



# Behavioural and hormonal effects of member replacement in captive groups of blue-fronted amazon parrots (*Amazona aestiva*)



Laerciana Silva de Souza Matos<sup>a,b</sup>, Rupert Palme<sup>c</sup>, Angélica Silva Vasconcellos<sup>a,\*</sup>

<sup>a</sup> Programa de Pós-graduação em Biologia de Vertebrados, Pontifícia Universidade Católica de Minas Gerais, Av. Dom José Gaspar, 500, Prédio 41, Coração Eucarístico, Belo Horizonte, Minas Gerais CEP 30535-901, Brazil

<sup>b</sup> Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis – IBAMA, Belo Horizonte, Minas Gerais, CEP 30110-051, Brazil

<sup>c</sup> Department of Biomedical Sciences, University of Veterinary Medicine, Veterinärplatz 1, 1210 Vienna, Austria

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## ABSTRACT

Social species in captivity may face allostatic overload due to artificial grouping and other social constraints. In rescue centres, groups of psittacines are constantly mixed due to the arrival and/or release of individuals; this procedure is potentially harmful to animal welfare. This study aimed at evaluating the possible impacts of mate replacement on the stress levels of captive blue-fronted amazon parrots (*Amazona aestiva*). During five weeks, we recorded agonistic interactions and dropping-glucocorticoid metabolites (GCM) concentrations of individuals allocated in a group whose members were kept constant and in a group subjected to frequent member replacement. In both groups, non-linear hierarchies developed, without sex differences regarding aggression or hierarchical positions. The replacement of individuals had no effect on the number of agonistic interactions or on the animals' stress levels. In both groups, higher-ranking individuals had higher stress loads than subordinates. Our study, the first to investigate the social dynamics of *A. aestiva*, indicated that introducing or removing individuals in captive groups does not seem to affect the welfare of the birds in the short term. This information favours release and reintroduction programs and is relevant for conservation management of this, and possibly other parrot species with similar environmental requirements.

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## 1. Introduction

The transfer of wild animals into captivity, and their management in the captive environment can induce a situation of allostatic overload in the animals (i.e., chronic stress, when environmental demands surpass the coping capacity of individuals, Morgan and Tromborg, 2007; Scheiber et al., 2015), especially for those born in the wild (Ferreira et al., 2015; Rose and Croft, 2015). Social stress is reported as one of the most important factors affecting the welfare of social animals in the captive environment (Young, 2003). Within many species, the frequency and severity of conflicts tend to increase immediately after unfamiliar individuals are introduced

to an existing group (Creel, 2001; Sapolsky, 2005). Although agonistic interactions are inevitable in society (Hobson and Dedeo, 2015; Rose and Croft, 2015), in stable hierarchies, social dominance tends to settle to avoid the costs and risks of increased and continual fighting (Creel, 2001; Enquist and Leimar, 1990). However, when the stability of the social group is compromised, higher levels of aggression and, consequently, greater stress loads are expected (Rose and Croft, 2015), often affecting more overtly higher ranking individuals (Flack et al., 2006; Mendonça-Furtado et al., 2014; Sands and Creel, 2004). Therefore, mixing groups of animals, a common procedure for some species in rescue centres – due to the arrival and/or release of individuals – may promote social distress (McCowan et al., 2008).

For a comprehensive assessment of stress levels, the concomitant evaluation of more than one parameter is highly recommended (Scheiber et al., 2015). Evidence of compromised welfare can be evaluated by using behavioural and physiological parameters, such as increased heart rate or adrenal activity, reduced immune response, reproductive suppression, etc. (Abbott et al., 2003; Broom and Molento, 2004). Social stress and, in particular, agonistic interactions can cause large and persistent increases in the secretion

Abbreviations: AICc, Akaikei's information criterion corrected for small samples; CETAS, Wild Animal Screening Centers (*Centros de Triagem de Animais Silvestres*); CRAS, Rehabilitation Center for Wild Animals (*Centro de Reabilitação de Animais Silvestres*); ER, Elo-rating; GC, glucocorticoids; GCM, glucocorticoid metabolites; GLM, generalised linear model.

\* Corresponding author.

E-mail address: [angelicavasconcellos@gmail.com](mailto:angelicavasconcellos@gmail.com) (A. Silva Vasconcellos).

of glucocorticoids – “GC” (Creel, 2001) – which are part of the cascade of response to stressors (Möstl and Palme, 2002). Non-invasive sampling methods – the best suited for assessing stress levels (Palme et al., 2005) – have been used to study social stress in birds. Kotrschal et al. (1998) evaluated social stress in graylag geese (*Anser anser*) and recorded different GC levels in distinct rank positions – pointing to the influence of social ranking in the stress loads of birds. The study of Stocker et al. (2016) pointed to the relevance of social integration for the stress conditions of ravens (*Corvus corax*): GC responses to individual separation depended on how well the individual was integrated in its group.

Parrots have been considered a group which develops stable associations, i.e., maintained over several years (Bernstein, 1981; Rowley, 1990), and exhibits complex social organisation (Hobson et al., 2014). However, the sociality of the group is poorly understood (Eberhard, 1998; Salinas-Melgoza and Wright, 2012; Seibert, 2006). For some species, dominance hierarchy is assumed, and its possible correlation with behavioural and/or ecological factors has been investigated (e.g., for orange-fronted conures – *Eupsittula aurea* – Balsby et al., 2012; blue-fronted amazon parrots – *A. aestiva* – Fernández-Juricic et al., 1998; budgerigars – *Melopsittacus undulatus* – Soma and Hasegawa, 2004), but the process of hierarchy development and its effects on animals have not been studied for most species.

Many parrot species are currently threatened, and a better understanding of their sociality may help improve our ability to manage their populations *ex-situ* and even *in-situ* (Hobson et al., 2014). The maintenance of wild animals in captivity may contribute to conservation only if such animals are kept in good conditions of welfare (Young, 2003); these are animals that may compose viable populations once released in the wild (Keulartz, 2015).

Blue-fronted amazon (*Amazona aestiva*) is one of the parrot species most often found in captivity (Freitas et al., 2015). This species is widely kept as a pet, mainly due to its ability to interact with humans (Ferreira et al., 2015; ICMBIO, 2011). In Brazil, it is the most common bird handled in the Wild Animal Screening Centres (CETAS), primarily as a result of apprehensions by environmental agencies of illegally possessed birds (Beissinger and Bucher, 1992; Seixas and Mourão, 2002). The study of this species may bring relevant information to its conservation and possibly other psittacine species with similar environmental requirements.

Our aim in this study was to investigate the process of hierarchy development in *A. aestiva* in captivity, and the possible impacts of group-member replacement on their stress levels. Based on studies on social stress in birds (Kotrschal et al., 1998; Stocker et al., 2016), our assumptions here are: 1) the replacement of individuals promotes an increase in the number of agonistic interactions within the group; 2) this creates greater stress loads for group members, measured through their glucocorticoid metabolite (GCM) concentrations; 3) dominant members have higher GCM concentrations than subordinates.

## 2. Material and methods

This project was approved by the Animal Ethics Committee of the Pontifical Catholic University of Minas Gerais, process no. 002/2015, and was conducted in accordance with the regulations of the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA – Normative Instruction 154/2007), the Forestry State Institute (IEF – Ordinance 148/2013), and the ethical guidelines published by the International Society for Applied Ethology (ISAE, 2002).

### 2.1. Subjects and facilities

Between February and May 2015, 60 individuals of *A. aestiva* were studied in captivity. There is great variation in the reports of the time of reproductive season in the species (e.g., from October to March – Del Hoyo et al., 2010; from August to December – Fernández-Juricic and Martella, 2000; Carrara et al., 2007). Therefore, one week before starting the experiment, we run observations of the birds, looking for reproductive behaviours. None of the birds exhibited such behaviours, so breeding behaviours or reproductive changes in the birds' physiology were not likely to introduce a confounding factor to the study. The subjects had been housed in the Rehabilitation Centre for Wild Animals (CRAS) Lagoa Grande/IBAMA in Nova Lima/MG for approximately 12 months before the start of this study. These animals were sent to CRAS because they had been apprehended or voluntarily surrendered for being illegally possessed. Although the ages of the individuals were unknown, since they were trafficked animals, all subjects were classified as adults through morphological analysis. The animals were fed twice a day with fruits and a crushed mixture of beetroot, carrots, corn and grain mixture for psittacines (MEGAZOO, Betim – MG, Brazil). Water was offered *ad libitum*.

