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1 **Bill covering and nape feather ruffling as indicators of calm states in the Sulphur-**
2 **crested cockatoo (*Cacatua galerita*)**

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19 *Keywords*

20 Animal sentience; Calmness; Facial expression; Positive emotions; Emotional expression

21 **Abstract**

22

23 Parrots are highly social birds that are recognized for their primate-like cognitive abilities but
24 their way to express emotions remain overlooked. Herein we explored potential facial
25 indicators of emotions in cockatoos. We predicted that facial feather ruffling is an indicator of
26 a cockatoo's emotional state and hypothesized that specific facial feather positions would be
27 present more during positive valence and low arousal situations. We observed feather position
28 on the crest, cheek and nape during the daily routine of a group of five captive, non-breeding,
29 Sulphur-crested cockatoos. The data show that cheek and nape feather ruffling occurred
30 significantly more during activities associated with low arousal levels and positive valence
31 such as maintenance behaviours, positive and quiet social contact and resting. Our data
32 suggest that ruffling feathers over the bill (i.e. cheek feather ruffling) and nape ruffling may
33 provide visual indicators of calm/relaxed states in cockatoos. Subtle movement of facial
34 feathers may be an effective close-ranged visual signal to communicate birds' affective states
35 or their intention to engage in specific activities. This work provides a novel approach to
36 assessing the positive welfare of captive cockatoos and to understanding emotional
37 communication in non-mammalian species.

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46 **1. Introduction**

47 Positive emotions have been recognized as adaptive as negative ones and as primary
48 component of animal well-being (Mendl, Burman, and Paul 2010; Panksepp 2004; Boissy et
49 al. 2007). Despite their importance, positive emotions have been less studied than negative
50 ones because they are more subtle and difficult to assess. Emotions are subjective experiences
51 composed of cognitive processes, neurophysiological and behavioural responses (Boissy et al.
52 2007). In mammals, movement of facial muscles provides species-specific repertoires of
53 facial expressions, which are one of the most studied and reliable behavioural tools to access
54 the emotional world of animals (Waller and Micheletta 2013). As birds lack a complex facial
55 musculature (Diogo et al. 2008), they have been discarded from this field of research.
56 However, birds do have the capacity to move their facial feathers due to the contractile
57 properties of the feather-bearing integument (Homburger and de Silva 2003). According to
58 anecdotal observations, facial/head feather movement including the crest may communicate
59 emotions or moods, like play mood in cockatoos (Kaplan 2015). In the few other crested-birds
60 studied so far, crest displaying was mainly observed in contexts of high arousal levels like
61 intra or interspecific aggression, courtship or defence from predators (Kumar 2010; Graves
62 1990; Goodwin 1956; Ruiz-Rodríguez, Martín-Vivaldi, and Avilés 2017).

63 Emotions are both characterized by their valence (positive or negative) and arousal
64 level (high or low) (Mendl, Burman, and Paul 2010). Two types of positive emotions or states
65 are commonly distinguished. Those characterized by high arousal levels such as joy,
66 excitement, consummatory or appetite motivational states and, those characterized by low
67 arousal levels such as calm, relaxed, safeness, social bonding or post-consummatory
68 behaviours (Mendl, Burman, and Paul 2010; Richardson et al. 2016; Carver 2001). In a
69 previous experiment on a group of captive blue-and-yellow macaws (*Ara aranauna*), we
70 followed the birds' routine activities and their associated facial display. We showed that

71 crown and nape ruffling were associated with activities with positive valence and low arousal
72 levels, like quiet positive social interactions, maintenance or resting (Bertin et al. 2018). As
73 these behavioural categories are commonly associated with post-consummatory behaviours
74 and positive welfare in mammals or birds (Mattiello et al. 2019; Ritters, Kelm-Nelson, Spool,
75 2019; Mendl, Burman, and Paul 2010; Richardson et al. 2016; Luescher 2006), we aimed to
76 expand this research on emotional communication in Psittaciformes by following the routine
77 activities of a group of cockatoos. Identifying indicators of positive welfare or calmness may
78 help improve the well-being of the millions of parrots and cockatoos (two families of the
79 order Psittaciformes) kept in captivity as pets, or for conservation programs.

