Captive Blue-and-yellow macaws (Ara ararauna) show facial indicators of positive affect when reunited with their caregiver

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1   **Captive Blue-and-yellow macaws (*Ara Ararauna*) show facial signs of positive affect**

2   **when reunited with their caregiver.**

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11   In mammals, human-animal bonding is recognized as a source of positive affect for

12   companion or farm animals. Because this remains unexplored in birds, we investigated

13   captive parrots' perspective of the human-animal relationship. We used a classical separation-

14   reunion paradigm and predicted that variations in parrots' facial displays and behaviours

15   would indicate their appraisal of the relationship. The test was divided into three phases of

16   two minutes each: the bird was placed in an unfamiliar environment with a familiar caregiver

17   (union), then the bird was left alone (separation) and finally, the caregiver returned (reunion).

18   The test was repeated 10 times for each bird and video recorded in order to analyze their

19   behaviour. The data show significantly higher crown and nape feather heights, higher redness

20   of the skin and higher frequency of contact-seeking behaviours during the union and reunion

21   phases than during the separation phase during which they expressed long distance contact

22   calls. We observed the expression of eye pinning during the union and reunion phases in one

23   out of five macaws. We argue that variation in facial displays provides indicators of parrot's

positive appraisal of the caretaker presence. Our results broaden the scope for further studies on parrots' expression of their subjective feelings.

1. Introduction

Interacting and bonding with companion animals such as dogs, cats, horses or birds is known to provide multiple benefits for human well-being (e.g. Beck 2014; Beck and Katcher 1996; Katcher and Beck, 1987). Comparatively, reciprocal studies dealing with the benefit for animals of bonding with humans are rarer and focused on mammals. To investigate this bond, the separation-reunion paradigm - derived from human psychology to investigate attachment-related behaviours (Ainsworth and Bell, 1970) - has been used on farm animals and more recently on companion dogs, cats or horses (Topál et al., 2005; Nagasawa et al., 2009; Payne et al., 2015; Rehn et al., 2014; Vitale et al., 2019; Lundberg et al., 2020). In farm animals, the existence of a positive affiliative bond towards humans was recognized as beneficial for animal welfare (Rault et al., 2020). For example, lambs express distress vocalizations when isolated but when they are reunited with a familiar caregiver they search physical contact and display appeasement. This indicates that the caregiver acts as a social support for the lambs (Nowak et al., 2015; Price and Thos, 1980; Boivin et al., 2001; Coulon et al., 2013; Rault et al., 2011). In dogs, the mere return of the owner after a brief separation is known to induce contact-seeking behaviour and to have a positive effect on oxytocin levels – a neuropeptide thought to be involved in the expression of prosocial behaviours and positive emotions - (Rhen, 2014).

Emotions are characterized by their valence (positive or negative) and arousal level (high or low; Mendl et al., 2010). Two types of positive emotions or states are commonly distinguished. Those characterized by high arousal levels such as joy, excitement,

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48 consummatory or appetite motivational states and, those characterized by low arousal levels

49 such as calmness, relaxation, safeness, social bonding or post-consummatory behaviours

50 (Mendl et al., 2010; Richardson et al., 2016; Carver, 2001). In previous studies, we showed

51 that specific facial displays such as crown and nape feather ruffling were associated with

52 activities having a positive valence and low arousal levels, like quiet positive social

53 interactions, maintenance or resting in Blue-and yellow macaws or Sulphur-crested cockatoo

54 *(Cacatua galerita)* (Bertin et al., 2018a; 2020). Macaws were also found to blush (i.e. increase

55 in blood flow in vascularized tissues) and ruffle their crown feathers when engaged in a

56 mutual interaction with their familiar caregiver (Bertin et al., 2018a), a context recognized as

57 rewarding for captive parrots (Pepperberg and McLaughlin 1996). Head feather ruffling was

58 also observed in Japanese quail performing dust-bathing, a behaviour considered as rewarding

59 with high arousal level (Bertin et al., 2018b).