In September 2014, the birds had their chest and cranio-cervical feathers marked with non-toxic dye for fabric (ACRILEX, São Bernardo do Campo – SP, Brazil) in various colour combinations in order to allow visual identification of individuals. In preliminary observations following this procedure, we found that the marking did not cause measurable changes in the animals' behaviour, including their interaction rates. During animal marking, blood samples of the birds were also collected for subsequent sexing by DNA testing. The day before the start of the study, the animals were randomly distributed into two groups of 30 subjects (later randomly named Alternate and Constant groups), and each group was kept in enclosures measuring 2.5 × 7.0 × 3.0 m, partially covered with ceramic tiles. Each enclosure contained: two wooden perches, free and suspended (approximately two metres from the ground), a six-level ladder-type perch, two feeders and a drinking water source made of stainless steel, suspended about two metres from the ground. The enclosures were cleaned every morning. Due to logistical reasons, it was not possible to perform the sexing before the start of the experiment. Thus, the initial composition of the groups by sex was as follows: a) Alternate group: 20 males, eight females and two individuals whose sex remained undefined due to inconclusive test results; b) Constant group: 12 males, 14 females and four individuals of undefined sex.

### 2.2. Procedures

Due to the difference in the male-female ratios between the two groups, we checked for the existence of a possible effect of sex on the individuals' ranking and number of agonistic interactions. There was no detectable effect of these factors on the tested variables (GLM, agonistic interactions:  $estimate \pm SE = 7.07 \pm 7.81$ ,  $t = 0.90$ ,  $P = 0.37$ ; ranking:  $estimate \pm SE = 6.90 \pm 5.25$ ,  $t = 1.31$ ,  $P = 0.19$ ;  $n = 63$ ).

Our study consisted of two stages: Pre-experimental and Experimental. In the Pre-experimental stage both groups were kept under the same management conditions (without introduction or removal of members) and all the animals' agonistic behaviours were regularly recorded (Albers and de Vries, 2001; Royer and Anderson, 2014). Dropping samples were also collected from both groups once a week, for GCM assessment. These samples were used to compare the mean levels of stress of the birds before and after hierarchy stabilisation. This stage was performed to determine the moment when the dominance hierarchies of both groups was established and stabilised, so the Experimental stage could start

from known stable hierarchies in both groups. The stabilisation of both hierarchies determined the end of the Pre-experimental stage, after five weeks. On the last day of the Pre-experimental stage, there was one death in the Alternate group (the bird had its foot stuck in the wire mesh that surrounded the enclosure). Thus, the next stage (Experimental) was conducted with one group of 30 individuals and one group of 29 individuals.

During the Experimental stage, which also lasted five weeks, in the Alternate group there was a weekly replacement of the dominant member by a non-familiar individual, selected at random from an external sample pool. Individuals composing this sample pool were kept in a separate enclosure prior to their introduction, two enclosures apart from the experimental animals, without visual contact with experimental groups. The Constant group remained under the same management conditions of the Pre-experimental stage. During the Experimental stage, all agonistic behaviours performed by members of both groups were also recorded. Dropping samples were collected from groups and from individuals in three different hierarchical positions: the most dominant individual, the individual in the most intermediate position and the most subordinate one. This procedure was performed to evaluate the possible effects of the replacement of individuals in the stress levels of the group as a whole, and in individuals in specific hierarchical positions.

### 2.3. Behavioural observations

Prior to the beginning of the study, we developed an ethogram, based on the studies of [Seibert and Crowell-Davis \(2001\)](#) and [Seibert \(2006\)](#), and on previous observations of 30 individuals housed at the CRAS Lagoa Grande/IBAMA in Nova Lima/MG ([Table 1](#)). The observations were made through the methods behaviour sampling and continuous recording ([Martin and Bateson, 2010](#)), by continuously recording all agonistic behaviours presented by the animals for 30 min in the morning and 30 min in the afternoon, for three days in September 2014.

During the Pre-experimental and Experimental stages, the animals were observed through the same methods used to build the ethogram. Additionally, we recorded the authors, targets, winners and losers of each agonistic interaction; these were defined according to the ethogram developed for the study ([Table 1](#)). Two daily observations sessions of 15 min were made for each group, one in the morning – between 08:00 h and 10:00 h, and one in the afternoon, between 12:30 h and 14:30 h, five times a week. The observation times were defined considering the activity pattern displayed by the animals during the execution of an activity budget ([Silva et al., 2011](#)). The frequency of agonistic interactions recorded in each group during the whole experiment was used for statistical analysis.

### 2.4. Collection of droppings

#### 2.4.1. Group samples

Throughout the experiment, all the fresh droppings found in the birds' enclosures were collected once a week, in the mornings, before the enclosure cleaning. The samples were then homogenised, generating a single sample per group per week. The collection of a single sample per group was necessary due to the reduced amount of faecal matter found in most samples at the time of collection. During the Pre-experimental stage, the collection was held on the first day of the week; during the Experimental stage, it was performed in both groups on the first day after the removal/insertion of individuals in the Alternate group.

#### 2.4.2. Individual samples

During the Experimental stage, a second weekly collection of droppings was performed on the fifth day following member replacement – therefore, after the new rank order could be determined. For this collection, the droppings of birds in three hierarchical positions were individually stored: a) dominant, b) intermediate and c) subordinate (three samples from each group). These collections were also performed in the morning, before the enclosure cleaning. For sample identification, at about 5 p.m. of the day before collection, food dye (ARCOLOR, São Paulo – SP, Brazil) was orally administered to the birds. Each hierarchically distinct individual received dye in a different colour, and the samples were identified and stored individually. The time spent in capture and handling for dye administration was less than two minutes; therefore, this restraint was considered unlikely to be enough to cause changes in the levels of GCM measured in the droppings ([Ferreira et al., 2015](#)).

Shortly after collection, all samples were homogenised, stored in labelled tubes, and frozen at  $-20^{\circ}$  C until extraction and analysis.

### 2.5. Extraction and analysis of GCM

Droppings were extracted according to the methanol-based protocol given in [Palme et al. \(2013\)](#). The dried down extracts were then shipped to the Vetmeduni Vienna, Austria for measuring GCM with a cortisone enzyme immunoassay (EIA) previously developed for chicken ([Rettenbacher et al., 2004](#)), and validated for use in the study species ([Ferreira et al., 2015](#)). All samples were assayed in duplicate, and all intra- and inter-assay coefficients of variation of pool samples were less than 12%. Concentrations of hormone metabolites are expressed as nanograms per gram of wet dropping (ng/g droppings).

### 2.6. Data analysis

#### 2.6.1. Hierarchy assessment

The assessment of the hierarchies was performed by weekly calculating the ranking of the birds in each group, with the use of the Elo-Rating method – “ER” ([Albers and de Vries, 2001](#); [Johnson et al., 2014](#); [Neumann et al., 2011](#)). The ER values are calculated for all group members, considering the probability that bird A beats bird B in a given contest. The ER values of the contestants were updated after each agonistic interaction, as a function of contest results (win, lose or draw), and the current difference in ranking between the two opponents. Higher-ranking individuals are most probable to win any contests; therefore, when a lower-ranking contestant wins, the consequent increase in its position (and decrease in the loser's position; [Albers and de Vries, 2001](#)) is greater than if the result had favoured the higher ranking animal.

In order to assess the stability of the hierarchies, we used the Stability Index (S). The hierarchies were considered stable when the values of S – ranging from 0 to 1 – were above 0.9 ([Correa et al., 2013](#)). All ER and S values were calculated using the R software, with the package ‘EloRating’ ([Neumann and Kulik, 2014](#); R package version 0.43; R version 3.1.3, R Foundation for Statistical Computing).

The linearity of the hierarchies was evaluated through the linearity index (de Vries index –  $h'$ – [De Vries, 1995](#); [Shizuka and McDonald, 2012](#)), with the SOCPROG 2.4 program ([Whitehead, 2009](#)), where 0 corresponds to a completely nonlinear hierarchy and 1 corresponds to a completely linear hierarchy.