80 Herein we provide a first exploration of potential facial indicators of emotions of
81 Sulphur-crested cockatoos - highly social Australian native birds living in stable family
82 groups and forming large feeding or resting flocks (Styche 2000). We observed a group of
83 non-breeding captive cockatoos in their aviary and recorded their crest, cheek and nape
84 feather ruffling during their routine daily activities. According to our previous findings on
85 macaws, we hypothesized that there would be a higher probability to observe feather ruffling
86 (i.e. erection of feathers), except for the crest, in activities associated with low arousal levels
87 and positive valence. The cognitive abilities of Psittaciformes showed striking convergence
88 with mammals (Emery 2016) and the present work provides new insights into facial
89 emotional communication systems across vertebrates.

90 **2. Material and methods**

91 *2.1. Birds and housing conditions*

92 We observed five hand-reared Sulphur-crested cockatoos (*Cacatua galerita*) (2 males,
93 1 female and 2 undetermined sex, between 3 and 4 years old), not exposed to the public but
94 part of a free-flying show (i.e. unrestrained outdoor flight), at the Zooparc de Beauval (Saint

95 Aignan, 41110, France). These birds were housed in an aviary with an indoor area (250 cm x
96 520 cm x 260 cm) freely connected to an outdoor area (250 cm x 850 cm x 260 cm) and
97 mixed with one citron-crested cockatoo (*Cacatua sulphurea citrinocristata*). The aviary
98 contained several tree branches, perches and cords. Enrichment was provided daily (cardboard
99 and journal paper). Birds were fed daily with fresh fruits and vegetables, germinated seeds
100 (wheat, corn, sunflower, rice, and oat), millet seeds, oyster shells, and a commercial mix for
101 exotic birds.

102 *2.2 Behaviour and feather postures*

103 To determine during which activity feathers were ruffled we used a focal sampling
104 method with a handheld video camera recorder (Sony HDRP PJ410) capturing 24 images per
105 second. Each day, we followed one focal bird's behaviour for twenty minutes, and
106 successively followed another bird, in a random order, until all the five birds had been
107 observed. These observations were repeated during three consecutive weeks until 5 hours of
108 recording per bird had been obtained. As birds were trained for free flight daily in the
109 morning, we observed the birds in the afternoon between 2 and 5 PM, outside of any
110 disturbance. The experimenter was familiar to them and moved around the aviary very quietly
111 only when necessary.

112 We used a scan sampling method to analyse the videos. Every 5 s, the experimenter
113 recorded the bird's feather position and behavioural activity: locomotion (walking, flying,
114 climbing on the grid); alimentation (ground-foraging and eating or drinking); chewing
115 (actively cutting and/or chewing pieces of paper, branches, cardboards, cords or the grid);
116 maintenance (preening, scratching, stretching); social contact (allopreening, perched in body
117 contact without or with interactions i.e. gently touching the conspecific with the beak or the
118 feet; resting (the bird is perched, the body is immobile with little or no movement of the
119 head). Agonistic interactions such as threat displays were extremely rarely observed.

120 We determined three areas where feathers can move independently from one another:
121 the crest, the cheek and the nape (Fig. 1). For the crest and the nape, when ruffled, individual
122 feathers can be distinguished. For the cheek, the feathers were over the bill when ruffled and
123 we considered there to be two possible positions: “lower” when part of the lower mandible
124 was covered and “upper” when any part of the upper mandible was covered in addition to the
125 entire lower mandible (Fig. 1 and supplementary data). When some parameters were
126 unobservable, the scan was not included. We obtained a mean total number of 3247.6 ± 114.6
127 scans per individual (minimum: 2915; maximum: 3566). The same experimenter conducted
128 all observations. We assessed observer reliability for the occurrence of feather ruffling and
129 activities by rescoring twice 20 min of video per bird. Intra-observer concordance was 96 %
130 (percentage of scans where the scans were scored the same).

131

132 *2.3 Statistical analyses*

133 For each behavioural category, we calculated the mean proportion of ruffled feather scans per
134 bird for the crest, the nape and the two categories of cheek feather positions. As the data were
135 not normally distributed, we used the function `aovp` of the `lmPerm` package in R 3.4.2, to run
136 permutation tests on the proportion of scans containing ruffled feathers during each activity.

137 Activity type was considered a fixed factor while the individual was considered as a random
138 factor. Two activity types were defined according to their presumed arousal levels (high or
139 low). Behavioural categories without locomotion including: “maintenance”, “social contact”
140 and “resting” were grouped and considered low arousal and positive valence activity type.

