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Aline Bertin[a], Baptiste Mulot[b], Raymond Nowak[a], Marie-Claire Blache[a], Scott Love[a] , Mathilde Arnold[b], Annabelle Pinateau[b] , Cécile Arnould[a*], Léa Lansade[a *]

[a] CNRS, IFCE, INRAE, Université de Tours, PRC, 37380, Nouzilly, France; [b]ZooParc de Beauval & Beauval Nature, Saint-Aignan, France

*****co-last authors

*corresponding author: aline.bertin@inrae.fr, [a]PRC, CNRS, IFCE, INRAE, Université de Tours, 37380, Nouzilly, France.

Baptiste Mulot : baptiste.mulot@zoobeauval.com; Raymond Nowak : raymond.nowak@inrae.fr; Marie-Claire Blache : marie-claire.blache@inrae.fr; Scott Love : scott.love@inrae.fr; Mathilde Arnold : mathilde.arnold@zoobeauval.com; Annabelle Pinateau : annabelle.pinateau@gmail.com; Léa Lansade : lea.lansade@inrae.fr; Cécile Arnould : cecile.arnould@inrae.fr.

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Abstract

In mammals, human-animal bonding is recognized as a source of positive affect for companion or farm animals. Because this remains unexplored in birds, we investigated captive parrots' perspective of the human-animal relationship. We used a classical separation-reunion paradigm and predicted that variations in parrots' facial displays and behaviours would indicate their appraisal of the relationship. The test was divided into three phases of two minutes each: the bird was placed in an unfamiliar environment with a familiar caregiver (union), then the bird was left alone (separation) and finally, the caregiver returned (reunion). The test was repeated 10 times for each bird and video recorded in order to analyze their behaviour. The data show significantly higher crown and nape feather heights, higher redness of the skin and higher frequency of contact-seeking behaviours during the union and reunion phases than during the separation phase during which they expressed long distance contact calls. We observed the expression of eye pinning during the union and reunion phases in one 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, consummatory or appetite motivational states and, those characterized by low arousal levels such as calmness, relaxation, safeness, social bonding or post-consummatory behaviours (Mendl et al., 2010; Richardson et al., 2016; Carver, 2001). In previous studies, we showed that specific facial displays such as crown and nape feather ruffling were associated with activities having a positive valence and low arousal levels, like quiet positive social interactions, maintenance or resting in Blue-and yellow macaws or Sulphur-crested cockatoo *(Cacatua galerita*) (Bertin et al., 2018a; 2020). Macaws were also found to blush (i.e. increase in blood flow in vascularized tissues) and ruffle their crown feathers when engaged in a mutual interaction with their familiar caregiver (Bertin et al., 2018a), a context recognized as rewarding for captive parrots (Pepperberg and McLaughlin 1996). Head feather ruffling was also observed in Japanese quail performing dust-bathing, a behaviour considered as rewarding with high arousal level (Bertin et al., 2018b).

Psittaciformes are highly social with primate-like cognitive capacities (Olkowicz et al. 2016; Gutiérrez-Ibáñez et al., 2018). Despite being wild non-domesticated animals, they form strong affiliative bonds with people when captive (Baker, 2012; Anderson, 2014; Bond and Diamond, 2019). We propose that, similarly to mammalian domesticated animals, a human-animal social bond is a source of positive affect for these birds. To reveal attachment-related behaviours, it is necessary to place the individual in a slightly stressful situation (Bowlby, 1982). Here we used a separation-reunion test in an unfamiliar environment as a slightly stressful situation. The test was an adaptation of the Ainsworth Strange Situation test in which human infants are separated and reunited from a parent or a stranger in a novel environment (Ainsworth 1979). The original test compared the child's proximity seeking, during distress, to the attachment figure or the stranger (Ainsworth 1979). Because our parrots were not used to being approached by strangers and they show fear or aggressive behaviours in general towards them, it was not possible to test parrots' behaviours when reunited with an unfamiliar human. As a consequence, our study did not aim to determine whether parrots show a preference for a specific attachment figure which, is one of the criteria that define a social bond as attachment *per se* (a special affectional and emotional relationship between two specific individuals).