#### 2.6.2. Statistical analysis

Data were analysed using General Linear Models (GLM), in the R 3.1.3 program (R Development CoreTeam, 2014), adjusted for a “norm” distribution. We started the analysis with full models,

**Table 1**  
Ethogram of agonistic behaviours exhibited by individuals of *A. aestiva* in this study.

Agonistic behaviour	Description
Attacking	The feathers of the head and body may be bristling, and the tail can open like a fan; the bird walks or runs toward the stimulus source with lowered head and semi-open beak; the head is kept facing forward, lowered or tilted sideways. The attacking bird can peck the opponent or not. If the individual who is attacked retreats, it will be deemed the loser.
Moving away	The bird turns sideways to the opponent, lowers his head and turns away quickly, keeps his head down and eyes away from the view of the opponent. The individual who adopts this attitude is considered the loser.
Grabbing	The bird raises one foot with claws spread towards another bird, and opens its beak; the wings are held close to the body or slightly turned back. If the individual who is attacked retreats, it will be deemed the loser.
Flapping	The bird hits the wings three to five times, stereotypically, while perched with an upright posture; the head is held high forward. If the individual who was attacked retreats, it will be deemed the loser.
Threatening	The bird bristles and briefly lowers all feathers of the cervical, dorsal and thoracic regions. If the individual who is threatened retreats, it will be deemed the loser.
Avoiding	The bird remains motionless, unresponsive, or turns his back to the opponent, hiding its head in the corner or pulling it down between its shoulders. The individual who adopts this attitude is considered the loser.
Extending wings	The bird raises the wings extended simultaneously. If the individual who was the aim of the display retreats, it will be deemed the loser.
Exhibiting	The bird walks quickly, showing off as he walks with his head upright. If the individual who is approached retreats, it will be deemed the loser.
Head-oscillating	The bird moves his head up and down, vertical and rhythmically, while the body is stationary. If the individual who is the aim of the display retreats, it will be deemed the loser.
Attacking on flight	The body feathers are kept tightly lowered. The bird, at the beginning, remains standing on both legs, with eyes wide open. Then, it flies towards the opponent, usually trying to beat him/her with its feet and/or beak during the flight. If the individual who is attacked retreats, it will be deemed the loser.

where all explanatory variables and their possible interactions were included. The minimum adequate models were obtained by comparing the values of the Akaike Information Criterion Fixed (AICc; the best model is the one with the lowest value of AICc). This method promotes a second-order bias correction for AIC, useful particularly for small sample sizes, often in behavioural studies (Burnham et al., 2011; Jolles et al., 2013). Data interpretation was based on significance level ( $p < 0.05$ ) and on effect size (*estimate*).

GLM models were selected to evaluate the following effects: a) member replacement on GCM levels of the group and of individuals in specific positions (dominant, intermediate and subordinate); b) ranking (dominant, intermediate and subordinate) on the GCM levels of individuals in these positions; c) sex, member replacement and ranking on the number of agonistic interactions; d) sex, member replacement, number of agonistic interactions and number of wins on the ranking of the birds.

Due to the dependence of the data of each group in the Pre-experimental and Experimental stages, to assess possible changes in GCM concentrations of groups between these stages, a Paired T-test was used through the program GraphPad InStat (version 3.00, GraphPad Software Inc 2000).

### 3. Results

#### 3.1. Pre-experimental stage: establishing hierarchy

During the Pre-experimental stage, 3290 agonistic interactions were recorded in both groups. The linearity indices indicated that non-linear hierarchies were established in both groups ( $h'_{\text{Constant}} = 0.181$ ,  $P = 0.020$  and  $h'_{\text{Alternate}} = 0.125$ ,  $P = 0.009$ ). The hierarchy was considered stable from the fifth week on in both groups ( $S_{\text{Alternate}} = 0.92$ ;  $S_{\text{Constant}} = 0.92$ , Fig. 1). There were no differences in the mean GCM concentrations in any of the groups between Pre-experimental and Experimental stages (Pre-experimental<sub>Constant</sub> =  $242 \pm 299$  ng/g, Experimental<sub>Constant</sub> =  $178 \pm 34$  ng/g,  $t = 0.5176$ ,

$P = 0.632$ ; Pre-experimental<sub>Alternate</sub> =  $614 \pm 416$  ng/g; Experimental<sub>Alternate</sub> =  $228 \pm 138$  ng/g,  $t = 1.763$ ,  $P = 0.1526$ ).

#### 3.2. Experimental stage: testing the effect of member replacement

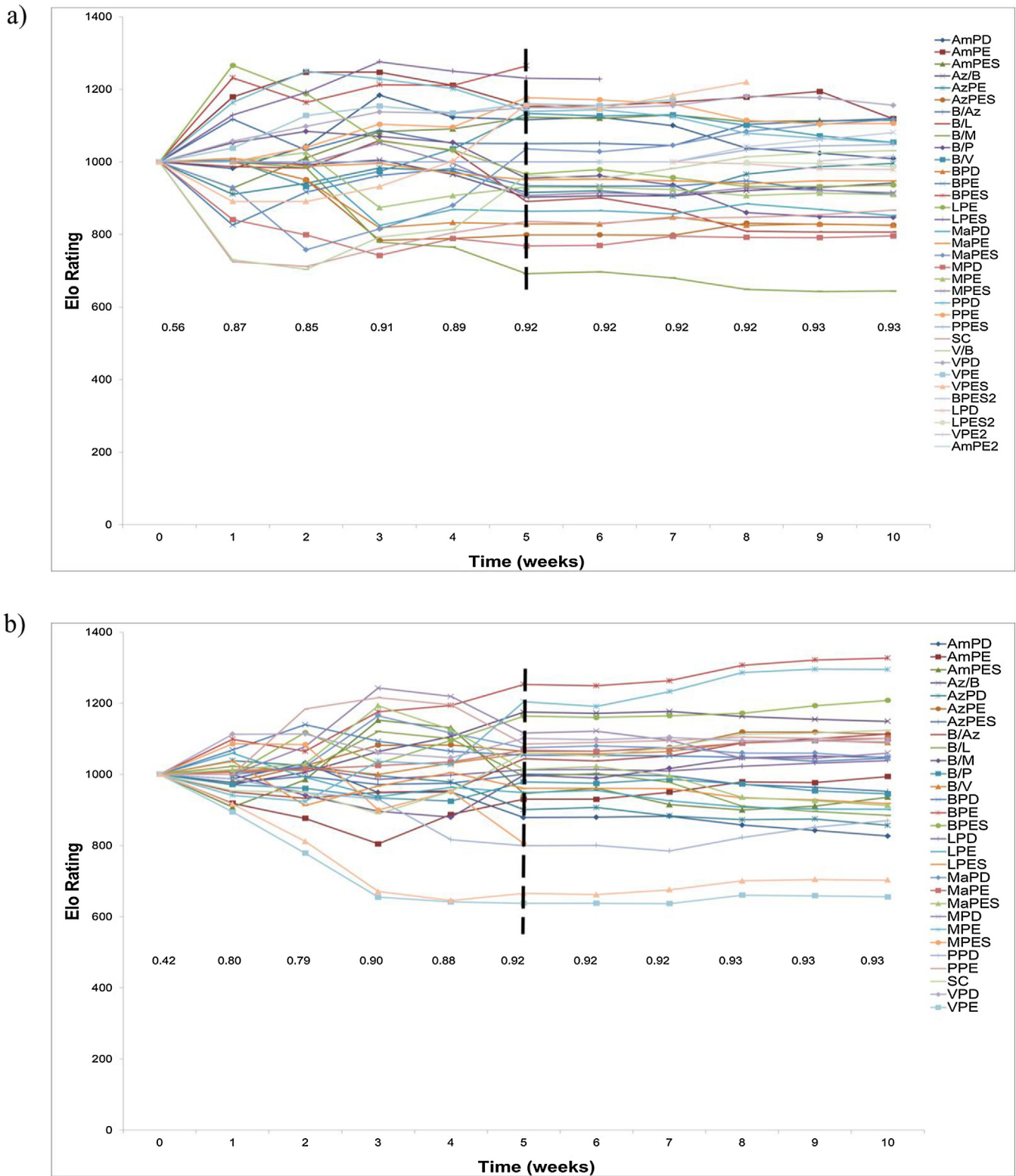
During the Experimental stage, 1846 agonistic interactions were recorded in both groups. The S values remained above 0.9 throughout the Experimental period in both groups, indicating that even with the weekly replacement of dominant individuals in the Alternate group, the hierarchy remained stable (Fig. 1). Data of the eight subjects whose sexing results were inconclusive were excluded from the analysis regarding sex.