60   Psittaciformes are highly social with primate-like cognitive capacities (Olkowicz et al.

61 2016; Gutiérrez-Ibáñez et al., 2018). Despite being wild non-domesticated animals, they form

62 strong affiliative bonds with people when captive (Baker, 2012; Anderson, 2014; Bond and

63 Diamond, 2019). We propose that, similarly to mammalian domesticated animals, a human-

64 animal social bond is a source of positive affect for these birds. To reveal attachment-related

65 behaviours, it is necessary to place the individual in a slightly stressful situation (Bowlby,

66 1982). Here we used a separation-reunion test in an unfamiliar environment as a slightly

67 stressful situation. The test was an adaptation of the Ainsworth Strange Situation test in which

68 human infants are separated and reunited from a parent or a stranger in a novel environment

69 (Ainsworth 1979). The original test compared the child's proximity seeking, during distress,

70 to the attachment figure or the stranger (Ainsworth 1979). Because our parrots were not used

71 to being approached by strangers and they show fear or aggressive behaviours in general

72 towards them, it was not possible to test parrots' behaviours when reunited with an unfamiliar

73 human. As a consequence, our study did not aim to determine whether parrots show a

74 preference for a specific attachment figure which, is one of the criteria that define a social

75 bond as attachment *per se* (a special affectional and emotional relationship between two

76 specific individuals).

77   We hypothesized that if the parrots were socially bonded toward their most familiar

78 caregiver then, this person should act as a social support to the birds (i.e: the ability of social

79 partners to enhance one's ability to cope with a challenging situation). Evidence of this social

80 support could consist of signs of positive-like emotional responses (e.g. calmness, relaxation)

81 during the test despite being placed in an unfamiliar environment and separated from

82 conspecifics. We predicted that this bond would be expressed by variations in behaviour

83 during the different phases of the test: union, separation, reunion. Specifically, based on our

84 previous research, we expected that macaws would express feather ruffling and blushing

85 when in presence of the familiar caregiver and a potentially enhanced response (rebound

86 effect) of these behaviours during the reunion phase.

87

88 **2. Animals and methods**

89 *2.1. Birds and housing conditions*

90 We observed five hand-reared Blue-and-yellow macaws (two males and three females

91 between 7 and 12 years old), not exposed to public visitors, at the Zooparc de Beauval Saint

92 Aignan (41110, France). All birds are part of a free-flying show. They had been trained daily

93 (i.e. handled daily) since weaning and were thus in close contact with humans, especially their

94 caregivers. During free-flight training the birds were taught to land on the caregivers' arm

95 when called after unrestricted outdoor flight. The five birds were housed in two adjacent

96 aviaries of similar sizes with an indoor area (250 cm x 520 cm x 260 cm) freely connected to

97 an outdoor area (250 cm x 850 cm x 260 cm) and were mixed with a pair of Sulphur-crested

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98   cockatoo. The aviaries were equipped with several tree branches, perches and ropes.

99   Enrichments were provided daily (cardboard and newspaper). Parrots were fed daily with

100   fresh fruits and vegetables, germinated seeds (wheat, corn, sunflower, rice, and oat), millet

101   seeds, oyster shells, and a commercial mix for exotic birds.

102   *2.2 Test apparatus and procedure*

103   All the tests took place inside a (3m l x 3m L x 2m h) barnum installed indoors,

104   unfamiliar to the birds and approximately 60 meters away from their aviaries. In order to

105   obtain profile images of the heads of the birds, the barnum was equipped with a perch (1.15 m

106   high, 80 cm long) placed perpendicularly to a small window allowing the passage of the

107   camera recorder mounted on a tripod. All the walls and the roof were opaque and composed

108   of white fabric. A lamp (Somikon photo light SLH3), placed on the floor, was used to have

109   even lighting conditions. All the tests were filmed by a Sony FS5 4K camera.