We hypothesized that if the parrots were socially bonded toward their most familiar caregiver then, this person should act as a social support to the birds (i.e: the ability of social partners to enhance one's ability to cope with a challenging situation). Evidence of this social support could consist of signs of positive-like emotional responses (e.g. calmness, relaxation) during the test despite being placed in an unfamiliar environment and separated from conspecifics. We predicted that this bond would be expressed by variations in behaviour during the different phases of the test: union, separation, reunion. Specifically, based on our previous research, we expected that macaws would express feather ruffling and blushing when in presence of the familiar caregiver and a potentially enhanced response (rebound effect) of these behaviours during the reunion phase.

2. Animals and methods

2.1. Birds and housing conditions

We observed five hand-reared Blue-and-yellow macaws (two males and three females between 7 and 12 years old), not exposed to public visitors, at the Zooparc de Beauval Saint Aignan (41110, France). All birds are part of a free-flying show. They had been trained daily (i.e. handled daily) since weaning and were thus in close contact with humans, especially their caregivers. During free-flight training the birds were taught to land on the caregivers' arm when called after unrestricted outdoor flight. The five birds were housed in two adjacent aviaries of similar sizes with an indoor area (250 cm x 520 cm x 260 cm) freely connected to an outdoor area (250 cm x 850 cm x 260 cm) and were mixed with a pair of Sulphur-crested cockatoo. The aviaries were equipped with several tree branches, perches and ropes. Enrichments were provided daily (cardboard and newspaper). Parrots were fed daily with fresh fruits and vegetables, germinated seeds (wheat, corn, sunflower, rice, and oat), millet seeds, oyster shells, and a commercial mix for exotic birds.

2.2 Test apparatus and procedure

All the tests took place inside a (3m l x 3m L x 2m h) barnum installed indoors, unfamiliar to the birds and approximately 60 meters away from their aviaries. In order to obtain profile images of the heads of the birds, the barnum was equipped with a perch (1.15 m high, 80 cm long) placed perpendicularly to a small window allowing the passage of the camera recorder mounted on a tripod. All the walls and the roof were opaque and composed of white fabric. A lamp (Somikon photo light SLH3), placed on the floor, was used to have even lighting conditions. All the tests were filmed by a Sony FS5 4K camera.

All birds were tested individually 10 times on 10 different days. All the tests were conducted between 10am and 12pm for two successive weeks. Each bird was tested only once per day and rank order of the birds was counterbalanced between days. All birds were tested with the same animal caretaker. We worked with the animal caretaker who was the most familiar to all of them (more than 10 years of caring for them). The caretaker chosen was also the only one spending quality time with them daily to work on bonding (like playing with them, providing tactile contacts or talking to them). As we observed pet-like behaviours (supplementary data, Figure S1) during the daily routine in presence of the caretaker - characteristic of an affiliative social bond with humans in pet macaws (Jordan, 2003) - we assumed that, more than being familiar, a positive social bond had been established between the birds and the caretaker. For each test session, a bird was called by its name, placed in its usual transport cage (the same used for transport before free-flight shows) and taken to the barnum. Then the bird was put on the perch by hand. The test was divided into three phases of 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).

On the first day of testing, the birds were not willing to stay on the perch. They flew back to their transport cage or perched on the caregiver's arms. Therefore, from day 2 to day 10, the transport cage was left outside of the barnum and the birds were brought by hand inside the barnum. The caregiver remained motionless in front of the bird at approximately 50 cm, was asked to keep the arms behind her back. The caregiver was allowed to whisper the same words to all parrots ("oui, c'est bien") to encourage them to stay on the perch. At the end, each parrot received a nut and was placed back in its transport cage.