The final GLM models are available on Table 2. No effect of member replacement was found on group GCM concentrations (Group<sub>Constant</sub> median = 175 ng/g, quartiles Q1 = 159 ng/g and Q3 = 205 ng/g; Group<sub>Alternate</sub> median = 196 ng/g, Q1 = 164 ng/g and Q3 = 246 ng/g,  $P > 0.05$ ), or on the GCM concentrations of subjects in specific hierarchical positions (Dominant<sub>Constant</sub> median = 381 ng/g, Q1 = 173 ng/g and Q3 = 576 ng/g, Dominant<sub>Alternate</sub> median = 225 ng/g, Q1 = 94 ng/g and Q3 = 359 ng/g; Intermediate<sub>Constant</sub> median = 255 ng/g, Q1 = 212 ng/g and Q3 = 736 ng/g; Intermediate<sub>Alternate</sub> median = 199 ng/g, Q1 = 185 ng/g and Q3 = 222 ng/g; Subordinate<sub>Constant</sub> median = 125 ng/g, Q1 = 77 ng/g and Q3 = 155 ng/g; Subordinate<sub>Alternate</sub> median = 135 ng/g, Q1 = 88 ng/g and 179 ng/g, Table 2).

As we did not find differences between GCM concentrations of subjects in specific positions allocated in different groups (Constant and Alternate), data from individuals in each hierarchical position from both groups were gathered in order to compare GCM concentrations between individuals in distinct positions. Ranking affected the GCM concentrations of individuals (*estimate* =  $-86.5$ ,  $P < 0.0001$ , Fig. 2, Table 2): dominant individuals had the highest GCM concentrations in the groups.

There was no effect of the sex of individuals on the number of agonistic interactions observed. Although there was an interaction between the number of agonistic interactions in which one individual took part and the number of its wins on their social ranking,

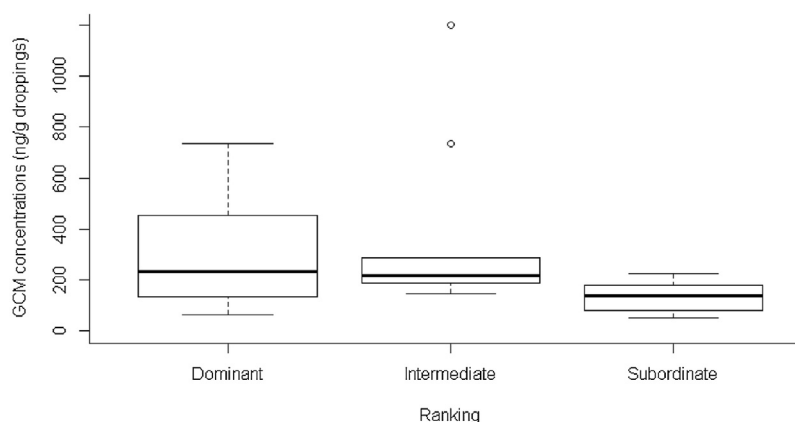




**Fig. 1.** Elo Rating-values of the *A. aestiva* groups: a) Alternate and b) Constant, throughout the ten weeks of study. The dashed lines indicate the point from which the hierarchies were considered stable (stability index above 0.9). The values below the lines represent the values of the stability index (S) for every week, and the codes in the right-hand side of the lines represent the individuals studied.

the effect was negligible (*estimate* = 0.01); therefore, we analysed the effects of the number of agonistic interactions and the number of wins separately. Individuals in lower positions participated in more agonistic interactions (*estimate* = 1.83,  $P < 0.0001$ , Table 2) and, as expected, the number of wins affected the position of the

individual (*estimate* = -4.3,  $P < 0.0001$ , Table 2): the more wins an individual had, the higher its position in the hierarchy. Member replacement did not affect the overall frequency of within group agonistic interactions ( $P > 0.05$ ).



**Fig. 2.** Glucocorticoid metabolite (GCM) concentrations (in ng per g droppings) of individuals of *A. aestiva* in Dominant, Intermediate and Subordinate positions during the Experimental Stage. Box plots show medians and quartiles, whiskers show 10th and 90th percentiles, and circles show outliers.

**Table 2**

Final, reduced models of fixed effects on the response variables Agonistic Interactions (AGI), Ranking, Individual Glucocorticoid Metabolites (GCM) and Group GCM of *A. aestiva*.

Response variables	Estimate $\pm$ SE	t	P
AGI <sup>a</sup>	22.90 $\pm$ 5.20	4.40	<0.0001
(Intercept)	-0.27 $\pm$ 0.14	-1.89	0.06
Ranking			
Ranking <sup>b,e</sup>	27.64 $\pm$ 5.73	4.82	<0.0001
(Intercept)	1.83 $\pm$ 0.41	4.44	<0.0001
AGI	-4.30 $\pm$ 0.70	-6.18	<0.0001
Wins	4.46 $\pm$ 2.56	1.74	0.09
Sex	0.01 $\pm$ 0.003	4.01	0.0002
AGI x Wins			
Individual	387.6 $\pm$ 67.7	5.728	<0.0001
GCM <sup>c</sup>	-86.5 $\pm$ 31.2	-2.774	0.01
(Intercept)			
Ranking <sup>e</sup>			
Group GCM <sup>d</sup>	632.0 $\pm$ 205.2	3.08	0.006
(Intercept)			

<sup>a</sup> The complete model for the variable Agonistic Interactions (AGI) included as explanatory variables: ranking, sex, group (Constant or Alternate) and the interactions: ranking\*sex, ranking\*group and sex\*group.

<sup>b</sup> The complete model for the variable Ranking included as explanatory variables: AGI, number of wins, sex, group and the interactions: AGI\*number of wins, AGI\*sex, AGI\*group, number of wins\*sex, number of wins\*group, sex\*group.

<sup>c</sup> The complete model for the variable Individual GCM included as explanatory variables: group, ranking and the interaction: group\*ranking.

<sup>d</sup> The complete model for the variable Group GCM includes as explanatory variable only group.

<sup>e</sup> The values used as indicators of individual positions in the ranking decrease with rank importance, i.e., the highest individual in the ranking occupies the position 1 and the lowest, occupies the position 63.

#### 4. Discussion

We investigated the process of hierarchy establishment in *A. aestiva* in captivity, and the behavioural and physiological responses of individuals to the replacement of dominant group members compared to the reactions of individuals housed in a group with constant composition. The established hierarchies were non-linear (all linearity indexes less than 0.2) and there was no measurable effect of group member replacement on the GCM levels of the birds, nor on the number of agonistic interactions between the animals. Individuals in the lowest hierarchical positions participated in more agonistic interactions, but individuals in the highest positions had the highest GCM levels.

We recorded the establishment of stable hierarchies within five weeks of group formation, as evidenced by a sharp drop in the average number of agonistic interactions within groups thereafter. After

this period, stability indexes of both groups were above 0.9 – the pre-defined criteria for considering hierarchies as stable (Correa et al., 2013), but since the second week of study, these indexes were already above 0.8, pointing to a rapid hierarchical stabilisation. For some species, stability is favourable, in other taxa disruption is part of the day-to-day social structure. Stable hierarchies have lower levels of aggression, since individuals know their positions and can avoid unnecessary confrontations (Rose and Croft, 2015). Predictable responses based on previous interactions collaborate to set up and maintain stable hierarchies, resulting in decreased aggression among group members, which favours energy saving and, therefore, is adaptive (Mendonça-Furtado et al., 2014; Seibert, 2006). Rapid hierarchical stabilisation was also observed in parakeets in semi-natural captivity (Hobson et al., 2014).

The dominance hierarchy established in *A. aestiva* was non-linear, with linearity indexes near zero. Non-linear hierarchies are seen as egalitarian, i.e., they tend to have intransitive dominance relations (for example, A dominates B, B dominates C, but C can dominate A; Chase et al., 2002) where agonistic interactions are not necessarily unidirectional, relationships are attained with the support of subordinate individuals, and distribution of resources is, usually, balanced among group members (Sapolsky, 2005; Thierry et al., 2004; Wittemyer and Getz, 2007). Examples of egalitarian hierarchies can be found in the northern muriqui (*Brachyteles hypoxanthus*; Strier et al., 2011), the Tonkean macaques (*Macaca tonkeana*; Ciani et al., 2012) and Mantled guerezas (*Colobus guereza*; Grunau and Kuester, 2001). Species that use resources that are hard to monopolise tend to develop such hierarchies, as is the case of parrots, which in the wild use mostly scattered and seasonal food resources, and travel long distances in search of food (Hobson et al., 2014; Juniper and Parr, 1998). Although in captivity, due to spatial constraints, resources may be more easily monopolised (Horova et al., 2015; McDougall et al., 2006), there were no records of food monopolisation in our study, which would be expected for an egalitarian hierarchy (Sapolsky, 2005).