110   All birds were tested individually 10 times on 10 different days. All the tests were

111   conducted between 10am and 12pm for two successive weeks. Each bird was tested only once

112   per day and rank order of the birds was counterbalanced between days. All birds were tested

113   with the same animal caretaker. We worked with the animal caretaker who was the most

114   familiar to all of them (more than 10 years of caring for them). The caretaker chosen is also

115   the only one spending quality time with them daily to work on bonding (like playing with

116   them, providing tactile contacts or talking to them). As we observed pet-like behaviours

117   (supplementary data, Figure S1) during the daily routine in presence of the caretaker -

118   characteristic of an affiliative social bond with humans in pet macaws (Jordan, 2003) - we

119   assumed that, more than being familiar, a positive social bond had been established between

120   the birds and the caretaker. For each test session, a bird was called by its name, placed in its

121   usual transport cage (the same used for transport before free-flight shows) and taken to the

122 barnum. Then the bird was put on the perch by hand. The test was divided into three phases of

123 two minutes each:

    1. Union: the familiar caregiver stayed with the bird

    2. Separation: the caregiver left the barnum and thus the bird alone

    3. Reunion: the caregiver returned (reunion).

127 On the first day of testing, the birds were not willing to stay on the perch. They flew back

128 to their transport cage or perched on the caregiver's arms. Therefore, from day 2 to day 10,

129 the transport cage was left outside of the barnum and the birds were brought by hand inside

130 the barnum. The caregiver remained motionless in front of the bird at approximately 50 cm,

131 was asked to keep the arms behind her back. The caregiver was allowed to whisper the same

132 words to all parrots ("oui, c'est bien") to encourage them to stay on the perch. At the end,

133 each parrot received a nut and was placed back in its transport cage.

134 *2.3. Facial display characterization*

135 We used a protocol similar to Bertin et al. (2018b) on video-recordings obtained from

136 day 2 to day 9. We used the VLC software to search images of clear profiles and extract them

137 (Fig. 1). To homogenize the time when the profiles were extracted between birds, the profiles

138 were searched within twelve 30-s sequences. We extracted images every second with the

139 software and kept the first clear profile found within the 30-s sequence for analysis. We

140 extracted one clear profile per 30-s sequence for all birds (12 images per bird per test). We

141 used the software ImageJ, an image analysis program, to measure crown feather height, nape

142 feather height and area of the pupil. To correct for variation in the distance of the bird from

143 the camera, we used an invariant distance on each bird. For each bird, we measured manually

144 before the experiment, the real distance between the top of the beak and its tip with a digital

145 calliper (± 0.01 mm) (Fig. 1; a). Then, for each image, we used the function "straight" to draw

146 this distance on the image and then the function "set scale" to convert the distance in pixels to

147 distance in real centimetres. To measure crown feather height, we drew an angle with a

148 vertical plane going from the top of the beak (boundary between the nostril and the beak) and

149 the middle of the pupil (Fig. 1; b) and a 90° angle from the middle of the pupil to the top of

150 the green feathers (Fig. 1; c). The length of the line was determined with the function

151 "analyse" and "measure". To measure nape feather height, we estimated the length of a line

152 adjacent to the white skin of the jaw and going from the top of the blue feathers on the head to

153 the tip of the black feathers of the throat (Fig. 1; d). The pupil area was assessed with the

154 function "oval", with which we circled the black pupil and then used the function "measure"

155 to obtain the area of the circle.

156   To assess the presence of blushing (redness of the skin), we drew a 10 x 10 pixels

157 square on the bare skin at the external corner of the eye, between the blue feathers of the head

158 and the black feathers of the jaw (Fig. 1; e). With the function "measure" of image J, we

159 obtained the mean red (R), mean green (G), and mean blue (B) values of the square. Similarly

160 to some carotenoid-based studies (Pérez-Rodríguez and Viñuela 2008; Passarotto et al.,

161 2021), we calculated the redness of the skin as $R/(R+G+B)$. In order to control for the

162 balance of the white within the images, a 10 x 10 pixels square was also drawn on the white

163 wall of the barnum for each image. Because the values of redness obtained in the white wall

164 (mean Redness: 0.33 ± 0.001) did not differ significantly from a theoretical redness obtained

165 in a white or grey standard reference (0.33) (t-test, $P > 0.05$), no colour correction of the

166 images was deemed necessary. The same well-trained experimenter, blind to the phase, made

167 all the measures (540 images in total).