2.3. Facial display characterization

We used a protocol similar to Bertin et al. (2018b) on video-recordings obtained from day 2 to day 9. We used the VLC software to search images of clear profiles and extract them (Fig. 1). To homogenize the time when the profiles were extracted between birds, the profiles were searched within twelve 30-s sequences. We extracted images every second with the software and kept the first clear profile found within the 30-s sequence for analysis. We extracted one clear profile per 30-s sequence for all birds (12 images per bird per test). We used the software ImageJ, an image analysis program, to measure crown feather height, nape feather height and area of the pupil. To correct for variation in the distance of the bird from the camera, we used an invariant distance on each bird. For each bird, we measured manually before the experiment, the real distance between the top of the beak and its tip with a digital calliper (± 0.01 mm) (Fig. 1; a). Then, for each image, we used the function "straight" to draw this distance on the image and then the function "set scale" to convert the distance in pixels to distance in real centimetres. To measure crown feather height, we drew an angle with a vertical plane going from the top of the beak (boundary between the nostril and the beak) and the middle of the pupil (Fig. 1; b) and a 90° angle from the middle of the pupil to the top of the green feathers (Fig. 1; c). The length of the line was determined with the function "analyse" and "measure". To measure nape feather height, we estimated the length of a line adjacent to the white skin of the jaw and going from the top of the blue feathers on the head to the tip of the black feathers of the throat (Fig. 1; d). The pupil area was assessed with the function "oval", with which we circled the black pupil and then used the function "measure" to obtain the area of the circle.

To assess the presence of blushing (redness of the skin), we drew a 10 x 10 pixels square on the bare skin at the external corner of the eye, between the blue feathers of the head and the black feathers of the jaw (Fig. 1; e). With the function "measure" of image J, we obtained the mean red (R), mean green (G), and mean blue (B) values of the square. Similarly to some carotenoid-based studies (Pérez-Rodríguez and Viñuela 2008; Passarotto et al., 2021), we calculated the redness of the skin as R/ (R+G+B). In order to control for the balance of the white within the images, a 10 x 10 pixels square was also drawn on the white wall of the barnum for each image. Because the values of redness obtained in the white wall (mean Redness: 0.33 ± 0.001) did not differ significantly from a theoretical redness obtained in a white or grey standard reference (0.33) (t-test, $P > 0.05$), no colour correction of the images was deemed necessary. The same well-trained experimenter, blind to the phase, made all the measures (540 images in total).

2.3 Analysis of behaviour

We assessed the number of times each bird expressed "contact seeking behaviours" towards the animal caregiver: the bird stretched his body horizontally towards the caregiver, and tried, or not, to grasp the caregiver's clothes with its beak, or the bird "begged" to be taken on hand by lifting one leg in front of its breast. These behaviours were scored during the three phases to make sure that they were specifically displayed in the presence of the caregiver. We also recorded the number of times the birds expressed "long distance contact calls" during the three phases. Macaws commonly emit these loud calls when they are separated from their flock (Luescher 2008) (Video 1, supplementary data). Furthermore, one out of the five birds expressed eye pinning (i.e. a rapid constriction of the pupil) (Gregory and Hopkins 1974). The occurrence of this behaviour (i.e. the number of times the pupil contracted to half its size, Figure S2, supplementary data) was recorded during the three phases for this bird by two independent observers.

2.4 Statistical analyses

For all the parameters recorded, data was averaged across sessions per phase and per individual. To test the effect of the phase we used the function aovperm of the Permuco package in R 3.4.2 to run permutation tests with the phase as a fixed factor and the individual as a random factor nested within phase with 10^6 permutations (Kherad-Pajouh and Renaud, 2015). All tests were two-tailed with significance considered at $P < 0.05$. The same function was used for post-hoc comparisons. Because the usefulness of using corrections for multiple comparisons in cases of low sample size is highly debated and results in a loss of power (Garcia 2004; Nakagawa 2004; Garamszegi 2006), we present the original *P*-values. The data are represented as boxplots with medians and interquartile distribution ranges. Only descriptive data were given for the occurrence of eye pinning as it was displayed only by one out of the five birds. The concordance between observers on the frequency of eye pinning was evaluated with a spearman test and was highly significant (Rho=0.97; $P < 0.01$).

2.5 Ethical note

The Zooparc de Beauval (41110, Saint Aignan) kindly provided access to their birds. Only video-recorded observations were conducted. Behavioural observations are not considered as animal experimentations and are beyond the scope for ethical consideration regarding French and European animal experimentation regulations. The Val de Loire Ethics

Committee for Animal Experimentation (N° CE19 – 2022-1503 – 5) reviewed the protocol and attributed a positive recommendation.