141 These three relatively motionless behavioural categories are commonly considered quiet
142 activities with low arousal levels and indicators of positive welfare across vertebrates
143 (Mattiello et al. 2019; Ritters, Kelm-Nelson, Spool, 2019; Mendl, Burman, and Paul 2010;
144 Richardson et al. 2016; Luescher 2006). Behavioural categories with active behaviours and

145 locomotion including “locomotion”, “alimentation” and “chewing” were grouped and
146 considered high arousal activity type. These behavioural categories might be associated with
147 consummatory behaviours and/or appetite motivational states with neutral or positive
148 emotional valence (Mendl et al. 2010) but the precise valence remains understudied so far in
149 birds. As agonistic interactions were rarely observed this category was not included in the
150 analysis. With our limited sample size, post-hoc analyses lead to a drastic loss of statistical
151 power and a high risk of type II error. However, a descriptive view of the data on behavioural
152 categories is represented in the form of median and interquartile distribution ranges. To
153 evaluate correlations between the proportions of ruffled feather scans observed on the
154 different areas we used Spearman correlations (N=5).

155 *2.4 Ethical note*

156 The Zooparc de Beauval (41110, Saint Aignan) kindly provided access to their birds.
157 Only video-recorded observations were conducted. These birds were trained since weaning to
158 perform unrestrained outdoor flights with their animal caretakers and the observer spent
159 several months in presence of the birds beforehand. No signs of avoidance behaviours to the
160 presence of the observer or the animal caretakers were observed.

161 **3. Results**

162 Crest displaying was rarely observed and did not show any significant variation
163 according to the bird’s activity type (Median [1st quartile-3rd quartile], lower arousal level vs.
164 higher arousal level, 0 [0-0] vs. 0 [0-0]; $df = 1$; Mean Square (MS) < 0.01; $P = 0.38$) (Fig. 2A).
165 The proportion of scans where feathers ruffling was observed was significantly higher during
166 activities with low arousal level (maintenance, social contact, resting) than during activities
167 with higher arousal level (locomotion, alimentation, chewing) for the two positions of cheek
168 feathers (lower mandible: 0.31 [0.05-0.80] vs. 0.05 [0.01-0.06]; $df = 1$; $MS = 0.29$; $P = 0.001$;
169 upper mandible: 0.48 [0.28-0.94] vs. 0.03 [0.01-0.06]; $df = 1$; $MS = 1.45$; $P < 0.001$) (Fig. 2B)

170 and for nape feathers (0.84 [0.66-0.91] vs. 0.05 [0.02-0.09]; $df = 1$; $MS = 3.13$; $P < 0.001$)
171 (Fig. 2C).

172 We found no significant effect of the random factor individual on the fixed effect
173 activity type for the crest ($df = 4$; $MS = 0.06$; $P = 1$), the cheek (lower; $df = 4$; $MS = 0.02$; $P =$
174 1; upper; $df = 4$; $MS = 0.12$; $P = 1$) or the nape ($df = 4$; $MS = 0.06$; $P = 1$).

175 We found a positive correlation between nape feather ruffling and both lower ($\rho =$
176 0.53, $P < 0.01$) and upper mandible cheek position ($\rho = 0.89$, $P < 0.01$) but not between the
177 two cheek feather positions lower and upper ($\rho = 0.29$, $P = 0.11$). Two few crest displaying
178 events were recorded to perform correlations.

179

180 **4. Discussion**

181 This study is the first to show variation in facial feather displays according to
182 cockatoos' activity and potential emotional state. Cheek and nape feather ruffling occurred
183 significantly more frequently during activities with low arousal levels and positive valence;
184 suggesting that calm or relaxed states may be indicated by bill covering and nape feather
185 ruffling.

186 Previously we found that activities with low arousal levels were associated with facial
187 and nape feather ruffling in blue-and-yellow macaws (Bertin et al., 2018). In the current work
188 with Sulphur-crested cockatoos we found, as hypothesized, a higher probability of ruffling
189 feathers over the bill and nape ruffling during low arousal positive valence activities such as
190 maintenance behaviours, social contact and resting. In the same direction, finches adopt a
191 more spheroid body posture by ruffling their feathers when clumping or resting, which may
192 be an effective signal inducing appeasement, clumping or allopreening in birds (Morris 1956;
193 Moynihan and Hall 1955). In our study, the activity "resting" was particularly associated with
194 nape ruffling and ruffling feathers over the upper mandible. Although speculative, this

195 position may provide a cryptic shape during resting by covering the black bill and decreasing
196 its contrast with the white plumage. The primary functions of a bird's feathers are flight and
197 thermoregulation of the body (Morris 1956). In addition to these functions, more subtle and
198 localized feather movements may provide social information about a bird's arousal level or
199 intention to engage in specific activities.