168

169 *2.3 Analysis of behaviour*

170   We assessed the number of times each bird expressed "contact seeking behaviours"

171 towards the animal caregiver: the bird stretched his body horizontally towards the caregiver,

7

172 and tried, or not, to grasp the caregiver's clothes with its beak, or the bird "begged" to be

173 taken on hand by lifting one leg in front of its breast. These behaviours were scored during the

174 three phases to make sure that they were specifically displayed in the presence of the

175 caregiver. We also recorded the number of times the birds expressed "long distance contact

176 calls" during the three phases. Macaws commonly emit these loud calls when they are

177 separated from their flock (Luescher 2008) (Video 1, supplementary data). Furthermore, one

178 out of the five birds expressed eye pinning (i.e. a rapid constriction of the pupil) (Gregory and

179 Hopkins 1974). The occurrence of this behaviour (i.e. the number of times the pupil

180 contracted to half its size, Figure S2, supplementary data) was recorded during the three

181 phases for this bird by two independent observers.

182

183 *2.4 Statistical analyses*

184 For all the parameters recorded, data was averaged across sessions per phase and per

185 individual. To test the effect of the phase we used the function aovperm of the Permuco

186 package in R 3.4.2 to run permutation tests with the phase as a fixed factor and the individual

187 as a random factor nested within phase with 10^6 permutations (Kherad-Pajouh and Renaud,

188 2015). All tests were two-tailed with significance considered at $P < 0.05$. The same function

189 was used for post-hoc comparisons. Because the usefulness of using corrections for multiple

190 comparisons in cases of low sample size is highly debated and results in a loss of power

191 (Garcia 2004; Nakagawa 2004; Garamszegi 2006), we present the original P-values. The data

192 are represented as boxplots with medians and interquartile distribution ranges. Only

193 descriptive data were given for the occurrence of eye pinning as it was displayed only by one

194 out of the five birds. The concordance between observers on the frequency of eye pinning was

195 evaluated with a spearman test and was highly significant (Rho=0.97; $P < 0.01$).

196

197 *2.5 Ethical note*

198   The Zooparc de Beauval (41110, Saint Aignan) kindly provided access to their birds.

199 Only video-recorded observations were conducted. Behavioural observations are not

200 considered as animal experimentations and are beyond the scope for ethical consideration

201 regarding French and European animal experimentation regulations. The Val de Loire Ethics

202 Committee for Animal Experimentation (N° CE19 – 2022-1503 – 5) reviewed the protocol

203 and attributed a positive recommendation.

204

205 **3. Results**

206   We found a significant effect of the phase on crown feather height ($F = 0.001$; $P =$

207 0.001) and nape feather height ($F < 0.001$; $P = 0.0008$) with in both cases the heights were

208 more important during the union and reunion phases compared to the separation phase

209 whereas heights did not differ significantly between the union and reunion phases (Fig. 2A

210 and 2B). We found a significant effect of the phase on redness of the skin ($F = 0.01$; $P =$

211 0.023) with post-hoc trends towards a higher redness during the union and reunion phases

212 than during the separation phase ($P = 0.06$ for all comparisons) whereas it did not differ

213 significantly between the union and reunion phases (Fig. 2C). The pupil surface did not differ

214 significantly between the three phases ($F = 0.14$; $P = 0.15$; Fig. 2D). The occurrence of

215 contact seeking behaviours differed significantly between the phases ($F = 0.09$; $P = 0.04$)

216 with higher occurrences during the union and reunion phases compared to the separation

217 phase whereas the occurrence did not differ significantly between the union and reunion

218 phases (Fig. 3A). The number of long distance contact calls differed significantly between the

219 phases ($F = 0.01$; $P = 0.001$) with a significant higher number of calls during the separation

220 phase than during the union and reunion phases (Fig. 3B). Eye pinning was observed in one

221 bird and only during the union and reunion phases (union: 3 [1-3]; separation: 0 [0-0];

222 reunion; 3 [1-3]).