3. Results

We found a significant effect of the phase on crown feather height ($F = 0.001$; $P = 0.001$) and nape feather height ($F < 0.001$; $P = 0.0008$) with in both cases the heights were more important during the union and reunion phases compared to the separation phase whereas heights did not differ significantly between the union and reunion phases (Fig. 2A and 2B). We found a significant effect of the phase on redness of the skin ($F = 0.01$; $P = 0.023$) with post-hoc trends towards a higher redness during the union and reunion phases than during the separation phase ($P = 0.06$ for all comparisons) whereas it did not differ significantly between the union and reunion phases (Fig. 2C). The pupil surface did not differ significantly between the three phases ($F = 0.14$; $P = 0.15$; Fig. 2D). The occurrence of contact seeking behaviours differed significantly between the phases ($F = 0.09$; $P = 0.04$) with higher occurrences during the union and reunion phases compared to the separation phase whereas the occurrence did not differ significantly between the union and reunion phases (Fig. 3A). The number of long distance contact calls differed significantly between the phases ($F = 0.01$; $P = 0.001$) with a significant higher number of calls during the separation phase than during the union and reunion phases (Fig. 3B). Eye pinning was observed in one bird and only during the union and reunion phases (union: 3 [1-3]; separation: 0 [0-0]; reunion; 3 [1-3]).

4. Discussion

Our study shows variations in facial displays and behaviours during the different phases of the tests. The presence of long distance calls during the separation phase and of specific facial displays associated with contact seeking behaviours during the union and reunion phases show that the familiar caregiver acted as a social support for the parrots placed in the unfamiliar environment.

As expected, we found variation in crown and nape feather heights and redness of the bare skin depending on the phase. We argue that lower heights of the crown and nape feathers, lower redness of the skin and the occurrence of long distance calls during the separation phase indicate that parrots have perceived this phase more negatively compared to the other two phases. Macaws are highly social birds inhabiting dense forest. They are known to produce loud calls also called “screams” especially at daybreak and dusk. These calls frequently emitted in the wild, are essential in keeping track of companions (Luescher 2008). For some authors, the sleeking of feathers might be associated with stressful situations and the activation of the sympathetic nervous system but this remains understudied (Moris 1956). In addition, feathers sleeking could also be observed in neutral situations such as locomotion (Bertin et al., 2018a). A control neutral situation would have been necessary to determine whether the feathers were sleeked or in a neutral position (neither sleeked or ruffled) during the separation phase. No fear-related behaviours were observed except on day 1 suggesting that the birds habituated to the experimental situation and that the phase of separation may only have had a mild negative valence for the birds.

Bare skin blushing and ruffling of crown and nape feathers were observed during the union and reunion phases. We previously observed ruffling of both crown and nape feathers in macaws or cockatoos engaged in intraspecific positive social interactions or comfort behaviours such as resting (Bertin et al., 2018a; Bertin et al., 2020); activities which are commonly considered as reflecting calm and relaxed states and low level of threat in birds and vertebrates (Mattiello et al., 2019; Riters et al., 2019; Mendl et al., 2010; Richardson et al., 2016; Luescher, 2006 (e.g. Mattiello et al., 2019; Riters et al., 2019; Richardson et al., 2016;

Luescher, 2006). The similar facial displays observed in the present study during the union and reunion phases suggest that these phases had a more positive emotional valence for the parrots than the separation phase during which head feathers were sleeked. In our previous study on macaws, crown ruffling and bare skin blushing were also more frequent when the caretaker was actively engaging with the parrot than during a control phase with no mutual interaction whereas nape feathers remained ruffled during both phases (Bertin et al., 2018a). In humans, consistent with Darwin's observation (Darwin 1872), recent research has demonstrated that faces do change color with emotion (Benitez-Quiroz et al., 2018; Thorstenson et al., 2018). For example, emotions such as anger and happiness elicit dilated arteries, facilitating blood flow to the skin surface and increasing facial redness. These changes in color allow the emitter to successfully transmit and observers to visually interpret emotion even in the absence of facial muscle movement (Benitez-Quiroz et al., 2018). Trichromatic color vision in humans is thought to have been naturally selected, in part, for detecting color changes on conspecific faces to discriminate emotions, or other socially relevant physiological states (Changizi, Zhang, & Shimojo, 2006). This capacity to produce and perceive facial color changes is also thought to facilitate adaptive social functioning by regulating approach-avoidance behaviours (Thorstenson and Pazda, 2021). In Blue-and-yellow macaws, evolution has favoured the development of a particularly complex face with mobile coloured feathers (black, green, blue, yellow) and bare skin. Given their tetrachromatic vision, it is conceivable that they have evolved a comparable mechanism conveying information about an individual's internal physiological and psychological state.