Parrots exhibit great diversity of social structures (Hobson et al., 2014). Non-linear hierarchies were found in kea in captivity (*Nestor notabilis* – seven animals; Tebbich et al., 1996), with numerous reversals of positions. In monk parakeets (*Myiopsitta monachus*), a moderately linear hierarchy was found in semi-natural conditions of captivity (21 and 19 animals; Hobson et al., 2014), and in captive cockatiels (*Nymphicus hollandicus*), a linear hierarchy (12 animals; Seibert and Crowell-Davis, 2001) was described. In addition to the characteristics of each species, the number of individuals studied may interfere in the variations found in the linearity of hierarchy among psittacine species. It was reported that the more intransitive relations a hierarchy has, the less linear the hierarchy

is (Chase et al., 2002); therefore, it is expected that linear hierarchies occur most often in smaller groups (Braun and Bugnyar, 2012; Chase et al., 2002; Drews, 1993; Jameson et al., 1999; Royer and Anderson, 2014). As group size increases, the likelihood of occurrence of intransitive interactions also increases and, as a consequence, the probability of a hierarchy being non-linear as well (Chase et al., 2002; Jameson et al., 1999). In our study, we reported non-linear hierarchies in groups of 30 individuals, the most numerous parrot groups studied in captivity. Although captive conditions may favour the formation of linear hierarchies (Horova et al., 2015; Hobson et al., 2014), group size may have contributed to the establishment of non-linear hierarchies in our birds. There are no data on the natural group size of *A. aestiva*; future studies with this species in the wild may shed more light in the matter.

There was no difference between the GCM concentrations of the groups in the Pre-experimental and Experimental stages. Although the establishment of the hierarchies occurred during the Pre-experimental stage, GCM levels of the animals did not point to a stress load greater than that observed after hierarchy stabilisation. This lack of increase in social stress during hierarchy establishment might be due to the non-linearity of the hierarchy: in this type of hierarchy, there is no individual who exerts dominance over the whole group, therefore the dominance tends to be more egalitarian (Sapolsky, 2005; Wittemyer and Getz, 2007). As a result, social interactions may cause lower stress loads in group members; in the case of our study, this can be inferred through the absence of increase in GCM concentrations during hierarchy establishment, as well as the lack of increase in GCM concentrations and in agonistic interactions even with the replacement of group members.

In contrast to our first and second hypotheses, we did not find evidence that the replacement of the dominant individual by non-familiar members intensely affected the social structure of the group: member replacement did not affect the number of agonistic interactions, nor promoted increases in the levels of GCM. In non-linear hierarchies, the removal of an individual, even a high-ranking one, would affect only a few birds with whom this individual regularly interacted, and not the whole group. In order to investigate the reason for the lack of effect we observed, we conducted a pilot project (unpublished results), in which we evaluated the effect of removing the four highest-ranking individuals on the stability of the Alternate group. Even though, no change in group stability was recorded; S values remained above 0.9, suggesting the non-linearity might have a buffer effect, preserving social stability. On the other hand, studies on species characterised by linear hierarchies have found a different pattern. In pig-tailed macaques (*Macaca nemestrina*; Flack et al., 2006), rhesus macaques (*Macaca mulatta*; McCowan et al., 2008) and chickens (*Gallus gallus domesticus*; Carvalho et al., unpublished results), the removal of individuals in the highest hierarchical positions caused rapid instability within the group, with a consequent increase in the levels of aggression and/or reduced affiliative behaviours.

Our results indicated that the relocation of individuals, as conducted in environmental agencies, might not affect the welfare of individuals in the short term. However, considering the positive effect of the formation of social bonds and associations on the health, well-being, adaptive value and reproductive success of animals (Asher et al., 2009; Rose and Croft, 2015), the breaking of these bonds may lead to group fragmentation in the long term (Asher et al., 2009; McCowan et al., 2008; Rose and Croft, 2015). Parrot species have been shown to flock preferentially in familiar groups (Gilardi and Munn, 1998; Seixas and Mourão, 2013), present better welfare conditions when pair-housed in comparison to individual housing (Meehan et al., 2003), may present social facilitation (Soma and Hasegawa, 2004), and even exhibit social play, which may function to strengthen social bonds (Skeate, 1985). All these data indicate the importance of social bonding in the species

(Hobson et al., 2014; Seibert, 2006; Salinas-Melgoza and Wrigh, 2012). Therefore, considering this study evaluated the short-term effect of the replacement of the dominant member in *A. aestiva* in the group, we suggest that future studies on the species investigate the existence of social preferences, and the long-term effect of social management on each member of the dyads that were separated.

Our third hypothesis – that dominant individuals would present larger allostatic loads than subordinates – was corroborated by our data. Individuals in the highest positions in the hierarchy had the highest GCM concentrations, indicating greater stress load in these positions. Higher levels of GCM in dominants have been associated with a function of appeasement within the group (Flack et al., 2006), defence and resource control as reported, for example, in capuchin monkeys (Mendonça-Furtado et al., 2014), wolves (Sands and Creel, 2004), and in fish (Dey et al., 2013). In timber wolves, (Sands and Creel, 2004; Vasconcellos et al., 2011), a positive correlation between the levels of GCM and hierarchical position was recorded, with no correlation between GCM levels and the number of agonistic or affiliative interactions in which the animals were involved. Similarly, in our study, although dominants had higher GCM concentrations than subordinates, no correlation between GCM levels and agonistic interactions was recorded, which suggests that the stress load to maintain dominance within a group whose hierarchy is not strict is perhaps influenced by more than the participation in interactions with group members; it might include the chronic stress of having to constantly monitor the group to maintain one's hierarchical position (Seibert, 2006; Vasconcellos et al., 2011).

Our intermediate subjects had GCM concentrations very close to concentrations of the dominants, while subordinates had lower levels than those in both other positions. In monk parakeets, a higher occurrence of aggression directed against individuals closer in ranking was reported (Hobson and Dedeo, 2015), indicating that during rank establishment, apparently the author “chooses its target, instead of directing aggression against any other individuals. Forkman and Haskell (2004) reported that 95% of the attacks in chickens are directed to individuals in a hierarchical position immediately below the aggressor, a possible strategy of dominant individuals for conditioning members hierarchically close to lose, thereby reducing the possibility of reversal in position due to similar physical conditions (the Suppression Hypothesis). This is possibly also the case of our animals.

In contrast to the above results, studies with some other species recorded higher allostatic load in subordinates than in dominants, for example: in Harris' sparrows (*Zonotrichia querula* – Rohwer and Wingfield, 1981), olive baboons (*Papio anubis* – Sapolsky, 1982), white-throated sparrows (*Zonotrichia albicollis* – Schwabl et al., 1988), naked mole-rats (*Heterocephalus glabe* – Faulkes and Abbott, 1997), and Assamese macaques (*Macaca assamensis* – Ostner et al., 2008). In white-throated sparrows, the authors interpret higher GCM concentrations in subordinates to be due to their exposure to greater risk of predation, since they forage away from the pack (Schwabl et al., 1988). In assamese macaques, the highest levels of GCM in subordinates are possibly an effect of the higher rate of aggression directed toward them during the breeding season (Ostner et al., 2008). In this species, dominance is not associated with high costs, since it is maintained mainly by demonstrations of submission, and dominants form strong bonds with each other through affiliative interactions, likely to prevent possible attacks by subordinates (Ostner et al., 2008). This way, they leave for the subordinates the greatest stress loads in the groups. In a linear hierarchy, where an individual who occupies a high position in the ranking dominates all the others below it, resource distribution is uneven, and this unevenness is maintained in most cases by aggression and intimidation (Shizuka and McDonald, 2012). In



such hierarchies, subordinates have lower chances of having access to resources, lower coping opportunities and, consequently, higher levels of physical and social stress. The higher concentrations of stress-hormones in subordinates may even mediate reproductive suppression in some species (e.g. in the African cichlid *Astatotilapia burtoni* – Korzan et al., 2014; and in common marmosets, *Callithrix jacchus* – Saltzman et al., 1998). Subordinates living in such hierarchies tend to have less control over the situation (Abbott et al., 2003; Ostner et al., 2008; Sapolsky, 2005), and this is a factor with recognised influence on stress levels in captivity (Bassett and Buchanan-Smith, 2007).

