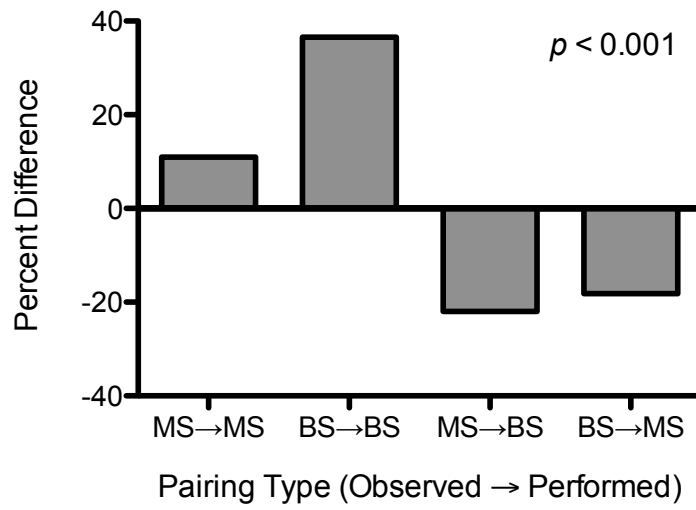
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revealing a uniform distribution at each time of day.



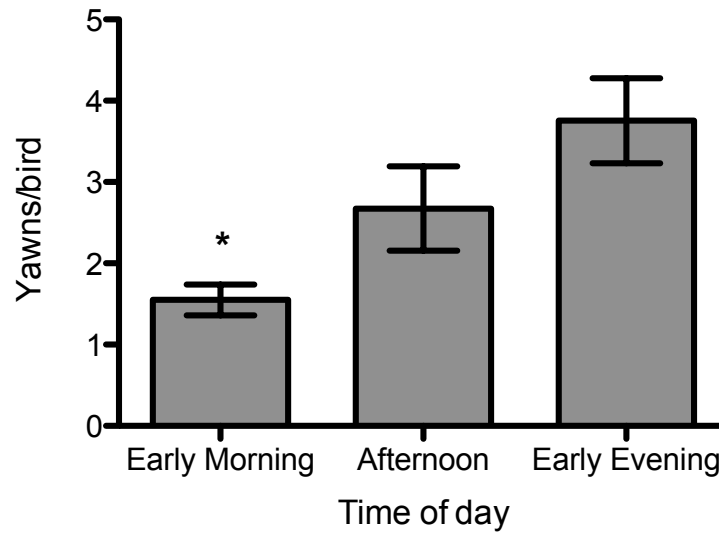
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494 **Figure 4.** Based on runs test analyses, both yawning and stretching were distributed non-
 495 randomly. (a) For yawns, 15 of the 23 sessions resulted in negative Z-scores, and of these, four
 496 sessions resulted in Z-scores significantly less than zero. (b) For stretches, 21 sessions resulted
 497 in negative Z-scores, and of these, 16 resulted in Z-scores significantly less than zero (bold line =
 498 average Z-score; Light Shading = +/- SEM; $n = 23$ sessions; $*p < 0.05$, $**p < 0.001$) (EM: early
 499 morning; AN: afternoon; EE: early evening).



500

501 **Figure 5.** The type of stretch performed by a different bird, within 20-seconds of the previous
502 stretch, was more likely to be matched (** $p < 0.001$).



503

504 **Figure 6.** Yawning frequency was affected by time of day. The frequency of yawns was

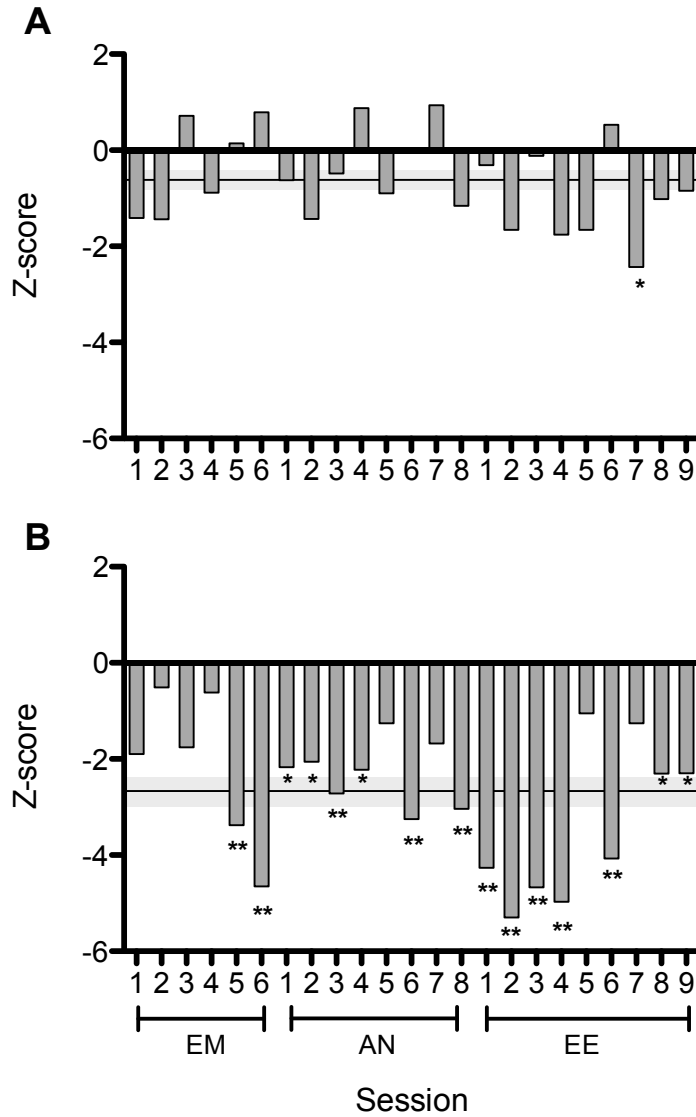
505 significantly lower in the early morning – relative to the early evening – and gradually increased

506 during the subsequent time-points (* $p < 0.05$ relative to early evening).

507

508

Supplemental Material



509

510 *Supplemental Figure S1.* Runs test analyses for both behaviors were re-performed after re-
 511 binning the data into 20-second intervals, and these yielded similar findings. The Z-scores for
 512 each session are separately shown for yawning (a) and stretching (b). For a descriptive
 513 comparison between two binning approaches, refer to *Supplemental Table S1* (bold line =
 514 average Z-score; light shading = +/- SEM; $n = 23$ sessions; * $p < 0.05$ and ** $p < 0.001$) (EM: early
 515 morning; AN: afternoon; EE: early evening).

Category	Binning method	
	20 sec	30 sec
(a) Yawning		
Average Z-score	-0.62	-0.59
Significantly clustered sessions (number)	1	4
Combined probabilities test (p value)	0.139	< 0.001
Total negative Z-values (number)	17	15
(b) Stretching		
Average Z-score	-2.67	-2.85
Significantly clustered sessions (number)	15	16
Combined probabilities test (p value)	< 0.001	< 0.001
Total negative Z-values (number)	23	21

516

517 Supplemental Table S1. Several parameters from both binning methods were compared to518 illustrate that the overall clustering pattern of each behavior was independent of binning519 method.