200 In the context of presumed higher arousal level activities such as locomotion,
201 foraging, actively interacting with enrichments, eating and drinking, nape and cheek feather
202 ruffling occurred significantly less. These behavioural categories might be associated with
203 consummatory behaviours and/or appetite motivational states with neutral or positive
204 emotional valence but this remains understudied so far in birds so caution must be taken. In
205 cockatoos, crest raising is probably more characteristic of states of high arousal levels as it
206 was reported in contexts of alertness, agonistic interactions or play readiness in cockatoos
207 (Kaplan 2015). Accordingly, we did observe crest raising when birds were excited after a free
208 flight or during the rare agonistic interactions we witnessed (pers. obs).

209 As we observed a stable group of healthy birds kept in a particularly enriched
210 environment, we cannot rule out that in other situations head feather ruffling, in combination
211 with specific body postures could also signal sickness or negative emotions in parrots. Our
212 sample size was low and the inter-individual variability was important therefore, additional
213 investigations with larger, diverse samples will be required to determine with precision the
214 function of bird facial displays. At term, it would be of interest to observe more extreme
215 emotional valences and different sensory channels (acoustic, visual) to understand better
216 parrots' emotional language. For example, contact calls or long distance calls may carry
217 information about parrots' intention to engage in specific activities and/or their emotional
218 states (New Zealand kea parrot, *Nestor notabilis*; Schwing, Parsons and Nelson 2012).

219 So far, avian visual communication is almost exclusively studied in ultimate,
220 evolutionary contexts such as sexual selection and focused on conspicuous signals like bright
221 colours or ornaments (e.g., Wachtmeister 2001; Gomes et al. 2017). Our study is
222 complementary and calls attention to the overlooked function of more subtle visual displays
223 (non-conspicuous facial feather movements). In social groups of birds emotion expression is
224 probably adaptive, contributing to social cohesion by regulating approach and avoidance
225 behaviours. Head feather displays may have similar function to facial expression in mammals,
226 which convey close-range public information regarding individuals' intention to engage in
227 specific activities or emotions (Waller and Micheletta 2013).

228 **5. Conclusion**

229 As the Psittaciformes are highly social with primate-like cognitive capacities
230 (Olkowicz et al. 2016; Gutiérrez-Ibáñez, Iwaniuk, and Wylie 2018), they are very popular as
231 companion animals. However, captive parrots and cockatoos are particularly sensitive to
232 feather plucking or stereotypic behaviours, which are signs of negative welfare (van Zeeland
233 et al. 2009). Wild parrots normally spend a large amount of their diurnal time engaged in
234 comfort, affiliative or resting behaviours (Rowley 1987; Bergman and Reinisch 2006). These
235 behavioural categories are commonly considered as reflecting calm and relaxed states and low
236 level of threat in birds and vertebrates (Mattiello et al. 2019; Ritters, Kelm-Nelson, Spool,
237 2019; Mendl, Burman, and Paul 2010; Richardson et al. 2016; Luescher 2006). Therefore,
238 assessing these positive low arousal states in captive birds could help to evaluate their well-
239 being and prevent damaging behaviours. Low arousal positive affect states have been less
240 studied due to practical limitations in assessment. Our data show that subtle facial feather
241 movements may provide reliable tools to assess calm or relaxed states. As for mammals,
242 species-specific repertoires of facial expressions could provide useful tools to better assess

243 well-being of captive birds and, more broadly, to better understand emotional communication
244 across vertebrate species.