In our study, the number of agonistic interactions in which individuals participated, and the number of victories they achieved were predictors of the position they occupied in the rankings. Individuals in lower positions in the hierarchy participated in more agonistic interactions, but dominant individuals were the ones who obtained more victories, as one might expect (Piper, 1997). Evidence of lack of increased aggressiveness in dominant parrot species has been found (e.g., in budgerigars – Soma and Hasegawa, 2004; monk parakeets – Hobson et al., 2014 and orange-fronted conures – Balsby et al., 2012). In budgerigars, although an effect of ranking was observed in foraging situations – through increased latency to start feeding by subordinates – higher ranking birds did not aggressively prevent lower ranking ones from feeding: the latter fed almost as much as the dominants (Soma and Hasegawa, 2004). Orange-fronted conures were found to avoid aggression by ‘negotiating’ dominance prior to flock fusion, through imitation of specific individuals (Balsby et al., 2012). In cockatiels, by contrast, a positive correlation between aggression and hierarchical position was reported (Seibert and Crowell-Davis, 2001). As we found evidence of an egalitarian hierarchy in our study, it is possible that the observed lack of increased aggressiveness in higher ranking birds is also related to such type of hierarchy. As described above, several studies on dominance hierarchy in terms of stability, aggressiveness and stress loads have found diverse results, with greater stress loads in different hierarchical positions. Social stress should not be considered as a unicausal factor, but rather as a consequence of a combination of dominance and subordination efforts (Vasconcellos et al., 2012), and their consequences on the construction of the social organisation. Therefore, the position in the hierarchy in itself does not seem to determine the stress loads of individuals; factors such as the possibilities of coping, and having control and predictability available for individuals may also influence the costs of being dominant or subordinate (Abbott et al., 2003; Ostner et al., 2008).

We found no difference between the participation in agonistic interactions of males and females, nor in their hierarchical positions in our study. Similar result was found in monk parakeets (Hobson et al., 2014). The parakeets study, although having been conducted during the breeding season, reported that their subjects were not actively breeding, perhaps because of some characteristics of the captive environment. In cockatiels, different results were found: higher rates of aggression in males (Seibert and Crowell-Davis, 2001), possibly due to activities of partner selection, at the start of the breeding season. During the breeding season, males show an increase in levels of circulating androgens in plasma and these, especially testosterone, are closely related to increased levels of aggression (Gould and Ziegler, 2007; Goymann et al., 2007; Mendonça-Furtado et al., 2014; Royer and Anderson, 2014). In monk parakeets, a seasonal variation in the dominant sex was described: males were dominant in the reproductive period, while females were dominant in the non-breeding period (Masure and Allee, 1934).

Our study, the first to investigate the process of development of hierarchy in *A. aestiva*, recorded the development of non-linear hierarchies in captivity, wherein male and female occupied similar

positions and exhibited similar number of agonistic interactions. The replacement of dominant individuals did not affect group stability, the average levels of GCM, or the number of agonistic interactions. Therefore, the management practice adopted by environmental agencies – i.e., the relocation of individuals between rehabilitation groups before release – may not measurably impact the welfare of the birds in the short-term, when out of the breeding season. Consequently, it is unlikely that there would be negative impacts of such management practice on the success in the survival of parrots to later be released. This management practice does not seem to represent an obstacle to the maintenance of psittacines in good conditions of welfare, and may contribute to the integration of *ex-situ* and *in-situ* parrot conservation. Our findings have implications for captive breeding and release/reintroduction programs of blue-fronted parrots, and may be useful also for conservation programs of other parrot species, with varying degrees of vulnerability.

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## References

- Abbott, D.H., Keverned, E.B., Bercovitch, F.B., Shively, C.A., Mendozag, S.P., Saltzman, W., Snowdon, C.T., Ziegler, T.E., Banjević, M., Garland, Jr. T., Sapolsky, R.M., 2003. Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Horm. Behav.* 43 (1), 67–82. [http://dx.doi.org/10.1016/S0018-506X\(02\)00037-5](http://dx.doi.org/10.1016/S0018-506X(02)00037-5).
- Albers, C.H., de Vries, H., 2001. Elo-rating as a tool in the sequential estimation of dominance strengths. *Anim. Behav.* 61 (2), 489–495. <http://dx.doi.org/10.1006/anbe.2000.1571>.
- Asher, L., Collins, L.M., Ortiz-Pelaez, A., Drewe, J.A., Nicol, C.J., Pfeiffer, D.U., 2009. Recent advances in the analysis of behavioural organization and interpretation as indicators of animal welfare. *J. R. Soc. Interface* 6 (41), 1103–1119. <http://dx.doi.org/10.1098/rsif.2009.0221>.
- Balsby, T.J.S., Momberg, J.V., Dabelsteen, T., 2012. Vocal imitation in parrots allows addressing of specific individuals in a dynamic communication network. *PLoS One* 7 (11), e49747.
- Bassett, L., Buchanan-Smith, H.M., 2007. Effects of predictability on the welfare of captive animals. *Appl. Anim. Behav. Sci.* 102, 223–245. <http://dx.doi.org/10.1016/j.applanim.2006.05.029>.
- Beissinger, S.R., Bucher, E.H., 1992. Sustainable harvesting of parrots for conservation. In: Beissinger, S.R., Snyder, N.E.R. (Eds.), *New World Parrots in Crisis: Solutions from Conservation Biology*. Smithsonian Institution Press, Washington, USA, pp. 73–115.
- Bernstein, I.S., 1981. Dominance: the baby and the bath water. *Behav. Brain Sci.* 4, 419–457.
- Braun, A., Bugnyar, T., 2012. Social bonds and rank acquisition in raven nonbreeder aggregations. *Anim. Behav.* 84 (6), 1507–1515. <http://dx.doi.org/10.1016/j.anbehav.2012.09.024>.
- Broom, D.M., Molento, C.F.M., 2004. Bem-estar animal: conceitos e questões relacionadas – Revisão. *Arch. Vet. Sci.* 9 (2), 1–11.
- Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* 65 (1), 23–35. <http://dx.doi.org/10.1007/s00265-010-1029-6>.