So far, studies on emotional facial expression in birds are scarce. Some authors also described subtle changes in crown and nape feather displays as indicators of the bird's social status during social interactions (Bond and Diamond 2019) or in warning threat in pet parrots (Simone-Freilicher 2015). In crested Psittaciformes like cockatoos, facial/head feather movement including the crest were reported in contexts of alertness, agonistic interactions or play readiness (Kaplan, 2015). All in all these results call attention to the overlooked function of subtle facial visual displays which, similarly to mammals, could convey close-range public information regarding individuals' intention to engage in specific activities or emotions (Waller and Micheletta 2013).

When reunited with the caregiver, macaws ceased calling and expressed contact seeking behaviours towards the caregiver as during the union phase. Most parrot species show complex social organization with flock members maintaining non-random affiliative relationships characterized by allopreening, allofeeding and maintenance of close proximity (Seibert 2006). Proximity searching with the caregiver indicated that she acted as a social support and a source of appeasement for the macaws which ceased calling for their mates. Separation distress, proximity seeking and appeasement are two out the three main features characterizing attachment namely: proximity seeking, appeasement (relief from stress due to the social support of the attachment figure); secure base (i.e. increase of exploration of the novel environment) and separation distress (Cassidy 1999). As we were not able to test macaws' responses towards a stranger, we cannot resolve whether our results fulfil all criteria for an attachment-bond. However, to our knowledge, our study constitutes the first attempt to investigate the human-animal bond in a bird species.

In humans, non-human primates and dogs, reunion following separation results in a positive emotional state, and an increase in affiliative behaviours (e.g. Kalin et al., 1995; Rhen, 2014). A higher frequency of contact seeking behaviours during the reunion phase than during the union phase could thus have been expected. Our sample size was relatively small and the inter-individual variability was high, which could have masked a potential rebound effect on affiliative behaviours. This high inter-individual variability was also observed for eye surface and the expression of eye pinning. Contrarily to mammals, birds have the control of the dilation and constriction of their pupils (Walls 1963). Unexplored by the scientific community, eye pinning describes the rapid dilation and contraction of the pupils of a bird's eye. In Psittacidae, eye pinning is reported when birds anticipate positive events like stroking, or during pleasant activities like eating a favourite food or courtship but also during negative events like defense of territory (Moustaki 2011). Eye pinning was also described, for the first time in a scientific journal, in a female pet Yellow-fronted amazon (*Amazona ochrocephala panamensis*) when she engaged in mutual vocal interactions with the owners (Gregory and Hopkins 1974). In our study, the production of eye pinning was observed only in an 8-year-old female that, according to the caregiver, was the most bonded to her out of the five macaws. It would be interesting to determine in future studies if the production of this behaviour varies according to the quality of the bond established between the bird and the caregiver and if, in a social group, this behaviour may constitute a close-range visual means to express affiliative behaviours towards preferred conspecifics.

From a general point of view, our results and interpretation warrant caution due to the lack of control situations. For example, we cannot rule out the hypothesis that the mere familiarity of the caregiver (and not a particular affiliative link) was enough to buffer the effects of social separation and novelty. In mammals, the effectiveness of social support is known to depend on both the familiarity and the nature of the relationship with the social partner (Rault, 2012 for a review). While 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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Figure captions

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.

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 ($0.05 < P < 0.1$).

Fig 3: **Median and interquartile distribution ranges of** A) frequency of contact seeking behaviours; B) frequency of long distance contact calls. Different letters indicate significant post-hoc differences.