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266 **References**

- 267 Bergman, L. and Reinisch, U.S. 2006. Comfort behavior and sleep. *Manual of parrot behavior*, 59.
- 268 Bertin, A., Beraud, A., Lansade, L., Blache, M.-C., Diot, A., Mulo, B. and Arnould, C. 2018. Facial
269 display and blushing: Means of visual communication in blue-and-yellow macaws (*Ara*
270 *Ararauna*)? *PLoS ONE*, 13: e0201762.
- 271 Boissy, A., Manteuffel, G., Jensen, M.B., Moe, R.O., Spruijt, B., Keeling, L.J., Winckler, C., Forkman, B.,
272 Dimitrov, I. and Langbein, J. 2007. Assessment of positive emotions in animals to improve
273 their welfare. *Physiology & Behavior*, 92: 375-397.
- 274 Carver, C.S. 2001. Affect and the functional bases of behavior: On the dimensional structure of
275 affective experience. *Personality and Social Psychology Review*, 5: 345-356.
- 276 Diogo, R., Abdala, V., Lonergan, N. and Wood, B. 2008. From fish to modern humans—comparative
277 anatomy, homologies and evolution of the head and neck musculature. *Journal of Anatomy*,
278 213: 391-424.
- 279 Emery, N. 2016. *Bird Brain: An exploration of avian intelligence*. Princeton University Press.
- 280 Gomes, A.C.R., Funghi, C., Soma, M., Sorenson, M.D. and Cardoso, G.C. 2017. Multimodal signalling in
281 estrildid finches: song, dance and colour are associated with different ecological and life-
282 history traits. *Journal of Evolutionary Biology*, 30: 1336-1346.
- 283 Goodwin, D. 1956. Further observations on the behaviour of the jay *Garrulus glandarius*. *Ibis*, 98:
284 186-219.
- 285 Graves, G.R. 1990. Function of crest displays in royal flycatchers (*Onychorhynchus*). *The Condor*, 92:
286 522-524.
- 287 Gutiérrez-Ibáñez, C., Iwaniuk, A.N. and Wylie, D.R. 2018. Parrots have evolved a primate-like
288 telencephalic-midbrain-cerebellar circuit. *Scientific reports*, 8: 9960.
- 289 Homberger, D.G. and de Silva, K.N. 2003. The role of mechanical forces on the patterning of the avian
290 feather bearing skin: A biomechanical analysis of the integumentary musculature in birds.
291 *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 298: 123-
292 139.
- 293 Kaplan, G. 2015. *Bird minds: cognition and behaviour of Australian native birds*. CSIRO PUBLISHING.
- 294 Kumar, A. 2010. Communication value of displays and postures in Red-vented Bulbul *Pycnonotus*
295 *cafer* (Aves: Pycnonotidae). *Journal of Threatened Taxa*, 2: 919-929.
- 296 Luescher, A.U. 2006. *Manual of parrot behavior*. doi:10.1002/9780470344651.fmatter
- 297 Mattiello, S., Battini, M., De Rosa, G., Napolitano, F. and Dwyer, C. 2019. How Can We Assess Positive
298 Welfare in Ruminants?. *Animals*, 9(10), 758.
- 299 Mendl, M., Burman, O.H. and Paul, E.S. 2010. An integrative and functional framework for the study
300 of animal emotion and mood. *Proceedings of the Royal Society of London B: Biological*
301 *Sciences*, 277: 2895-2904.
- 302 Morris, D. 1956. The Feather Postures of Birds and the Problem of the Origin of Social Signals.
303 *Behaviour*, 9: 75-113.
- 304 Moynihan, M. and Hall, M.F. 1955. Hostile, Sexual, and Other Social Behaviour Patterns of the Spice
305 Finch (*Lonchura Punctulata*) in Captivity. *Behaviour*, 7: 33-75.
- 306 Olkowicz, S., Kocourek, M., Lucan, R.K., Portes, M., Fitch, W.T., Herculano-Houzel, S. and Nemeč, P.
307 2016. Birds have primate-like numbers of neurons in the forebrain. *Proceedings of the*
308 *National Academy of Sciences*, 113: 7255-60.
- 309 Panksepp, J. 2004. *Affective neuroscience: The foundations of human and animal emotions*. Oxford
310 university press.
- 311 Schwing, R., Parsons, S. and Nelson, X.J. 2012. Vocal repertoire of the New Zealand kea parrot *Nestor*
312 *notabilis*, *Current Zoology*, 58: 727–740.
- 313 Richardson, M., McEwan, K., Maratos, F. and Sheffield, D. 2016. Joy and Calm: How an Evolutionary
314 Functional Model of Affect Regulation Informs Positive Emotions in Nature. *Evolutionary*
315 *Psychological Science*, 2: 308-320.