- Carrara, L.A., Faria, L.P., Amaral, F.Q., Rodrigues, M., 2007. *Dormitórios do papagaio-verdadeiro A. aestiva e do papagaio-galego Salvia xanthops em plantio comercial de eucalipto*. Rev. Bras. Ornitol. 15 (1), 135–138.
- Chase, I.D., Tovey, C., Spangler-Martin, D., Manfredonia, M., 2002. Individual differences versus social dynamics in the formation of animal dominance hierarchies. Proc. Nat. Acad. Sci. 99 (8), 5744–5749, <http://dx.doi.org/10.1073/pnas.082104199>.
- Ciani, F., Dall'Olio, S., Stanyon, R., Palagi, E., 2012. Social tolerance and adult play in macaque societies: a comparison with different human cultures. Anim. Behav. 84, 1313–1322, <http://dx.doi.org/10.1016/j.anbehav.2012.09.002>.
- Correa, L.A., Zapata, B., Samaniego, H., Soto-Gamboa, M., 2013. Social structure in a family group of Guanaco (*Lama guanicoe*, Ungulate): Is female hierarchy based on 'prior attributes' or 'social dynamics'? Behav. Process. 98, 92–97, <http://dx.doi.org/10.1016/j.beproc.2013.05.003>.
- Creel, S., 2001. Social dominance and stress hormones. Trends Ecol. Evol. 16, 491–497, [http://dx.doi.org/10.1016/S0169-5347\(01\)02227-3](http://dx.doi.org/10.1016/S0169-5347(01)02227-3).
- De Vries, H., 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Anim. Behav. 50 (5), 1375–1389, [http://dx.doi.org/10.1016/0003-3472\(95\)80053-0](http://dx.doi.org/10.1016/0003-3472(95)80053-0).
- Del Hoyo, J., Elliott, A., Sargatal, J., 2010. *Handbook of the Birds of the World. Vol. 15: Weavers to New World Warblers*. Lynx Edicions, Barcelona.
- Dey, C.J., Reddon, A.R., O'Connor, C.M., Balshine, S., 2013. Network structure is related to social conflict in a cooperatively breeding fish. Anim. Behav. 85 (2), 395–402, <http://dx.doi.org/10.1016/j.anbehav.2012.11.012>.
- Drews, C., 1993. *The concept and definition of dominance in animal behaviour*. Behaviour 125 (3), 283–313.
- Eberhard, J.R., 1998. Breeding biology of the monk parakeet. Wilson Bull. 110, 463–473.
- Enquist, M., Leimar, O., 1990. The evolution of fatal fighting. Anim. Behav. 39 (1), 1–9, [http://dx.doi.org/10.1016/S0003-3472\(05\)80721-3](http://dx.doi.org/10.1016/S0003-3472(05)80721-3).
- Faulkes, C.G., Abbott, D.H., 1997. The physiology of a reproductive dictatorship: regulation of male and female reproduction by a single breeding female in colonies of naked mole-rats. In: Solomon, N.G., French, J.A. (Eds.), *Cooperative Breeding in Mammals*. Cambridge University Press, Cambridge, pp. 302–334.
- Fernández-Juricic, E.E., Martella, M.B., 2000. Guttural calls of blue-fronted amazons: structure, context, and their possible role in short range communication. Wilson Bull. 112 (1), 35–43.
- Fernández-Juricic, E., Alvarez, E.V., Martella, M.B., 1998. *vocalizations of the bluecrowned conures (Aratinga acuticaudata) in the Chancani Reserve Córdoba, Argentina*. Ornitol. Neotrop. 9, 31–40.
- Ferreira, J.C.P., Fujihara, C.J., Fruhvald, E., Trevisol, E., Destro, F.C., Teixeira, C.R., Pantoja, J.C.F., Schmidt, E.M.S., Palme, R., 2015. Non-invasive measurement of adrenocortical activity in blue-fronted parrots (*A. aestiva*, Linnaeus, 1758). PLoS One 10 (12), e0145909, <http://dx.doi.org/10.1371/journal.pone.0145909>.
- Flack, J.C., Girvan, M., de Waal, F.B.M., Krakauer, D.C., 2006. Policing stabilizes construction of social niches in primates. Nature 439 (7075), 426–429, <http://dx.doi.org/10.1038/nature04326>.
- Forkman, B., Haskell, M.J., 2004. The maintenance of stable dominance hierarchies and the pattern of aggression: support for the suppression hypothesis. Ethology 110, 737–744, <http://dx.doi.org/10.1111/j.1439-0310.2004.01009.x>.
- Freitas, A.C.P., Oviedo-Pastrana, M.E., Vilela, D.A.R., Pereira, P.L.L., Loureiro, L.O.C., Haddad, J.P.A., Martins, N.R.S., Soares, D.F.M., 2015. Diagnóstico de animais ilegais recebidos no centro de triagem de animais silvestres de Belo Horizonte, Estado de Minas Gerais, no ano de 2011. Cienc. Rural. 45, 163–170, <http://dx.doi.org/10.1590/0103-8478cr20131212>.
- Gilardi, J.D., Munn, C.A., 1998. *Patterns of activity flocking, and habitat use in parrots of the Peruvian Amazon*. Condor 100, 641–653.
- Gould, L., Ziegler, T.E., 2007. Variation in fecal testosterone levels, inter-male aggression, dominance rank and age during mating and post-mating periods in wild adult male ring-tailed lemurs (*Lemur catta*). Am. J. Primatol. 69, 1325–1339, <http://dx.doi.org/10.1002/ajp.20438>.
- Goymann, W., Landys, M.M., Wingfield, J.C., 2007. Distinguishing seasonal androgen responses from male–male androgen responsiveness – revisiting the challenge hypothesis. Horm. Behav. 51 (4), 463–476, <http://dx.doi.org/10.1016/j.yhbeh.2007.01.007>.
- Grunau, T., Kuester, J., 2001. *Dominance style in female guerezas (Colobus guereza RISPPELL 1835)*. Primates 42 (4), 301–307.
- Hobson, E.A., Dedeo, S., 2015. Social feedback and the emergence of rank in animal society. PLoS Comput. Biol. 11 (9), e1004411, <http://dx.doi.org/10.1371/journal.pcbi.1004411>.
- Hobson, E.A., Avery, M.L., Wright, T., 2014. The socioecology of Monk Parakeets: insights into parrot social complexity, USA. Auk 131 (4), 756–775, <http://dx.doi.org/10.1642/AUK-14-14.1>.
- Horova, E., Brandlova, K., Glonekova, M., 2015. The first description of dominance hierarchy in captive giraffe: not loose and egalitarian, but clear and linear. PLoS One 10 (5), e0124570, <http://dx.doi.org/10.1371/journal.pone.0124570>.
- ICMBIO, 2011. *Plano de ação nacional para a conservação dos papagaios da Mata Atlântica*. Instituto Chico Mendes MMA, ICMBIO, Brasília.
- ISAE Ethics Committee, 2002. *Ethical Treatment of Animals in Applied Animal Behaviour Research*. Available at [http://www.applied-ethology.org/ethical\\_guidelines.html](http://www.applied-ethology.org/ethical_guidelines.html) (Accessed in 04 February 2015).
- Jameson, K.A., Appleby, M.C., Freeman, L.C., 1999. Finding an appropriate order for a hierarchy based on probabilistic dominance. Anim. Behav. 57 (5), 991–998, <http://dx.doi.org/10.1006/anbe.1998.1077>.
- Johnson, E.T., Snyder-Mackler, N., Beehner, J.C., Bergman, T.J., 2014. Kinship and dominance rank influence the strength of social bonds in female geladas (*Theropithecus gelada*). Int. J. Primatol. 35 (1), 288–304, <http://dx.doi.org/10.1007/s10764-013-9733-5>.
- Jolles, J.W., Ostojić, L., Clayton, N.S., 2013. Dominance, pair bonds and boldness determine social-foraging tactics in rooks, *Corvus frugilegus*. Anim. Behav. 85 (6), 1261–1269, <http://dx.doi.org/10.1016/j.anbehav.2013.03.013>.
- Juniper, T., Parr, M., 1998. *Parrots: A Guide to Parrots of the World*. Pica Press, Sussex, UK, 594 p.
- Keulartz, J., 2015. Captivity for conservation? Zoos at a crossroads. J. Agric. Environ. Ethics 28 (2), 335–351, <http://dx.doi.org/10.1007/s10806-015-9537-z>.
- Korzan, W.J., Grone, B.P., Fernald, R.D., 2014. Social regulation of cortisol receptor gene expression. J. Exp. Biol. 217 (18), 3221–3228, <http://dx.doi.org/10.1242/jeb.104430>.
- Kotschal, K., Hirschenhauser, K., Möstl, E., 1998. *The relationship between social stress and dominance is seasonal in greylag geese*. Anim. Behav. 55 (1), 171–176.
- Möstl, E., Palme, R., 2002. Hormones as indicators of stress. Domest. Anim. Endocrinol. 23, 67–74, [http://dx.doi.org/10.1016/S0739-7240\(02\)00146-7](http://dx.doi.org/10.1016/S0739-7240(02)00146-7).
- Martin, P.H., Bateson, P.P.G.B., 2010. *Measuring Behavior*, 3 ed. Cambridge University, Cambridge, England, 186 p.
- Masure, R.H., Allee, W.C., 1934. Flock organization of the shell parakeet *Melospittacus undulatus* shaw. Ecology 15 (4), 388–398, <http://dx.doi.org/10.2307/1932354>.
- McCowan, B., Anderson, K., Heagarty, A., Cameron, A., 2008. Utility of social network analysis for primate behavioural management and wellbeing. Appl. Anim. Behav. Sci. 109 (2), 396–405, <http://dx.doi.org/10.1016/j.applanim.2007.02.009>.
- McDougall, P.T., Réale, D., Sol, D., Reader, S.M., 2006. *Wildlife conservation and animal temperament: an evolutionary overview*. Anim. Conserv. 9, 39–48.
- Meehan, C.L., Garner, J.P., Mench, J.A., 2003. *Isosexual pair housing improves the welfare of young Amazon parrots*. Appl. Anim. Behav. Sci. 81, 73–88.
- Mendonça-Furtado, O., Eades, M., Palme, R., Rodrigues, A., Siqueira, J., Izar, P., 2014. Does hierarchy stability influence testosterone and cortisol levels of bearded capuchin monkeys (*Sapajus libidinosus*) adult males? A comparison between two wild groups. Behav. Process. 109, 79–88, <http://dx.doi.org/10.1016/j.beproc.2014.09.010>.
- Morgan, K.N., Tromborg, C.T., 2007. Sources of stress in captivity. Appl. Anim. Behav. Sci. 102, 262–302, <http://dx.doi.org/10.1016/j.applanim.2006.05.032>.
- Neumann, C., Kulik, L., 2014. *EloRating-a Brief Tutorial*. R package versão 0.41; R version 3.1.1. Disponível em <http://CRAN.R-project.org/package=Elo-Rating> (Acesso in 02 May 2015).
- Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A.M., Agil, M., Engelhardt, A., 2011. Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. Anim. Behav. 82 (4), 911–921, <http://dx.doi.org/10.1016/j.anbehav.2011.07.016>.
- Ostner, J., Heistermann, M., Schülke, O., 2008. Dominance, aggression and physiological stress in wild male Assamese macaques (*Macaca assamensis*). Horm. Behav. 54 (5), 613–619, <http://dx.doi.org/10.1016/j.yhbeh.2008.05.020>.
- Palme, R., Rettenbacher, S., Touma, C., El-Bahr, S.M., Möstl, E., 2005. Stress hormones in mammals and birds: comparative aspects regarding metabolism, excretion and noninvasive measurement in fecal samples. Ann. N. Y. Acad. Sci. 1040, 162–171, <http://dx.doi.org/10.1196/annals.1327.021>.
- Palme, R., Touma, C., Arias, N., Dominchin, M., Lepshy, M., 2013. *Steroid extraction: get the best out of faecal samples*. Wien. Tierarztl. Monat. 100, 238–246.
- Piper, W.H., 1997. *Social dominance in birds: early findings and new horizons*. Curr. Ornithol. 14, 125–187.
- Rettenbacher, S., Möstl, E., Hackl, R., Ghareeb, K., Palme, R., 2004. Measurement of corticosterone metabolites in chicken droppings. Brit. Poult. Sci. 45 (5), 704–711, <http://dx.doi.org/10.1080/00071660400006156>.
- Rohwer, S., Wingfield, J.C., 1981. A field study of dominance, plasma levels of luteinizing hormone and steroid hormones in wintering Harris' sparrows. Z. Tierpsychol. 57, 173–183, <http://dx.doi.org/10.1111/j.1439-0310.1981.tb01321.x>.
- Rose, P.E., Croft, D.P., 2015. The potential of Social Network Analysis as a tool for the management of zoo animals. Anim. Welf. 24 (2), 123–138, <http://dx.doi.org/10.7120/09672786.24.2.123>.
- Rowley, I., 1990. *Behavioural Ecology of the Galah, Eolophus roseicapillus, in the Wheatbelt of Western Australia*. Surrey Beatty & Sons, Chipping Norton, New South Wales, 188 p.
- Royer, E.A., Anderson, M.J., 2014. Evidence of a dominance hierarchy in captive Caribbean flamingos and its relation to pair bonding and physiological measures of health. Behav. Process. 105, 60–70, <http://dx.doi.org/10.1016/j.beproc.2014.03.005>.
- Salinas-Melgoza, A., Wright, T.F., 2012. Evidence for vocal learning and limited dispersal as dual mechanisms for dialect maintenance in a parrot. PLoS One 7 (11), e48667, <http://dx.doi.org/10.1371/journal.pone.0048667>.
- Saltzman, W., Schultz-Darken, N.J., Wegner, F.H., Wittwer, D.J., Abbott, D.H., 1998. *Suppression of cortisol levels in subordinate female marmosets: reproductive and social contributions*. Horm. Behav. 33, 58–74.
- Sands, J., Creel, S., 2004. Social dominance, aggression and faecal glucocorticoid levels in a wild population of wolves, *Canis lupus*. Anim. Behav. 67, 387–396, <http://dx.doi.org/10.1016/j.anbehav.2003.03.019>.
- Sapolsky, R.M., 1982. The endocrine stress-response and social status in the wild baboon. Horm. Behav. 16 (3), 279–292, [http://dx.doi.org/10.1016/0018-506X\(82\)90027-7](http://dx.doi.org/10.1016/0018-506X(82)90027-7).
- Sapolsky, R.M., 2005. The influence of social hierarchy on primate health. Science 308 (5722), 648–652, <http://dx.doi.org/10.1126/science.1106477>.