223

224 **4. Discussion**

225   Our study shows variations in facial displays and behaviours during the different

226 phases of the tests. The presence of long distance calls during the separation phase and of

227 specific facial displays associated with contact seeking behaviours during the union and

228 reunion phases show that the familiar caregiver acted as a social support for the parrots placed

229 in the unfamiliar environment.

230   As expected, we found variation in crown and nape feather heights and redness of the

231 bare skin depending on the phase. We argue that lower heights of the crown and nape

232 feathers, lower redness of the skin and the occurrence of long distance calls during the

233 separation phase indicate that parrots have perceived this phase more negatively compared to

234 the other two phases. Macaws are highly social birds inhabiting dense forest. They are known

235 to produce loud calls also called "screams" especially at daybreak and dusk. These calls

236 frequently emitted in the wild, are essential in keeping track of companions (Luescher 2008).

237 For some authors, the sleeking of feathers might be associated with stressful situations and the

238 activation of the sympathetic nervous system but this remains understudied (Moris 1956). In

239 addition, feathers sleeking could also be observed in neutral situations such as locomotion

240 (Bertin et al., 2018a). A control neutral situation would have been necessary to determine

241 whether the feathers were sleeked or in a neutral position (neither sleeked or ruffled) during

242 the separation phase. No fear-related behaviours were observed except on day 1 suggesting

243 that the birds habituated to the experimental situation and that the phase of separation may

244 only have had a mild negative valence for the birds.

245   Bare skin blushing and ruffling of crown and nape feathers were observed during the

246   union and reunion phases. We previously observed ruffling of both crown and nape feathers

247   in macaws or cockatoos engaged in intraspecific positive social interactions or comfort

248   behaviours such as resting (Bertin et al., 2018a; Bertin et al., 2020); activities which are

249   commonly considered as reflecting calm and relaxed states and low level of threat in birds and

250   vertebrates (Mattiello et al., 2019; Riters et al., 2019; Mendl et al., 2010; Richardson et al.,

251   2016; Luescher, 2006 (e.g. Mattiello et al., 2019; Riters et al., 2019; Richardson et al., 2016;

252   Luescher, 2006). The similar facial displays observed in the present study during the union

253   and reunion phases suggest that these phases had a more positive emotional valence for the

254   parrots than the separation phase during which head feathers were sleeked. In our previous

255   study on macaws, crown ruffling and bare skin blushing were also more frequent when the

256   caretaker was actively engaging with the parrot than during a control phase with no mutual

257   interaction whereas nape feathers remained ruffled during both phases (Bertin et al., 2018a).

258   In humans, consistent with Darwin's observation (Darwin 1872), recent research has

259   demonstrated that faces do change color with emotion (Benitez-Quiroz et al., 2018;

260   Thorstenson et al., 2018). For example, emotions such as anger and happiness elicit dilated

261   arteries, facilitating blood flow to the skin surface and increasing facial redness. These

262   changes in color allow the emitter to successfully transmit and observers to visually interpret

263   emotion even in the absence of facial muscle movement (Benitez-Quiroz et al., 2018).

264   Trichromatic color vision in humans is thought to have been naturally selected, in part, for

265   detecting color changes on conspecific faces to discriminate emotions, or other socially

266   relevant physiological states (Changizi, Zhang, & Shimojo, 2006). This capacity to produce

267   and perceive facial color changes is also thought to facilitate adaptive social functioning by

268   regulating approach-avoidance behaviours (Thorstenson and Pazda, 2021). In Blue-and-

269   yellow macaws, evolution has favoured the development of a particularly complex face with

270   mobile coloured feathers (black, green, blue, yellow) and bare skin. Given their

271   tetrachromatic vision, it is conceivable that they have evolved a comparable mechanism

272   conveying information about an individual's internal physiological and psychological state.

273   So far, studies on emotional facial expression in birds are scarce. Some authors also

274   described subtle changes in crown and nape feather displays as indicators of the bird's social

275   status during social interactions (Bond and Diamond 2019) or in warning threat in pet parrots

276   (Simone-Freilicher 2015). In crested Psittaciformes like cockatoos, facial/head feather

277   movement including the crest were reported in contexts of alertness, agonistic interactions or

278   play readiness (Kaplan, 2015). All in all these results call attention to the overlooked function

279   of subtle facial visual displays which, similarly to mammals, could convey close-range public

280   information regarding individuals' intention to engage in specific activities or emotions

281   (Waller and Micheletta 2013).