316 Ritters, L. V., Kelm-Nelson, C. A. and Spool, J. A. 2019. Why do birds flock? A role for opioids in the
317 reinforcement of gregarious social interactions. *Frontiers in Physiology*, 10, 421.
318 Rowley, I. 1990. Behavioural ecology of the galah, *Eolophus roseicapillus*, in the wheatbelt of
319 Western Australia. Surrey Beatty & Sons Pty Limited.
320 Ruiz-Rodríguez, M., Martín-Vivaldi, M. and Avilés, J.M. 2017. Multi-functional crest display in
321 hoopoes *Upupa epops*. *Journal of Avian Biology*, 48: 1425-1431.
322 Styche, A. 2000. Distribution and behavioural ecology of the sulphur-crested cockatoo (*Cacatua*
323 *galerita* L.) in New Zealand. PhD thesis, Victoria University, Wellington/New Zealand.
324 van Zeeland, Y.R.A., Spruit, B.M., Rodenburg, T.B., Riedstra, B., van Hierden, Y.M., Buitenhuis, B.,
325 Korte, S.M. and Lumeij, J.T. 2009. Feather damaging behaviour in parrots: A review with
326 consideration of comparative aspects. *Applied Animal Behaviour Science*, 121: 75-95.
327 Wachtmeister, C.-A. 2001. Display in monogamous pairs: a review of empirical data and evolutionary
328 explanations. *Animal Behaviour*, 61: 861-868.
329 Waller, B.M. and Micheletta, J. 2013. Facial expression in nonhuman animals. *Emotion Review*, 5: 54-
330 59.

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351 **Figure captions**

352

353 **Fig 1. Repertoire of head feather displays:** Photographic representation of the position of
354 crest, cheek and nape feathers.

355

356 **Fig 2: Median and interquartile distribution ranges of the proportions of scans where**
357 **feathers ruffling was observed** on A) the crest, B) the cheek, C) the nape. The proportions of
358 scans are represented for the behavioural categories: locomotion (total mean \pm SE number of
359 scans = 226 ± 26), alimentation (215 ± 57 scans), chewing (1038 ± 115 scans), maintenance
360 (322 ± 51 scans), social contact (84 ± 40 scans), resting (1356 ± 115 scans). Higher arousal
361 level *versus* lower arousal level, NS = not significant, **: $P < 0.01$.

362

363

Crest feathers

Cheek feathers

Nape feathers

Ruffled



Lower mandible

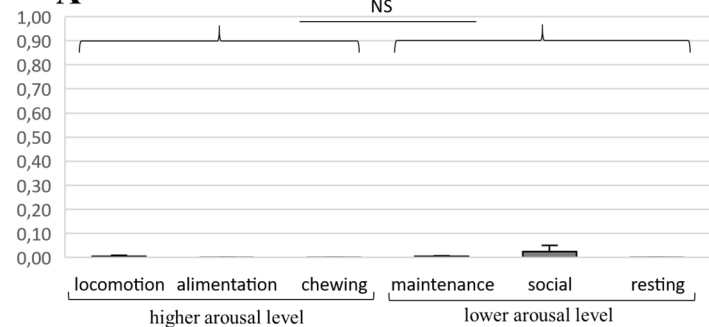
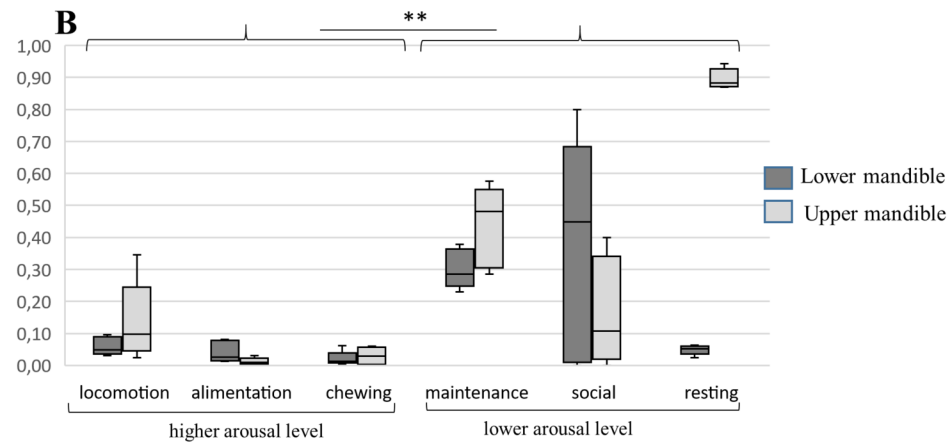


Upper mandible



Sleeked



A**B****C**