- Scheiber, I.B.R., Sterenborg, M.E., Komdeur, J., 2015. Stress assessment in captive graylag geese (*Anser anser*). *J. Anim. Sci.* 93, 2124–2133, <http://dx.doi.org/10.2527/jas.2014-8523>.
- Schwabl, H., Ramenofsky, M., Schwabl-Benzinger, I., Farner, D.S., Wingfield, J.C., 1988. Social status, circulating levels of hormones, and competition for food in winter flocks of the white-throated sparrow. *Behaviour* 107 (1), 107–121.
- Seibert, L.M., Crowell-Davis, S.L., 2001. Gender effects on aggression, dominance rank, and affiliative behaviors in a flock of captive adult cockatiels (*Nymphicus hollandicus*). *Appl. Anim. Behav. Sci.* 71 (2), 155–170.
- Seibert, L.M., 2006. Social behavior of psittacine birds. In: Luescher, A.U. (Ed.), *Manual of Parrot Behavior*, 1 ed. Blackwell Publishing, IOWA, USA, 332 p.
- Seixas, V.H.F., Mourão, G.M., 2002. Nesting success and hatching survival of the blue-fronted Amazon (*A. aestiva*) in the Pantanal of Mato Grosso do Sul, Brazil. *J. Field Ornithol.* 73 (4), 399–409, <http://dx.doi.org/10.1648/0273-8570-73.4.399>.
- Shizuka, D., McDonald, D.B., 2012. A social network perspective on measurements of dominance hierarchies. *Anim. Behav.* 83 (4), 925–934, <http://dx.doi.org/10.1016/j.anbehav.2012.01.011>.
- Silva, G.M.M., Veríssimo, K.C.S., Oliveira, M.A.B., 2011. Orçamento das atividades diárias de dois grupos de *Callithrix jacchus* em área urbana. *Rev. Etol.* 10 (2), 57–63.
- Skeate, S.T., 1985. Social play behaviour in captive white-fronted Amazon parrots *Amazona albifrons*. *Bird Behav.* 6 (1), 46–48.
- Soma, M., Hasegawa, T., 2004. The effect of social facilitation and social dominance on foraging success of budgerigars in an unfamiliar environment. *Behaviour* 141, 1121–1134.
- Stocker, M., Munteanu, A., Stöwe, M., Schwab, C., Palme, R., Bugnyar, T., 2016. Loner or socializer? Ravens' adrenocortical response to individual separation depends on social integration. *Horm. Behav.* 78, 194–199, <http://dx.doi.org/10.1016/j.yhbeh.2015.11.009>.
- Strier, K.B., Chaves, P.B., Mendes, S.L., Fagundes, V., Di Fiore, A., 2011. Low paternity skew and the influence of maternal kin in an egalitarian, patrilocal primate. *PNAS* 108 (47), 18915–18919, <http://dx.doi.org/10.1073/pnas.1116737108>.
- Tebbich, S., Taborsky, M., Winkler, H., 1996. Social manipulation causes cooperation in keas. *Anim. Behav.* 52 (1), 1–10, <http://dx.doi.org/10.1006/anbe.1996.0147>.
- Thierry, B., Singh, M., Kaumanns, W., 2004. *Macaque Societies: A Model for the Study of Social Organization*. Oxford University Press, New York.
- Vasconcellos, A.S., Virányi, Z., Range, F., Möstl, E., Ades, C., Kotrschal, K., 2011. Social interactions and non-invasive stress monitoring in captive timber wolves (*Canis lupus*). *J. Vet. Behav.* 6 (1), 71–72, <http://dx.doi.org/10.1016/j.jvbeh.2010.09.030>.
- Vasconcellos, A.S., Ades, C., Kotrschal, K., 2012. Social stress in wolves. In: Maia, A.P., Crussi, H.F. (Eds.), *Wolves: Biology, Behavior and Conservation*. Nova Science Publishers, Inc, New York, USA, pp. 157–175, 210 p.
- Whitehead, H., 2009. SOCPROG programs: analyzing animal social structures. *Behav. Ecol. Sociobiol.* 63 (5), 765–778, <http://dx.doi.org/10.1007/s00265-008-0697-y>.
- Wittemyer, G., Getz, W.M., 2007. Hierarchical dominance structure and social organization in African elephants, *Loxodonta africana*. *Anim. Behav.* 73, 671–681, <http://dx.doi.org/10.1016/j.anbehav.2006.10.008>.
- Young, R.J., 2003. *Environmental Enrichment for Captive Animals*. Universities Federation for Animal Welfare, Oxford, UK, 240 p.