Figure 1

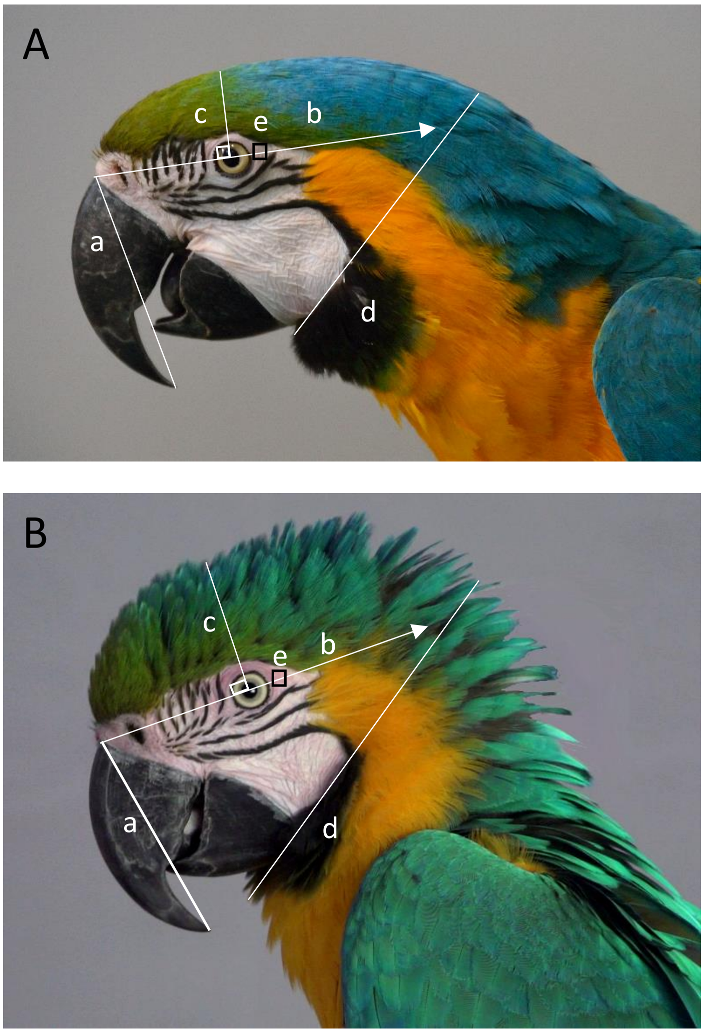


Figure 2

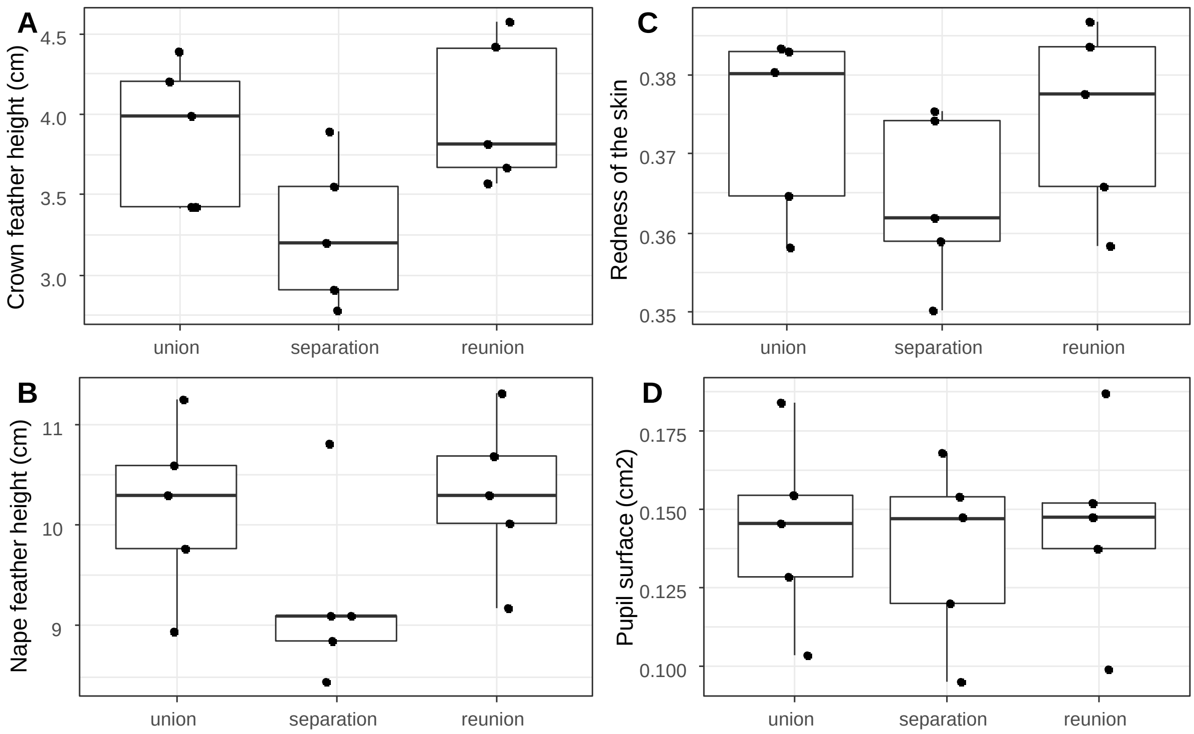
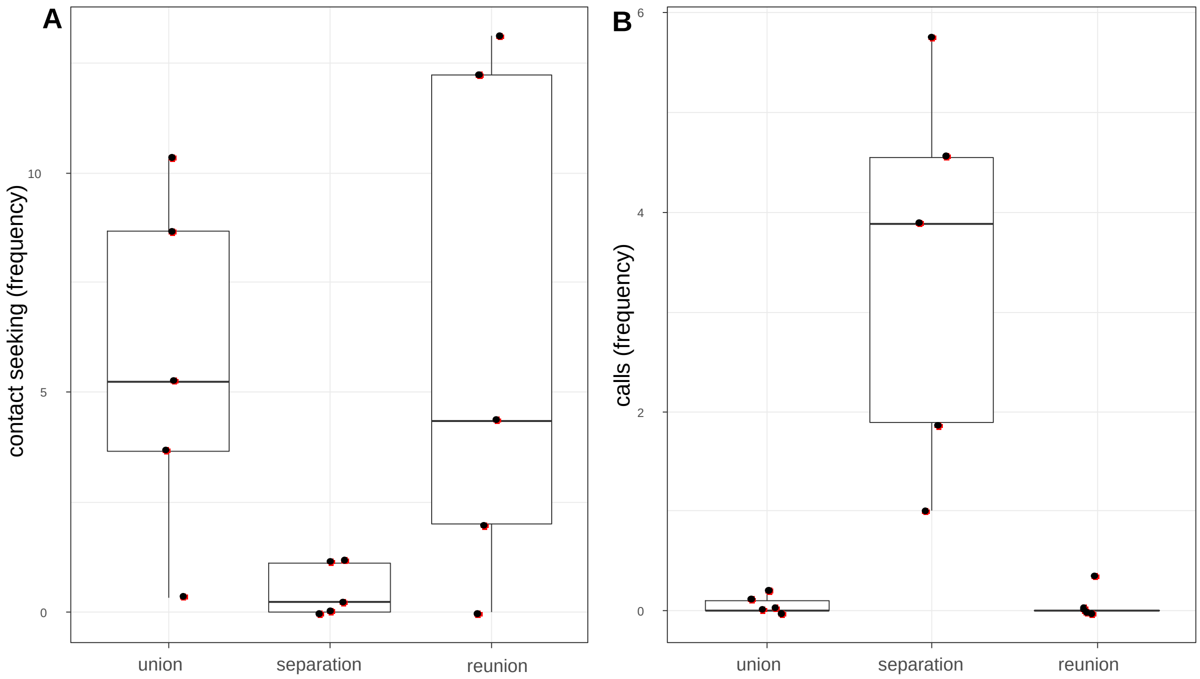

A
Crown feather height (cm)
4.5
4.0
3.5
3.0
union
separation
reunion
C
Redness of the skin
0.38
0.37
0.36
0.35
union
separation
reunion
B
Nape feather height (cm)
11
10
9
union
separation
reunion
D
Pupil surface (cm2)
0.175
0.150
0.125
0.100
union
separation
reunion

Figure 3


A
contact seeking (frequency)
10
5
0
union
separation
reunion
B
calls (frequency)
6
4
2
0
union
separation
reunion

Supplementary data

Figure S1: Examples of pet-like behaviours expressed by the birds in presence of their animal caretaker during their routine interactions. A) cuddling behaviour; B) rolling on the back to have the belly rubbed.

A)

B)

Figure S2: photography showing the reduction of the pupillary size during the expression of eye-pinning.

Movie 1: expression of long distance contact calls during the separation phase.