282   When reunited with the caregiver, macaws ceased calling and expressed contact

283   seeking behaviours towards the caregiver as during the union phase. Most parrot species show

284   complex social organization with flock members maintaining non-random affiliative

285   relationships characterized by allopreening, allofeeding and maintenance of close proximity

286   (Seibert 2006). Proximity searching with the caregiver indicated that she acted as a social

287   support and a source of appeasement for the macaws which ceased calling for their mates.

288   Separation distress, proximity seeking and appeasement are two out the three main features

289   characterizing attachment namely: proximity seeking, appeasement (relief from stress due to

290   the social support of the attachment figure); secure base (i.e. increase of exploration of the

291   novel environment) and separation distress (Cassidy 1999). As we were not able to test

292   macaws' responses towards a stranger, we cannot resolve whether our results fulfil all criteria

293   for an attachment-bond. However, to our knowledge, our study constitutes the first attempt to

294   investigate the human-animal bond in a bird species.

295   In humans, non-human primates and dogs, reunion following separation results in a

296   positive emotional state, and an increase in affiliative behaviours (e.g. Kalin et al., 1995;

297   Rhen, 2014). A higher frequency of contact seeking behaviours during the reunion phase than

298   during the union phase could thus have been expected. Our sample size was relatively small

299   and the inter-individual variability was high, which could have masked a potential rebound

300   effect on affiliative behaviours. This high inter-individual variability was also observed for

301   eye surface and the expression of eye pinning. Contrarily to mammals, birds have the control

302   of the dilation and constriction of their pupils (Walls 1963). Unexplored by the scientific

303   community, eye pinning describes the rapid dilation and contraction of the pupils of a bird's

304   eye. In Psittacidae, eye pinning is reported when birds anticipate positive events like stroking,

305   or during pleasant activities like eating a favourite food or courtship but also during negative

306   events like defense of territory (Moustaki 2011). Eye pinning was also described, for the first

307   time in a scientific journal, in a female pet Yellow-fronted amazon (*Amazona ochrocephala*

308   *panamensis*) when she engaged in mutual vocal interactions with the owners (Gregory and

309   Hopkins 1974). In our study, the production of eye pinning was observed only in an 8-year-

310   old female that, according to the caregiver, was the most bonded to her out of the five

311   macaws. It would be interesting to determine in future studies if the production of this

312   behaviour varies according to the quality of the bond established between the bird and the

313   caregiver and if, in a social group, this behaviour may constitute a close-range visual means to

314   express affiliative behaviours towards preferred conspecifics.

315   From a general point of view, our results and interpretation warrant caution due to the

316   lack of control situations. For example, we cannot rule out the hypothesis that the mere

317   familiarity of the caregiver (and not a particular affiliative link) was enough to buffer the

318   effects of social separation and novelty. In mammals, depending of the social organization,

319   both familiarity and identity of the social partner on social support effectiveness are crucial

(Rault, 2012 for a review). Although macaws are known to form strong exclusive bonds with humans (Blanchard, 1997), it would be of interest to conduct further studies with caretakers more or less familiar or affiliated to the tested birds. Observations of facial displays in larger groups of macaws will also be needed to further investigate the function of facial displays and blushing in social interactions varying in emotional valence and intensity.

5. Conclusion

Our data reinforce the idea that parrots have the capacity to produce diverse rapid changes in their facial displays according to situations differing in their emotional valence and/or arousal level. Psittaciformes are highly social and very popular as companion animals but the way they perceived humans, is yet relatively unknown. Captive parrots are particularly sensitive to feather plucking or stereotypic behaviours, which are signs of negative welfare (van Zeeland et al. 2009). Care should be taken at the fact that they are very social birds while being almost exclusively raised as a single individual by pet owners. Identifying signs of positive emotions will provide a better understanding of parrots' affiliative behaviours and emotional expression, which is crucial in order to satisfy their social needs. Species-specific repertoires of facial expressions could provide useful tools to better assess their well-being and provide for their needs. Although additional works are needed, our work suggests that facial displays may be used to identify whether captive parrots perceived positively the human-parrot relationships in which they are engaged.

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490 **Figure captions**

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Fig 1. Characterization of facial displays: Photographs with schematic representation of the measures of beak height (a); crown feather height (b and c); nape feather height (d) and the position of the 10 x 10 pixels scare for the assessment of redness of the skin (e). A) Head and nape feathers were sleeked. B) Head and nape feathers were ruffled.

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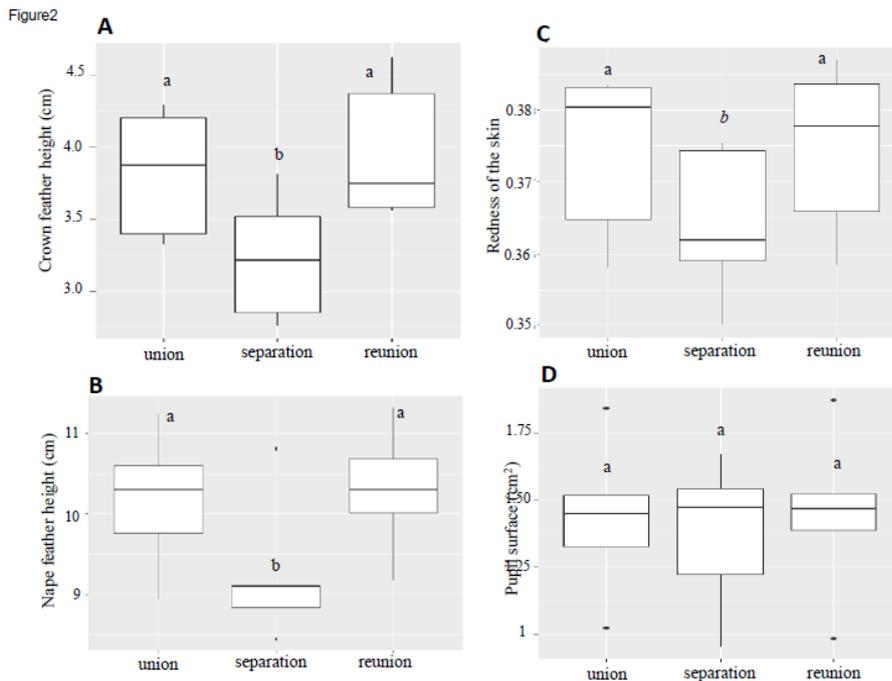
Fig 2: **Median and interquartile distribution ranges of** A) crown feather height; B) nape feather height; C) redness of the skin; D) pupil surface. Different letters indicate significant post-hoc differences. A letter in italic indicates a trend ($0.05 < P < 0.1$).

Figure3
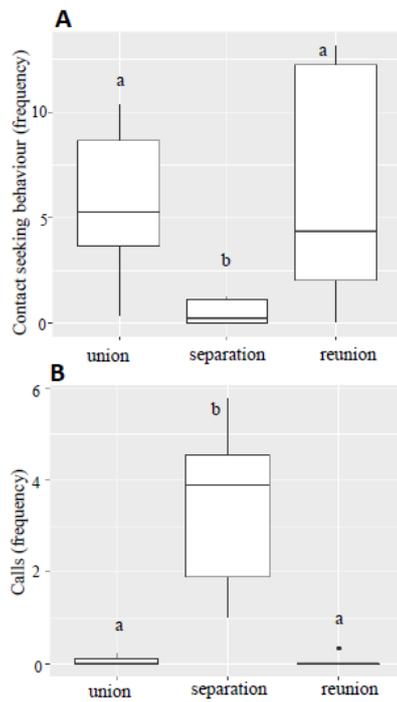
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501 **Fig 3**: **Median and interquartile distribution ranges of** A) frequency of contact seeking

502 behaviours; B) frequency of long distance contact calls. Different letters indicate significant

503 post-hoc differences.